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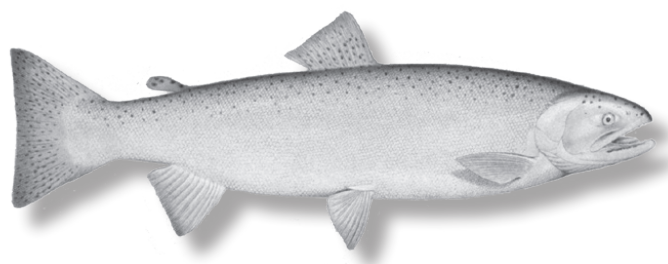
# Survival of Summer Steelhead Caught and Released from an Experimental Seine Fishery in the Lower Columbia River



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# Survival of Summer Steelhead Caught and Released from an Experimental Seine Fishery in the Lower Columbia River

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# Executive Summary

A study to determine the survival of adult summer steelhead released from commercial fishing gear occurred from 2011 to 2013. Steelhead were incidentally captured in an experimental Columbia River salmon beach and purse seine fishery (fishery) below Bonneville Dam (BON). Survival estimates were divided into short-term (between the fishery and BON), intermediate-term (between Bonneville and McNary (MCN) dams including tributaries and fisheries between BON and MCN), and cumulative (between the fishery and MCN, including tributaries and fisheries between BON and MCN). Steelhead survival was estimated based on a Ricker-Two-Release (R2R) study design. Summer steelhead were tagged with Passive Integrated Transponder (PIT) tags prior to release from the seines and tag "recoveries" were detections of the PIT tags at mainstem Columbia River dams, tributary interrogation sites, and in fisheries above BON. A control group of fish was captured at BON, PIT tagged, trucked downstream, and released into the fishery area.

Based on R2R model selection, the most parsimonious model for short-term and intermediate-term survival included a constant survival probability across years and seine type, and a capture probability that varied by year. For summer steelhead released from seines, the short-term survival was estimated to be 97.8% (95% CI: 96.4%-99.2%). Two alternate methods were used to estimate short-term survival. The first method used adult steelhead captured in seines and at BON that were previously tagged as juveniles and analyzed using the same Ricker-Two-Release design, which resulted in a survival estimate of 97.1%. The second method estimated the survival of seine caught steelhead, without a control group, by adjusting survival based on tag effects and tag detection efficiency at BON. The pooled survival estimate using this method was 96.8%. The weight of evidence from the three different analyses provides very strong support that the short-term survival of steelhead is greater than 96%. Based on the best model the intermediate-term survival was 99.8% (95% CI: 98.4%-100%). A second intermediate-term survival estimate calculated using previously tagged juvenile was 96.2% (95% CI: 77.4%-100%). Based on the overlap of the 95% CI there was no difference in the survival estimates using both approaches. This suggests that almost all the fishery mortality occurred between the fishery and BON, which represents 21 km of river and typically takes steelhead 1.9 days to navigate. The cumulative survival of steelhead from the fishery to MCN including the fishery and tributary PIT tag detections was 97.5% (95% CI: 95.7%-99.0%).

Logistic regression was used to explore variables that may explain the recovery of steelhead from the fishery to BON. We considered tagging location (control vs. treatment), origin (natural vs. hatchery), group (A vs. B steelhead), and water temperature as possible covariates with year modeled as a random effect. The most important covariates in the model were the random effect of year and tagging location. The best model, which included the intercept and year, had a 0.95 posterior model probability. Analysis of contingency tables indicated very strong support for association between recovery at BON and injury. During seining, fish that were classified as

wedged/gilled or tangled in the seines were 11.7 and 1.9 times less likely to be recovered than fish that were uninjured. The condition of each fish was also classified at both capture and release. Fish that were classified as lethargic at the time of capture or release were 2.3 times less likely to be recovered than those fish classified as vigorous. These results suggest that fish injury and condition are associated with the recovery of steelhead at BON.

Our adult steelhead survival results are similar to those reported from seining on the Rogue River (96%) but generally much higher than those reported in the literature for salmon caught in seines or tangle nets. We believe the low number of steelhead (mean=1.24) and salmon (mean=11.49) caught per set, short set times, and the strict fish handling guidelines contributed to the high survival rates observed in our study. Due to a combination of fish behavior, gear type, and soak time, 96.5% of all captured steelhead showed no signs of injury and only 1.5% of fish had injuries associated with high mortality (e.g. gilled or wedged). In addition, most fish were individually removed from the seine with rubber nets, which limited the typical seine mortalities resulting from fish being crushed or compressed by hoisting large numbers of fish from the water. The high survival rate of summer steelhead caught and released through seines determined through this analysis provides evidence that seines, when employing best management practices, can be an effective management tool in minimizing steelhead bycatch mortality in seine fisheries targeting salmon.

# Introduction

One of the guiding principles of the Washington Fish and Wildlife Commission's Columbia River Basin Salmon Management policy (WDFW POL-C3620) is the directive to "develop and implement alternative selective-fishing gear and techniques for commercial mainstem fisheries to optimize conservation and economic benefits". Implementation of selective commercial fisheries requires accurate estimates of release mortality rates by gear type so that the impacts on non-targeted fish can be accounted for in the fishery management and planning processes. The use of tangle nets in Columbia River salmon fisheries has been previously evaluated (Vander Haegen et al. 2004, Ashbrook et al. 2008, and Ashbrook 2008). However, the use of beach and purse seines has not been assessed and these gear types are currently being explored as options to maximize the benefits of hatchery salmon harvest in selective fisheries, while protecting wild and at-risk salmon and steelhead populations in the Columbia River.

Previous studies have demonstrated that many factors can contribute to survival rates of fish released from commercial fishing gear (Dunning et al. 1989, Chopin and Arimoto 1995, Baker and Schindler 2009, Cook et al. 2015). Although lower Columbia River non-Indian commercial fishers target Chinook (*Oncorhynchus tshawytscha)* and coho (*Oncorhynchus kisutch*) salmon in fall fisheries, summer steelhead (*Oncorhynchus mykiss)* are incidentally caught in these fisheries. Since all steelhead captured in non-Indian commercial fisheries below Bonneville Dam (BON) are required to be released, a survival study for steelhead captured and released from seines was needed to develop management options for a possible lower Columbia River commercial seine fishery targeting healthy salmon populations. Therefore, the primary purpose of our study was to evaluate the short-term, intermediate- term, and cumulative survival of adult summer steelhead released from selective commercial fishing gears.

Survival of fish caught and released from different fishing gears can be assessed in many ways. One of the most common methods for estimating survival is to hold fish in net pens after capture (Ruggerone and June 1996, Raby et al. 2015). However this method is limited to estimating short-term survival (Rogers et al. 2014) and may be subject to the "cage effect", where the survival of individuals may be negatively influenced by migration impedance and the holding of wild animals in a confined space (Schill 1996, Donaldson et al. 2008, Raby et al. 2013). In contrast, survival may be estimated using a Ricker-Two-Release (R2R) model (Ricker 1958, Seber 1982), which involves capturing, marking, and recapturing a paired (control and treatment) release group of fish. Here, the first sample consists of a representative sample of treatment fish (e.g. fish caught in seines) that are tagged and released. In the second sample, control fish, which are assumed to be from the same population of fish as the treatment group, are tagged and released at the same time and in the same geographic area. Subsequently, a single recapture sample is collected that is comprised of the tagged recoveries from both release groups, in which both groups are assumed to have the same probability of recapture. Since the method of moments estimate of survival in the R2R model is the ratio of the treatment to the control recovery rate this model is referred to as the relative recovery rate method (Burnham et al. 1987).

There are several advantages to using a R2R survival study design. First, the paired release study design utilizes a control group that accounts for common mortality experienced by both the control and treatment groups, which can include tagging and handling effects, along with other unaccounted mortality not due to the experiment (Burnham et al. 1987, Giorgi et al. 2010). If tagging, handling, and natural mortality are present and not accounted for through the use of a control group, the resulting estimates of survival will be biased low. Second, compared to the short-term holding of fish, capture-mark-recapture methods allow for estimates of longer-term survival and avoid negative impacts to wild anadromous fish caused by confinement. It is important to note that one main assumption of the R2R model is that the identified control group is representative of the treatment group, which can be challenging to verify and implement. The R2R model has been broadly applied to estimate the survival of bluegills in lakes (Ricker 1958), salmon in the marine environment (Mathews and Buckley 1974), and flounder (Howe et al. 1976). In addition, this model is used to estimate the smolt-to-adult survival benefit of transporting juvenile salmon around Columbia River dams using barges (treatment group) relative to those that remain in-river (control group; Sandford and Smith 2002), and the survival of salmon caught and released from commercial and recreational fisheries compared to a control group (Vander Haegen et al. 2004, Lindsay et al. 2004, Ashbrook et al. 2008).

Ricker (1958) proposed unbiased estimates of survival and capture for the R2R model based on the maximum likelihood method, which assumes the estimates are asymptotically normal. Analyses to estimate survival have often used the method of moments to obtain point estimates for recovery probabilities and survival (Ricker 1958, Mathews and Buckley 1974, Ashbrook et al. 2008). However, when data are sparse, Lee et al. (2006) found that Ricker's bias corrected survival estimates are still biased and provide poor interval coverage using simulations. In addition, when survival or capture estimates approach or exceed the boundary of their domain (0 or 1), Lowther and Skalski (1998) found confidence intervals based on normal approximation have poor interval coverage and survival estimates may exceed 1, which is not biologically defensible. When the 95% CI for the survival estimate includes 1, authors may truncate survival to the boundary or report that there is no difference in between control and treatment survival. In the case of sparse data, and/or when recapture estimates exceed the boundaries, constraining of the parameter space between zero and one (Schwarz et al. 1993) and using likelihood profile or Bayesian methods provide better alternatives to the method of moments estimators and large sample variance approximations (Gimenez et al. 2005). In this paper, we used a modified version of the Bayesian R2R model developed by Lee et al. (2006) to obtain survival estimates of steelhead released from seines that were biologically consistent.

In 2011, the Washington Department of Fish and Wildlife (WDFW) initiated a three year study to: 1) estimate the survival of steelhead released from both purse and beach seines caught in a Columbia River experimental salmon seine fishery (hereafter referred to as "fishery"), and 2) assess biological and environmental factors in predicting post-release survival of steelhead from seines. Survival was estimated using a R2R study design, which included the release of Passive Integrated Transponder (PIT) tagged control fish captured at a fish trap in the BON adult fish ladder and treatment fish captured in beach and purse seines below BON (Ricker 1958, Ashbrook 2008). Tag recoveries occurred in the extensive PIT tag monitoring network within the Columbia River basin (Prentice et al. 1990, Buchanan and Skalski 2007). Biological and environmental conditions that may influence survival were recorded at the time of tagging to determine if these factors could help explain the variation in the survival of released fish.

# Methods

*Study Site*

The experimental seine fishery was conducted on the Columbia River between Rooster Rock, river kilometer (rkm) 207 and just below Ives Island, rkm 228; this area is slightly downstream of BON at rkm 234. The average flows in the study area in the late summer and fall generally range from 75,000 to 100,000 cubic feet per second (cfs). The river width in this area ranges from 0.25 to 2 kilometers wide. River depths are highly variable, ranging less than three meters over large flats to depths of over 15 meters in the shipping channel. Control fish were collected at the Bonneville Dam Adult Fish Facility (AFF) located in the Washington Shore fish ladder at BON and released near the upstream extent of the fishery area at rkm 225 from either Skamania Landing, WA or Dodson, OR (Figure 1). Since PIT tags were used to evaluate survival, PIT tag detections were obtained from the network of fixed PIT tag detection sites at mainstem Columbia River dams, at instream PIT tag detection sites (IPITDS) in tributaries to the Columbia River between BON and McNary (MCN) dams, and through sampling of fisheries above and below BON. PIT tags were recovered at detection sites at BON and MCN on the mainstem Columbia River and in most major tributaries between BON and MCN, including the Wind, Hood, Klickitat, Deschutes, John Day, and Umatilla rivers. Detections at The Dalles Dam, located between BON and MCN, were only available for one year of the study (2013) and for consistency were not used in the analysis.

*Fish Collection*

Fish were captured in seines between late August and October from 2011 to 2013. Purse seines were deployed by a motorized skiff pulling the seine away from the seiner. After encircling the fishing area the skiff returned to the seiner and the purse line was tightened to close the bottom of the seine. After pursing, the seine was hauled aboard using a power block while the crew stacked the seine net on the deck. The last portion of the seine (bunt end) was hauled in slowly to allow the fish to become acclimated to confinement. Most fish were removed individually from the seine using a rubberized net and released into a tote on the deck of the seiner for tagging and sampling. The purse seine had a minimum length of 150 fathoms (~274 m) and a maximum length of 250 fathoms (~457 m) based on previous assessments of this gear type (WDFW, unpublished data). The seine had a mesh and bunt (i.e., bag of the net) size of 8.9 and 2.5 cm, respectively. The mesh size in the bunt was smaller than the remainder of the net because this is thought to result in less entanglement of fish thereby reducing potential injury to the fish. The depth of the net was determined based on the fishing area, but was typically 12 m or deeper. Fishing time for a set was recorded as the time that the first cork was observed on the water to the time the last fish was removed from the seine. The mean set time for purse seines, in which set time was recorded, was 71 minutes (SD = 28).

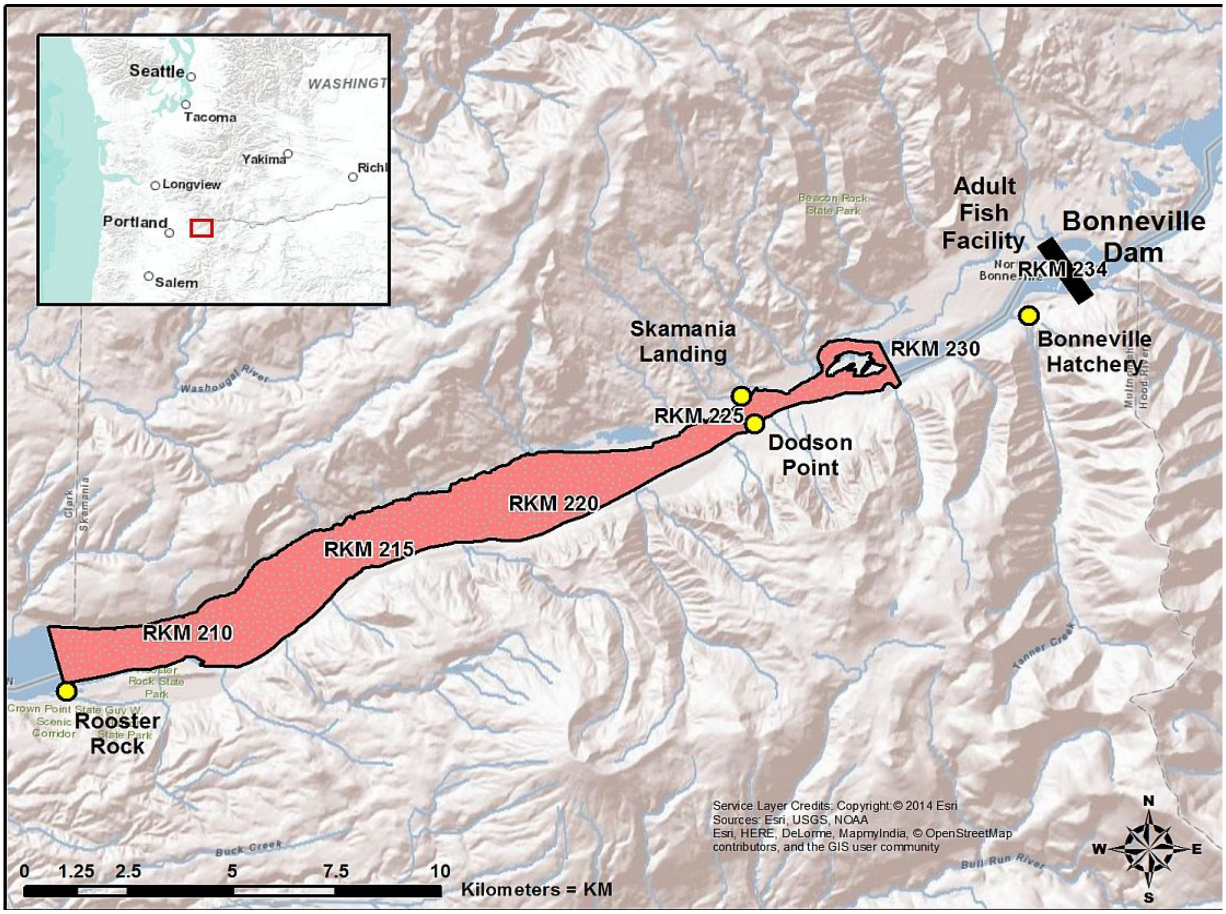


Figure 1. Map of study area which includes the experimental seine fishery (highlighted in red) where treatment fish were captured, tagged, and released and the Bonneville Adult Fish Facility (BON AFF) where control fish were captured and tagged before being transported down river and released at Skamania Landing or Dodson Point. Also shown are Bonneville Dam and Hatchery where PIT tag interrogation sites are located.

Beach seine fishing areas were cleared of obstructions prior to the fishery to maximize gear effectiveness. A motorized boat was used to deploy beach seines. After encircling the fishing area, the boat returned to shore and the net was pulled to shore through a block on shore. Care was taken to ensure the lead line maintained contact with the river bottom so that fish could not escape under the net. A maximum length of 250 fathoms (~458 m) was proposed based on previous evaluations with commercial fishers (WDFW, unpublished data). The beach seine mesh size of 8.9 cm was the same as the purse seine mesh size. A rubberized net was used to transfer fish from the seine into a tagging tote, which was placed in the river to minimize the impact of warm air temperatures on the water temperature in the tote. The mean set time for beach seines, in which set time was recorded, was 44 minutes (SD = 18), which was less than the mean set time for purse seines.

Fish sampling at the BON AFF to collect control fish was scheduled to occur concurrently with the fishery. However, during the study some periods of time were missed because of trapping constraints related to warm water temperatures. Fish collection and handling at the BON AFF followed methods similar to previous Columbia River gear evaluation studies (Vander Haegen et al. 2004). After tagging, the control fish were place in a holding tank for transport, and allowed to recover before being released, which is a standard handling procedure at the AFF (Keefer et al. 2004a). Steelhead were release downstream at either Skamania Landing or Dodson Point, which were the same release sites used in prior Columbia River R2R study designs (Vander Haegen et al. 2004, Ashbrook 2008). Fish handling protocols were in compliance with AFF guidelines established by the Fish Passage Operation and Maintenance Coordination Team, as detailed in the Fish Passage Plan for BON (USACE 2010). Other long-term ongoing research studies were also collecting salmon and steelhead at the AFF during the same time period, so the weekly steelhead sampling targets for this study were not always achieved.

*Fish Sampling, Tagging, and Tag Detection*

The following data were collected from each control and treatment fish: species, stock group (A vs. B), origin (natural vs. hatchery), fork length, gear type (purse, beach), injury type, and fish condition. In addition, we obtained daily mean temperature data for the study area below BON, which is available at [http://www.nwd-wc.usace.army.mil/cgi-bin/dataquery.pl?k=id:BON+record://BON/TW//IR-MONTH/IRXZZBZD/+psy:+psm:+psd:+pey:+pem:+ped:+pk:bonneville](http://www.nwd-wc.usace.army.mil/cgi-bin/dataquery.pl?k=id:BON+record://BON/TW//IR-MONTH/IRXZZBZD/+psy:+psm:+psd:+pey:+pem:+ped:+pk:bonneville) . Since Columbia River fishery managers have classified steelhead into Group A (<78 cm) and Group B (≥78cm) for management purposes, this study also tracked these stock groups based on fork lengths. When fish were captured they were assigned an injury type based on visible marks assumed to be inflicted by the seine gear. Fish were classified as: 1) tangled if they had net marks on their snout or were observed to be tangled, 2) gilled if they had net marks around their gills or were observed to be gilled, 3) wedged if they had net marks posterior of the gills and anterior of the dorsal fin or were observed to be wedged, and 4) none of the above. Upon capture and again upon release fish were assigned a condition ranging from 1 to 5 (1=vigorous, not bleeding; 2=vigorous, bleeding; 3=lethargic, not bleeding; 4=lethargic, bleeding; 5=moribund). These visual classification categories were developed by Vander Haegen et al. (2004). All fish were scanned for existing PIT tags using established PIT sampling protocols (Rawding et al. 2014b). Fish with existing PIT tags were recorded as previously tagged and were released as part of the study. All fish not previously tagged were implanted with a 12.5 mm 134.2 kHz full duplex PIT tag using a MK-25 Rapid Implant Gun (Biomark, Boise, ID). The PIT tags were injected into the peritoneal cavity using standard Columbia River protocols (CBFWA 1999). The control group, collected at BON AFF, was similarly sampled and tagged and assumed to be representative of the population. All data were recorded into a digital hand held data logger (Psion Workabout Pro, Strategic Mobility Group; Schaumburg, IL). PIT tagging data were uploaded to the PIT Tag Information System (PTAGIS) database.

Following release, PIT tagged fish were detected at fixed sites and in fisheries. Fixed PIT detection sites consisted of antenna arrays located at the mainstem Columbia River dams (BON and MCN) and various tributaries between these two dams. In addition to fixed site detections, PIT tags were sampled in fisheries (Rawding et al. 2014a). PIT tag detection data for this analysis were downloaded from the PTAGIS database on June 29, 2015.

*Data Management*

Over 28,000 salmon and steelhead were caught in seines and at BON over the three years of the study period, which resulted in over 790,000 PIT tag detections. Although PIT tag data was recorded electronically to minimize error, a rigorous QA/QC process was developed to minimize the errors in this large database. First, it was ensured that the tag data was based on PIT tags WDFW had purchased based on the tag list provided from the manufacturer. Second, using the unique 13 digit alpha numeric PIT tag code, a relational databased was developed that linked the biological data collected at the time of tagging or recapture with the PIT tag detection history of each individual fish. In addition, PIT tagged fish were classified into three categories: 1) steelhead that we PIT tagged as adults in the fishery or at BON AFF based on our tag list (N=2954), 2) steelhead that were caught in the fishery or at BON AFF that were previously tagged as juveniles by others (N=63), and 3) steelhead that were previously tagged by others (N=6) as adults. There were 13 additional fish captured in seines that were not tagged because they were moribund or escaped before being tagged and 1 control fish that was not tagged. Since the database and QA/QC steps were not complete at the time of the previous analysis, the reported results in this document supersede those previously reported by Holowatz et al. (2014).

*Bayesian Statistical Framework*

In the last two decades, Bayesian methods have increasingly been used to estimate survival due to available software, the ability to formally incorporate prior information into the estimation process, and to estimate survival from highly parameterized models (Brooks et al. 2000, McCarthy 2007, King et al. 2009, Link and Barker 2010, Kery and Schaub 2012). The Bayesian framework allows the use of previous data to be updated with new data via the likelihood function. Bayes theorem states the posterior distribution, or posterior [$p(\theta|y)$], is proportional to the prior distribution, or prior [$p(\theta)$], times the likelihood of parameter $\theta$ given the observed data [$p(y|\theta)$] (Gelman et al. 2004). Bayesian analysis can also be contentious because all priors are informative and may influence the results (Irony and Singpurwalla 1997, Dennis 1996). This study adopted objective Bayesian methods and used a vague or reference prior so that the posterior was heavily influenced by the collected data (Press 2003). The Berstien Von Mises Theorem implies that as the sample size of the data set increases, the posterior becomes less sensitive to the choice of prior (Link and Barker 2004). With sufficient data, survival estimates from objective Bayesian and maximum likelihood estimation approaches are similar (Maunder et al. 2009, Kery and Schaub 2012). Bayesian approaches were chosen for this study due to the complexity of the survival estimates and the need to constrain the survival estimates to less than 100%, which can be a problem using the R2R model when treatment and control survivals are similar (Lindsay et al. 2004).

The Bayesian analysis was conducted using Markov Chain Monte Carlo (MCMC) methods to sample the posterior probability density function using the Just Another Gibbs Sampler (JAGS) software (Gilks et al.1996, Plummer 2003). JAGS was called from the statistical package R (R Development Core Team 2014) using R2jags (Su and Yajima 2015). All of the modeling results described in this paper has been assessed for chain convergence and uncertainty in the parameter estimates due to Markov Chain variability (Plummer et al. 2006). Multiple chains were used starting at divergent initial values and the chains were monitored until they reached equilibrium. Convergence was assessed by visually inspecting the MCMC chains and using the Brooks-Gelman-Rubin (BGR) statistic (Lunn et al. 2013). BGR values less than 1.1 are considered to have converged (Gelman et al. 2004). After reaching equilibrium, the number of independent samples, as measured by effective sample size (ESS), was monitored to ensure a minimum of 4,000 was reached. This provides 95% credible intervals (CI) that have posterior probabilities between 0.94 and 0.96 (Lunn et al. 2013). Based on this approach, it was assumed that the reported posterior distributions were accurate and represented the underlying stationary distributions of the estimated parameters. The exception to this was that after the burn-in only 3,000 iterations were used in analyzing residuals from the logistic regression because of limited computer memory.

Bayesian and classical statistics use model selection and residual analysis to test model adequacy (Quinn and Keogh 2002, Lunn et al. 2013). In the Bayesian paradigm, the Bayes Factor (BF) is used as the summary of evidence in favor of one model compared to another model based on the data, prior, and statistical model (Kass and Raftery 1995). The BF uses a scale for comparing the best model to alternative models, where by convention the best model receives a score of 1. A BF of 1-3.2, 3.2-10, 10-32, 32-100, and >100 indicate support for the best model compared to the alternative model that is negligible, substantial, strong, very strong, and decisive, respectively. Posterior predictive checks were used to assess goodness of fit (GOF) through a comparison of the posterior predictive distribution of replicated data from the model with the data analyzed by the model (Gelman et al. 1996). These were measured with a Bayesian *p*-value, which is the proportion of the times the replicated data or discrepancy measure is more extreme than the observed data or discrepancy measure. If there is a good fit of the model to the data, the replicated data would be expected to be similar to the observed data, resulting in a Bayesian *p*-value of 0.50, while values near 0 or 1 would indicate that the model does not fit the data. The conditional posterior ordinate (CPO), also known as the leave-one-out cross-validation predictive density, expresses the posterior probability of observing the value when the model is fitted to all data excluding one data point (Gelfand 1996). A MCMC estimate of the approximate $CPO_i$ is obtained without actually omitting a value and is estimated by the inverse likelihood (Carlin and Louis 2009). $CPO_i$ values of less than 0.01 can be viewed as possible outliers with high leverage (Ntzoufras 2009, Congdon 2005).

Since it was challenging to compute the marginal likelihood or posterior model probabilities required for the R2R model selection using BF, we used the Deviance Information Criteria (DIC) rather than BF for model selection for the R2R models. DIC is a Bayesian measure of model fit and complexity and the model that best fits the data has the smallest DIC (Spiegelhalter et al. 2002). Since DIC is a Bayesian analog of Akiake Information Criteria (AIC), the same scale for model support developed by Burnham and Anderson (2002) was for model comparison. Models with a ΔDIC of less than 2 have considerable support, ΔDIC of 3-7 have less support, and models with ΔDIC > 10 have negligible support. We estimated model support using the equation DIC = Dev($\theta_m$) + pV, where Dev($\theta_m$) is the posterior mean deviance for the model and pV = Var(D(θ|Y))/2 and is a measure of the number of effective terms in the model (Gelman et al. 2004).

*Survival Analysis*

The R2R design has been used to estimate survival of a treatment group relative to a control group across time or space (Seber 1982, Burnham et al. 1987). In our case, short-term survival, which includes immediate mortality, was estimated by tagging a control group (*C*) at the BON AFF and transporting these fish to the upper end of the fishery zone. During the same time frame, treatment fish (*T*) were caught, tagged and released from the fishery. Both groups were subsequently recovered at BON (*c*, *t*) (Figure 2, upper panel). The estimate of survival (ϕ) for the treatment group was from release in the fishery to BON, and the probability of capture (p) of the control group was based on PIT tag detection at BON. The R2R model assumes the probability of capture is equivalent for the control and treatment groups. Control fish were released below BON to expose them to additional mortality that may also occur for treatment fish following their release from the fishery. Additional mortality may be due to fish being captured in sport and commercial fisheries between the release site and BON, predation by marine mammals, and adult mortality that is related to fish passage at BON (Vander Haegen et al. 2004, Ashbrook et al. 2008). Intermediate-term survival from BON to MCN, including tagged recoveries detected at MCN, caught in treaty commercial fisheries, and fish that entered Columbia River tributaries between BON and MCN, was also assessed using the R2R design (Figure 2, lower panel). The control (*C*) and treatment (*T*) fish from the short-term survival study detected at BON(*t*,*c*) and the recoveries from these two groups was the sum of treaty fishery (tf, cf), tributary (tt, tc), and MCN detections (tm, cm). While the short-term and intermediate-term estimates provide insight into the spatial distribution of mortality, fishery managers have asked for a survival estimate for fish from their release from the fishery to recovery at MCN, which also includes the tributary and fishery recoveries between BON and MCN. This overall estimate has been termed “cumulative survival”.

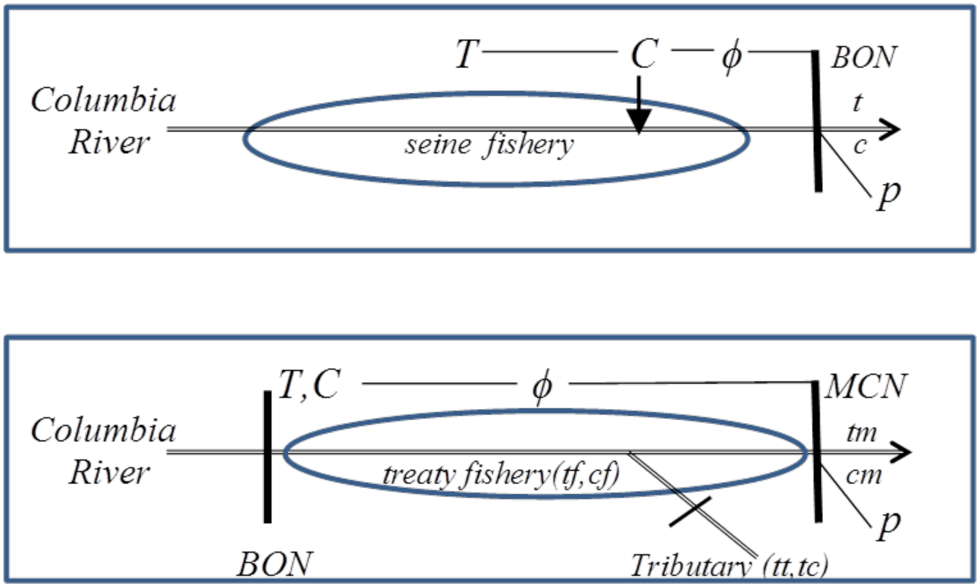


Figure 2. Diagram of Ricker-Two-Release (R2R) method used to estimate short-term (upper panel) and intermediate-term (lower panel) fishery survival, where p is the probability of capture, $\phi$ is the apparent survival from the fishery, $C$ and $T$ are the number of fish released from the control and treatment groups respectively, and $t$ and $c$ are the number of recaptures from each of these groups. Fish are moving upstream from left to right.

Lee et al. (2006) extended Ricker's original model to include the number of deaths in the treatment group and re-expressing the R2R model as three binomials using a Bayesian framework. Since this study had no specific interest in deaths, Ricker's two binomials model (equations 1 and 2) was used:

$$c_{jk} \sim Binomial(p_{jk}, C_{jk}) \quad (1)$$
$$t_{ijk} \sim Binomial(\phi_{ijk} p_{jk}, T_{ijk}) \quad (2)$$
$$\phi_{ij3} = \phi_{ij1}\phi_{ij2} \quad (3)$$

where $C_{jk}$ and $T_{ijk}$ are the number of fish released in the control and treatment groups, $c_{jk}$ and $t_{ijk}$ are the recoveries from these groups, $p_{jk}$ is the probability of capture, $\phi_{ijk}$ is the apparent survival, $i$ is an index where 1 is purse seine and 2 is beach seine, and $k$ is an index where 1 is the short-term survival (release to BON), 2 is the intermediate-term survival (BON to MCN including sport and commercial fishery and tributary detections), 3 is the cumulative survival, and $j$ is an index for year. The estimate of cumulative survival is the product of the short-term and intermediate-term survivals (equation 3). At the suggestion of one reviewer, estimates using Ricker's normal approximations were also included for a comparison with the Bayesian approach (Ricker 1958, Lee et al. 2006).

In addition to the R2R approached outlined above, we used two alternate methods to estimate post-release survival of steelhead. For the first alternate approach, we only used the returning adults that were previously tagged as outmigrating juveniles above BON. This approach is the same as the R2R method previously described except that these fish were not subjected to the short-term effect of tagging that can confound survival estimates (e.g. tag loss and tag induced mortality). Survival was estimated using equations 1 and 2. In the second alternate approach, we noted that the minimum survival of seine caught fish was the proportion of the tagged group that reached BON. However, to estimate the survival to BON it is necessary to account for tag loss, tag induced mortality and the PIT tag detection probability at BON. This approach was referred to as the "adjusted survival method" and is expressed as:

$$t_i \sim Binomial(p_i, T_i) \quad (4)$$
$$m_j \sim Binomial(p\_det_j, M_j) \quad (5)$$
$$ta \sim Binomial(p\_s, TA) \quad (6)$$
$$\phi_{ij1} = p_i/(p\_s \;\; p\_det_j) \quad (7)$$

where $T_i$ are the number of fish released in the treatment groups, $t_i$ are the recoveries from these groups, $p_i$ is the probability of capture, $\phi_{ij}$ is the apparent survival, $i$ is an index where 1 is purse seine and 2 is beach seine, $M_j$ are the PIT tag detections at MCN, $m_j$ are the subset $M_j$ also detected at BON, $j$ is an index for year, $p\_det_j$ is the proportion of $M_j$ detected at BON, $TA$ are the number of PIT tagged fish released alive during a hatchery study, $ta$ is the number recovered alive with PIT tags, $p\_s$ is the proportion of $TA$ that retained tags and survived in the hatchery study, and $\phi_{ij1}$ is the survival to BON. Since the adjusted survival estimate does not use a control group, it will be biased low if there is unreported harvest or natural mortality between the tagging site and BON. Using this approach it is possible that survival estimates may exceed 100%.

Jeffreys reference priors were used for all survival models since the analysis consisted of binomial distributions and an objective analysis was desired to "let the data speak for themselves". The Jeffreys prior for the binomial distribution is a beta distribution [Beta(0.5, 0.5)] and is considered the most appropriate reference prior for binomial data (Bernardo 1979). To test the sensitivity of our posterior to our priors, the posteriors from the Jeffreys prior were compared to the Bayes-LaPlace uniform prior [Beta (1, 1)] and the Haldane prior [Beta (0, 0)], which are also common reference priors (Tuyl et al. 2009, Lee 2004). Since the Haldane prior is an improper prior, it is often approximated with beta distribution with both values equal to 0.01.

*Logistic Regression*

An objective Bayesian analysis was used to determine the covariates that influenced the recovery rates of steelhead released from the fishery to BON using biological and environmental data (Tenan et al. 2014). A simple approach for indicator variable selection is to introduce a binary indicator to track if a regression coefficient is present (1) or absent (0) from the model (Kuo and

Mallick 1998). The posterior inclusion probability for a covariate ranges from 0 to 1 and is the mean of the binary indicator (O'Hara and Sillanpaa 2009). Indicator variable selection is a recommended approach for an integrating variable and model selection (Hooten and Hobbs 2015). To improve MCMC convergence and interpretation all variables were placed on the same scale; continuous variables were centered and divided by two standard deviations and all non-continuous variables were centered to ensure all variables have a mean = 0 with a standard deviation (SD) = 0.5 (Gelman et al. 2008).

The logistic regression model for steelhead recovery is expressed as:

$$y_i \sim Bernoulli(pi_i) \quad (8)$$
$$Logit(pi_i) = B_0 + \sum_{j=1}^{np} \gamma_j B_j X_{ij} + \varepsilon_y \quad (9)$$
$$B_j = (1-\gamma_j) Normal(\mu_j, S_j) + \gamma_j Normal(0, \Sigma_j) \quad (10)$$

where $y_i$ is the detection outcome (1=detected, 0 = not detected), $pi_i$ is the estimate of survival for each fish, *np* is the number of regression coefficients, $\gamma_j$ is the inclusion probability for regression coefficients $B_j$, $B_j$ with j=1,…,*np* are the regression coefficients, $X_{ij}$ is the data matrix, and $\varepsilon_y$ is the random effect for year assuming a normal distribution with a uniform prior (0-2) on SD (Gelman 2006). The method used for covariate and model selection was Gibbs variable selection (GVS; Dellaportas et al. 2000). This approach uses a mixture prior (equation 9) for the regression coefficients where hyperparameters $u_j$ and the variance $S_j$ are obtained from a pilot run of the full model, and $\Sigma_j$ is the fixed prior variance. The pseudoprior [Normal($u_j, S_j$)] has no effect on the posterior distribution and is used to improve the efficiency of the Gibbs sampler (Dellaportas et al. 2002). The recommended prior for the inclusion parameter is $\gamma_j \sim Bernoulli$ (0.5) because it gives the same weight to all possible covariates and models (George and McCulloch 1993). The prior for regression coefficients was $B_j \sim Normal(0, \Sigma_j)$. While Berstien Von Mises Theorem indicates that posterior parameter estimates are insensitive to vague priors when there are sufficient data, Bayes Factors with vague priors favor simpler models due to the Lindley-Bartlett paradox (Link and Barker 2006, Ntzoufras 2009). The fixed prior variance ( $\Sigma_j$) was set to four times the number of observations as recommended by Ntzoufras (2009). This prior supports the simplest model but in a minimal way because this prior is equal to adding one observation (Ntzoufras 2009). Key assumption of linearity on the logit scale was assessed using visual assessment and the correlation matrix of covariates was used to examine multicollinearity (Hilbe 2009, Quinn and Keogh 2002). Correlation coefficients less than 0.6 are judged to be less than the threshold where multicollinearity is a concern (Burnham and Anderson 2002).

Following Burnham and Anderson (2002), a set of candidate regression models was developed based on an understanding of steelhead biology in the Columbia River basin. The regression coefficients in estimating recovery from the fishery to BON include: 1) Location (L; seine (treatment) vs. BON (control)), 2) origin (O; natural vs. hatchery), 3) group (G; A vs. B steelhead), 4) water temperature (T), and year (Y). Time is often modeled as a random effect and we took this approach because we were not interested in the survival by year but wanted to account for this covariate in our model. For short-term survival it was hypothesized that temperature at the time of capture may lead to lower survivals. Since temperature and date were correlated (-0.86), we believed that temperature would be better covariate then date to explain recovery probabilities at BON.

*Contingency Tables*
Log linear models were used to determine associations between variables collected in the study. Models were fit using a hierarchical approach that automatically includes all lower order terms when higher order terms are included in the model (Agresti 2007). Binary indicators were used to estimate the inclusion probabilities of interaction terms along with posterior model probabilities (Kuo and Mallick 1998, Ntzoufras 2002). For example, the highest interaction term in a three way contingency table is only included in one of nine possible models, the prior inclusion probability for this term was $\delta_4$ ~Bernoulli (1/9) with remaining priors for the two way interaction terms $\delta_1$, $\delta_2$, and $\delta_3 = \pi$, with $\pi = \delta_4+0.5(1-\delta_4)$. This same approach was used in two way contingency tables. Counts were assumed to be Poisson distributed and regression coefficients were assigned a Normal (0,10) prior (Congdon 2005). In addition to the test of independence based on the interaction terms, a more detailed analysis of conditional dependence was conducted by calculating the odds ratio (OR) from the subset of two-way contingency or partial tables based on the preferred model (Agresti 2007). The OR from a marginal table was also calculated where appropriate, which was based on a combination of partial tables. To streamline analysis reporting of two way contingency tables we reported on the posterior model probability for independence (MPI) and the corresponding Bayes Factor (BF) supporting independence.

# Results

*Catch Composition*

The range of dates for the fishery was from August 24 – October 28, August 20 – October 23, and August 21 – October 22 for 2011, 2012, and 2013, respectively. During the three year study the seine fishery catch was comprised of 2,047 (10%) steelhead, 15,678 (75%) Chinook salmon, 3,065 (15%) coho salmon, and 35 (<1%) pink salmon (*Oncorhynchus gorbuscha*), and 1 chum salmon (*Oncorhynchus keta*). A total of 1,994 and 960 steelhead were caught and tagged in seines (treatment) and at the BON AFF (control), respectively. The range of dates for trapping at the BON AFF was from August 24 – October 11, 2011, August 29 – October 12, 2012, and September 20 – October 24, 2013. A total of 40 and 23 steelhead that were previously tagged as juveniles were caught in seines and the BON AFF, respectively. In addition, six adult steelhead were caught that were tagged at BON by other researchers. A total of 13 seine caught steelhead were not tagged including five immediate mortalities, seven fish released in vigorous condition, and one released in lethargic condition. One control fish was not tagged for unknown reasons but was caught and released in vigorous condition. The six adult steelhead previously tagged as adults by others were not used in any further analysis. Over the three years, a total of 1,635 sets were completed, including 1,315 (79%) in which at least one adult salmon or steelhead was caught, 1,273 (76%) in which at least one salmon was caught, and 702 (43%) in which at least one steelhead was caught. The mean steelhead catch per set was 1.24 (SD 2.33), which is consistent with the negative binomial distribution (Figure 3). The mean salmon catch per set was 11.49 fish and the mean ratio of salmon to steelhead caught was 8.62:1 when at least one steelhead was caught.

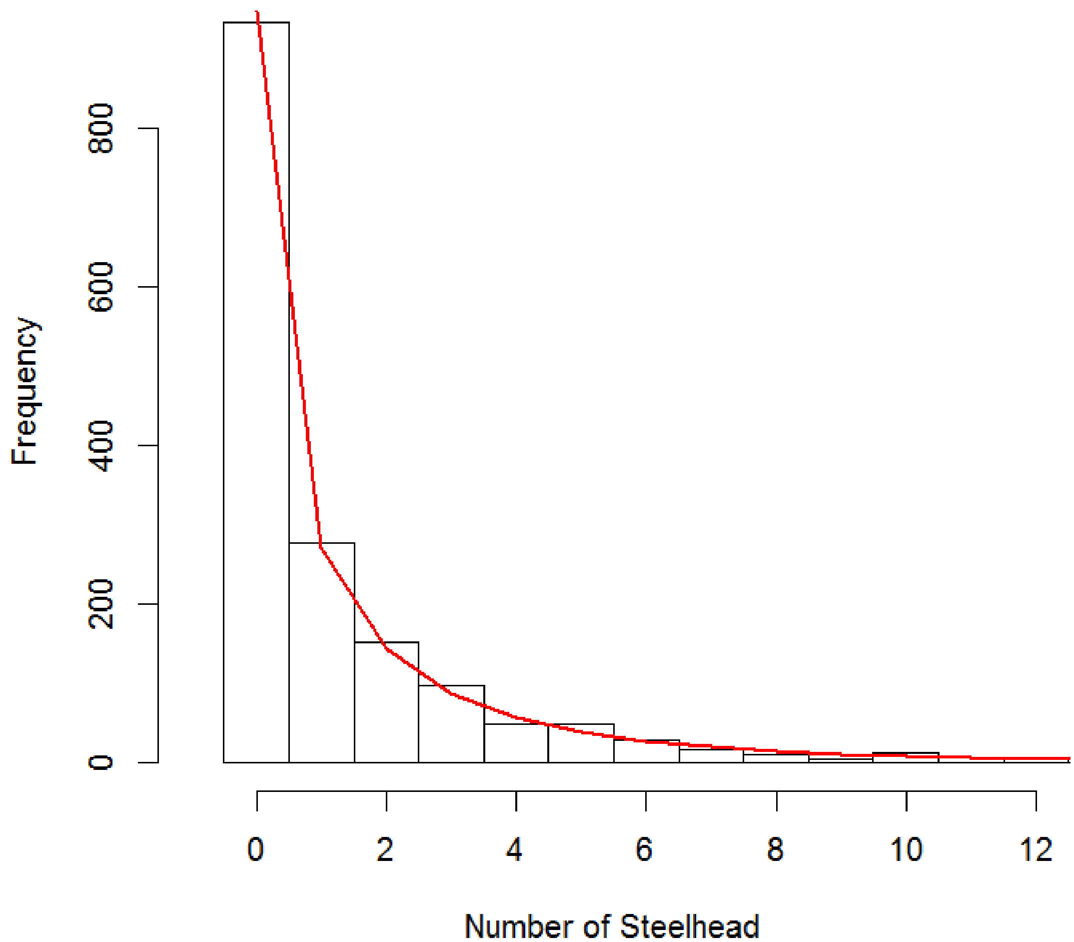


Figure 3. Observed (histogram) and expected (line) number of steelhead caught per seine set in the Columbia River experimental seine fishery based on the negative binomial distribution from 2011 to 2013. The upper limit of x-axis was reduced from 24 to 12 to better illustrate the goodness of fit between the observed data and expected fit.

Since a key assumption of the R2R model is that control and treatment fish are from the same population, we used log linear models to compare the association between origin and location (seines vs. BON) and between group (A vs. B) and location. The results from the first analysis found independence between origin and location (PMI=0.97. BF=36). This provides very strong support that the proportion of natural origin steelhead caught in seines (31.5%) and at BON

(31.9%) were similar. We found support of independence between group A steelhead (<78cm) caught and tagged in seines and at BON (PMI=0.89, BF=7.7). This provides substantial support that the percentage of group A steelhead caught in seines (63.7%) and at BON (60.3%) were similar. Bayesian *p*-values were near 0.5 and analysis of residuals did not indicate a lack of fit for either analysis.

The mean fork length for the treatment groups was 71.9 cm (range 42 – 105 cm) and the mean fork length for the control group was 71.6 (range 44 to 98). Fork lengths had exhibited a bi-modal distribution consistent with the Group A and B designations. A total of five steelhead (0.25%) from the treatment group and two steelhead (0.20%) from the control group were recaptured once in the seine fishery and six of these seven fish were subsequently detected at BON. Results from the contingency table analysis provides substantial support that the recapture of PIT tagged fish in subsequent fisheries was the same (PMI=0.78, BF=3.6). Since this was a control treatment design these fish were included in the analysis. The median travel time from the fishery to BON was 1.9 days (range 0-60) and 0.8 days (range 0-12) for the treatment and control groups, respectively. The median travel time from BON to MCN was 10.7 days (range 5-197) and 8.5 days (range 4-210) for treatment and control groups, respectively. The cumulative travel time for the control group from the fishery to MCN was 9.1 days (range 4-197) and the travel time for the treatment group was 13.1 days (range 5-215). The wide range of travel times to MCN is not unexpected since summer steelhead are stream-maturing fish and there is no urgency to immediately migrate to spawning areas because they are not spawning until the spring following tagging.

Since steelhead are iteroparous, the detection of PIT tags moving downstream after spawning was observed. Therefore, rather than rely on the last detection, we chose the upper most detection above BON to describe the recovery location of steelhead. Individual fish locations were pooled into distinct population segments such as the Upper Columbia River [>Priest Rapids Dam (PRD)] and Snake River [> Ice Harbor Dam (IHR)]. In addition, we kept track of upper most detection in the combined Lower and Middle Columbia DPS by recovery type (i.e., fishery and tributary detection) (Table 1). A 2x5 way contingency table was used to examine the association between the uppermost detection by recovery location and tag location (PMI=1.00, BF>100). This indicated decisive support that the recovery location was the same for control and treatment groups and pooling of recovery locations by tagging location to estimate intermediate-term survival in the R2R model is appropriate. The best model fits from these two models was consistent with the data based on the goodness of fit (GOF) test using the posterior predictive check (Bayesian *p*-value = 0.49) and all standardized Pearson residuals ranged from -0.28 to 0.17.

Table 1. The number and relative proportion of steelhead by their corresponding upper most recovery location by catch location (BON = control; fishery = treatment) from 2011-2013.

| Location | Controls | % Controls | Treatment | % Treatments |
|---|---|---|---|---|
| BON-MCN Fishery | 7 | 0.9% | 29 | 1.9% |
| BON-MCN Tributaries | 45 | 6.0% | 118 | 7.6% |
| MCN-IHR,PRD | 51 | 6.8% | 106 | 6.8% |
| Above IHR | 616 | 82.1% | 1250 | 80.6% |
| Above PRD | 31 | 4.1% | 48 | 3.1% |
| Total | 750 | | 1551 | |

*Survival*

We observed only five immediate mortalities (0.3%) of the 2,007 steelhead captured in seines that were not previously tagged. The median annual estimate of short-term survival of summer steelhead, which included immediate mortality, released from the beach seines in 2011 to 2013 ranged from 96.9 to 98.5% and from 98.0 to 99.0% for steelhead caught in purse seines (Tables 2-4). The annual median intermediate-term survival for fish released from beach seines was high but more variable then the short-term survival and ranged from 98.2 to 98.8%. The intermediate-term survival of steelhead released from purse seines was similar to the short-term survival and ranged from 99.1 to 99.6%. The annual cumulative median survival, which was the product of short-term and intermediate-term survival ranged from 94.9 to 96.5% for beach seined fish and ranged from 97.3 to 97.7% for purse seined fish (Tables 2-4).

The pooled seine survival estimates were 96.8% (95% CI: 95.3%-98.6%) for short-term, 99.7% (95% CI: 98.0%-100%) for intermediate-term, and 96.4% (95% CI: 94.3%-98.3%) for cumulative survival (Table 5). Ricker's annual and pooled estimates were generally higher than the Bayesian estimates and often yielded an unrealistic estimate with a point estimate or upper 95% CI that exceeded 100%, which is not biologically possible.

Due to the small sample sizes, all adult steelhead captured in seines and at BON that were PIT tagged as juveniles were pooled across all years. The short-term survival was estimated based on the proportion of treatment fish arriving at BON (equation 3) because the survival of control fish was 100%, intermediate-term survival was estimated using the R2R, and cumulative survival was estimated as the product of the two survivals. The short-term, intermediate-term, and cumulative survival for juvenile tagged steelhead were 97.1% (95% CI: 89.0% – 99.7%), 96.2% (95% CI: 77.4%-100%), and 92.2% (95% CI: 73.9%-98.9%), respectively (Table 6, Figure 4). Based on overlapping 95% CI these estimates were similar to the pooled survival estimates from steelhead tagged as adults (Table 5, Figure 4).

Table 2**.** Summer steelhead survival estimates based on Ricker-Two-Release (R2R) model in 2011. Survival estimates are the median point estimates and 95% credible interval (95% CI) of the posterior distribution. For comparison, R2R estimates based in Ricker's formula are provided in the last two columns. Since the cumulative estimate is the product of the short-term and intermediate-term survival, release and recapture sample sizes are not available.

| Short-term survival from fishery to BON | | | | | | |
|---|---|---|---|---|---|---|
| | | | Bayesian Analysis | | Ricker's Equations | |
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95% CI |
| Control | 458 | 443 | --- | --- | --- | --- |
| Purse | 316 | 300 | 0.985 | (0.952-1.000) | 0.981 | (0.951-1.011) |
| Beach | 231 | 219 | 0.984 | (0.946-1.000) | 0.980 | (0.946-1.014) |

| Intermediate-term survival from BON to MCN (including tributary & fishery recoveries) | | | | | | |
|---|---|---|---|---|---|---|
| | | | Bayesian Analysis | | Ricker's Equations | |
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95% CI |
| Control | 443 | 331 | --- | --- | --- | --- |
| Purse | 300 | 246 | 0.996 | (0.965-1.000) | 1.097 | (1.014-1.180) |
| Beach | 219 | 163 | 0.984 | (0.911-1.000) | 0.995 | (0.901-1.090) |

| Cumulative survival from fishery to MCN (including tributary & fishery recoveries) | | | | | | |
|---|---|---|---|---|---|---|
| | | | Bayesian Analysis | | Ricker's Equations | |
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95% CI |
| Control | --- | --- | --- | --- | --- | --- |
| Purse | --- | --- | 0.977 | (0.937-0.998) | 1.076 | --- |
| Beach | --- | --- | 0.962 | (0.888-0.996) | 0.976 | --- |

Table 3. Summer steelhead survival estimates based on Ricker-Two-Release (R2R) model in 2012. Survival estimates are the median point estimates and 95% CI of the posterior distribution. For comparison, R2R estimates based in Ricker's formula are provided in the last two columns. Since the cumulative estimate is the product of the short-term and intermediate-term survival, release and recapture sample sizes are not available.

| Short-term survival from fishery to BON | | | | | | |
|---|---|---|---|---|---|---|
| | | | Bayesian Analysis | | Ricker's Equations | |
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95% CI |
| Control | 424 | 415 | --- | --- | --- | --- |
| Purse | 460 | 440 | 0.980 | (0.955-0.999) | 0.977 | (0.954-1.001) |
| Beach | 371 | 351 | 0.969 | (0.939-0.997) | 0.967 | (0.939-0.994) |

| Intermediate-term survival from BON to MCN (including tributary & fishery recoveries) | | | | | | |
|---|---|---|---|---|---|---|
| | | | Bayesian Analysis | | Ricker's Equations | |
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95% CI |
| Control | 415 | 338 | --- | --- | --- | --- |
| Purse | 440 | 366 | 0.995 | (0.966-1.000) | 1.021 | (0.957-1.084) |
| Beach | 349* | 279 | 0.982 | (0.920-1.000) | 0.981 | (0.913-1.049) |

| Cumulative survival from fishery to MCN (including tributary & fishery recoveries) | | | | | | |
|---|---|---|---|---|---|---|
| | | | Bayesian Analysis | | Ricker's Equations | |
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95% CI |
| Control | --- | --- | --- | --- | --- | --- |
| Purse | --- | --- | 0.973 | (0.939-0.996) | 0.997 | --- |
| Beach | --- | --- | 0.949 | (0.886-0.987) | 0.948 | --- |

*Difference due to 2 fish that were detected at Bonneville Hatchery and not BON

Table 4. Summer steelhead survival estimates based on Ricker-Two-Release (R2R) model in 2013. Survival estimates are the median point estimates and 95% CI of the posterior distribution. For comparison, R2R estimates based in Ricker's formula are provided in the last two columns. Since the cumulative estimate is the product of the short-term and intermediate-term survival, release and recapture sample sizes are not available.

Short-term survival from fishery to BON

| | | | Bayesian Analysis | | Ricker's Equations | |
|---|---|---|---|---|---|---|
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95% CI |
| Control | 78 | 70 | --- | --- | --- | --- |
| Purse | 269 | 245 | 0.990 | (0.941-1.00) | 1.013 | (0.930-1.097) |
| Beach | 352 | 314 | 0.985 | (0.927-1.000) | 0.993 | (0.911-1.074) |

Intermediate-term survival from BON to MCN (including tributary & fishery recoveries)

| | | | Bayesian Analysis | | Ricker's Equations | |
|---|---|---|---|---|---|---|
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95% CI |
| Control | 70 | 53 | --- | --- | --- | --- |
| Purse | 245 | 204 | 0.991 | (0.935-1.000) | 1.095 | (0.940-1.249) |
| Beach | 313* | 252 | 0.988 | (0.919-1.000) | 1.059 | (0.910-1.207) |

Cumulative survival from fishery to MCN (including tributary & fishery recoveries)

| | | | Bayesian Analysis | | Ricker's Equations | |
|---|---|---|---|---|---|---|
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95% CI |
| Control | --- | --- | --- | --- | --- | --- |
| Purse | --- | --- | 0.974 | (0.909-0.998) | 1.109 | --- |
| Beach | --- | --- | 0.965 | (0.889-0.997) | 1.051 | --- |

*Difference due to 1 fish that was detected at Bonneville Hatchery and not BON

Table 5. Summer steelhead survival estimates based on Ricker-Two-Release (R2R) model for beach and purse seines combined in 2011-13. Survival estimates are the median point estimates and 95% CI of the posterior distribution. For comparison, R2R estimates based in Ricker's formula are provided in the last two columns. Since the cumulative estimate is the product of the short-term and intermediate-term survival, release and recapture sample sizes are not available.

Short-term survival from fishery to BON

| | | | Bayesian Analysis | | Ricker's Equations | |
|---|---|---|---|---|---|---|
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95% CI |
| Control | 960 | 928 | --- | --- | --- | --- |
| Seine | 1999 | 1869 | 0.968 | (0.953-0.986) | 0.967 | (0.951-0.983) |

Intermediate-term survival from BON to MCN (including tributary & fishery recoveries)

| | | | Bayesian Analysis | | Ricker's Equations | |
|---|---|---|---|---|---|---|
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95%,CI |
| Control | 928 | 722 | --- | --- | --- | --- |
| Seine | 1866* | 1510 | 0.997 | (0.980-1.000) | 1.040 | (0.997-1.082) |

Cumulative survival from fishery to MCN (including tributary & fishery recoveries)

| | | | Bayesian Analysis | | Ricker's Equations | |
|---|---|---|---|---|---|---|
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95% CI |
| Control | --- | --- | --- | --- | --- | --- |
| Seine | --- | --- | 0.964 | (0.943-0.983) | 1.006 | --- |

*Difference due to 3 fish that were detected at Bonneville Hatchery and not BON

Table 6. Summer steelhead survival estimates based on Ricker-Two-Release (R2R) model for steelhead adults caught in beach and purse seines combined in 2011-13 that were previously tagged as juveniles. Survival estimates are the median point estimates and 95% CI of the posterior distribution. For comparison, R2R estimates based in Ricker's formula are provided in the last two columns. Since the cumulative estimate is the product of the short-term and intermediate-term survival, release and recapture numbers are not available.

| Short-term survival from fishery to BON | | | | | | |
|---|---|---|---|---|---|---|
| | | | Bayesian Analysis | | Ricker's Equations | |
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95% CI |
| Control | 23 | 23 | --- | --- | --- | --- |
| Seine | 40 | 39 | 0.971 | (0.890-0.997) | 0.975 | (0.926-1.024) |

| Intermediate-term survival from BON to MCN (including tributary & fishery recoveries) | | | | | | |
|---|---|---|---|---|---|---|
| | | | Bayesian Analysis | | Ricker's Equations | |
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95% CI |
| Control | 23 | 16 | --- | --- | --- | --- |
| Seine | 39 | 29 | 0.962 | (0.774-1.000) | 1.050 | (0.724-1.376) |

| Cumulative survival from fishery to MCN (including tributary & fishery recoveries) | | | | | | |
|---|---|---|---|---|---|---|
| | | | Bayesian Analysis | | Ricker's Equations | |
| Treatment | Released | Recaptured | Survival | 95% CI | Survival | 95% CI |
| Control | --- | --- | --- | --- | --- | --- |
| Seine | --- | --- | 0.922 | (0.739-0.989) | 1.024 | --- |

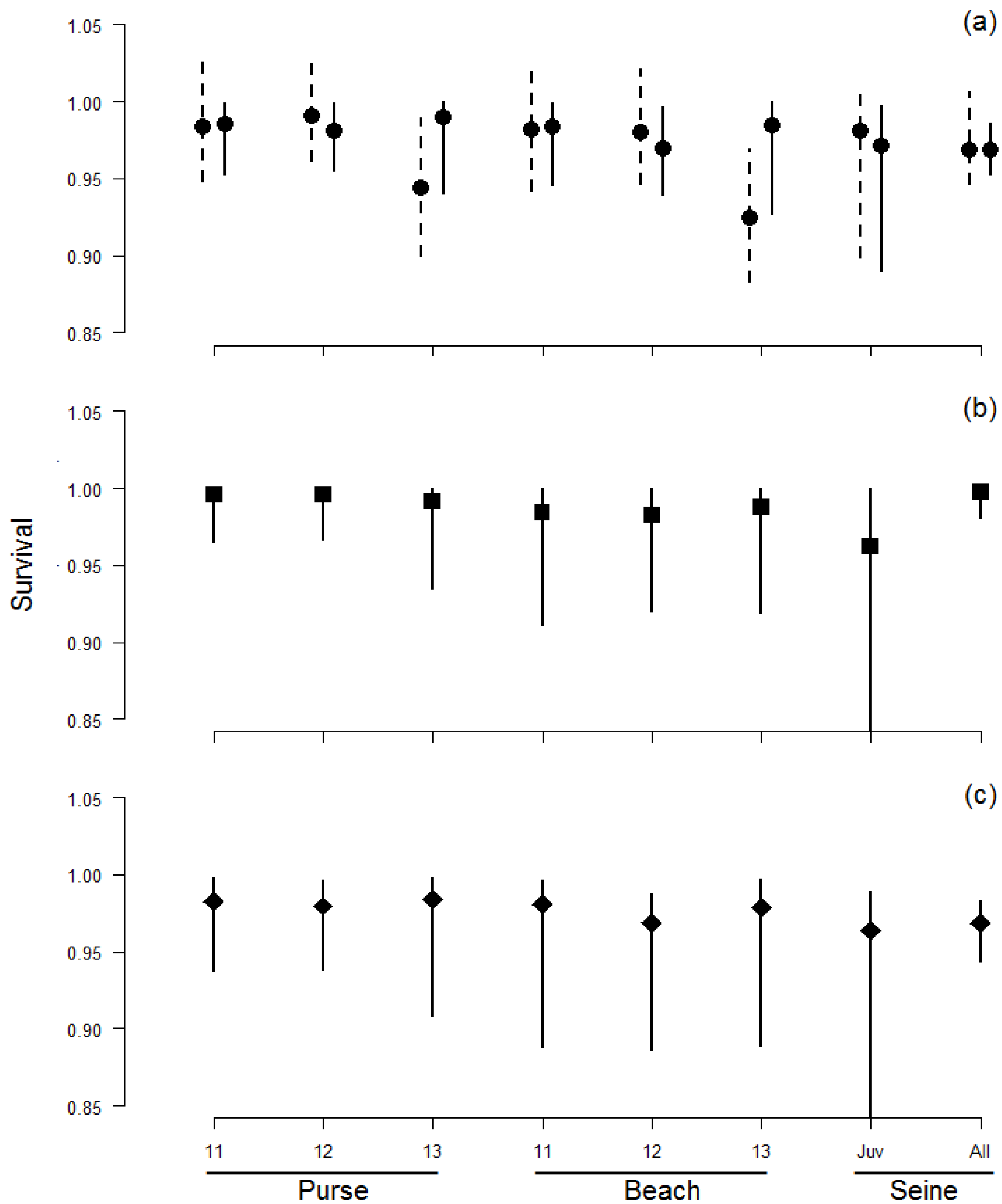


Figure 4. Short-term (panel a), intermediate-term (panel b) and cumulative (panel c) median survival estimates and 95% CI of Columbia River summer steelhead released from seines. The lower 95% CI are truncated at 0.85. The first three annual survival estimates are for steelhead released from purse seines for 2011 to 2013, the next three are for fish released from beach seines, the seventh survival estimate is the pooled survival for steelhead tagged as juveniles caught in seines, and the final estimate is the pooled beach and purse seine survival excluding fish tagged as juveniles. In the first panel the solid line/circle are the R2R estimates and the solid circle/dotted line are the "adjusted survival" estimates.

A total of nine possible models were considered for model selection for short-term and intermediate-term survival (Table 7). We considered constant (.) models that had the same capture or survival estimates by group (beach & purse) and across the three years, yearly (y) models that combined beach and purse seining parameters by year for each of the three years, and independent models (i) that separately estimated the beach and purse seine parameters across the years. For shorter-term and intermediate-term R2R models, DIC supported the model where capture probabilities varied yearly and survival probabilities were constant [$\rho(y)\ \phi(.)$]. This resulted in a median short-term survival estimate of 97.8% (95% CI: 96.4%-99.2%) and estimates of short-term survivals from the second best model were 98.4%, 97.4%, and 99.1% for 2011, 2012, and 2013, respectively. These estimates are slightly higher than the pooled estimate (96.8%) reported above, which is not supported by DIC (Table 7). The median intermediate-term survival estimate for the best model was 99.8% (95% CI: 98.4%-100). The second best intermediate-term model had the same estimate as the best model; this is similar to the pooled estimate of 99.7%, which is not supported by DIC (Table 7). The cumulative survival estimate for the best short and intermediate-term models is 97.5% (95% CI: 95.7-99.0%).

Table 7. The model selection results including number of effective parameters (pV), deviance information criteria (DIC), the change in DIC (Δ DIC), and DIC model weight (ω DIC) for short-term (left panel) and intermediate-term (right panel) summer steelhead survival estimates based on Ricker-Two-Release (R2R) model for steelhead adults caught in beach and purse seines combined from 2011 to 2013 that were tagged as adults.

| Short-term Survival | | | | |
|---|---|---|---|---|
| Model | pV | DIC | Δ DIC | ω DIC |
| ρ(y) ϕ(.) | 4.1 | 64.1 | 0.0 | 0.60 |
| ρ(y) ϕ(y) | 5.4 | 65.6 | 1.5 | 0.28 |
| ρ(y) ϕ(i) | 7.2 | 69.0 | 4.9 | 0.05 |
| ρ(i) ϕ(.) | 7.0 | 69.3 | 5.2 | 0.04 |
| ρ(i) ϕ(y) | 8.4 | 71.1 | 7.0 | 0.02 |
| ρ(i) ϕ(i) | 9.8 | 74.2 | 10.1 | 0.00 |
| ρ(.) ϕ(i) | 5.1 | 84.4 | 20.3 | 0.00 |
| ρ(.) ϕ(y) | 3.4 | 85.1 | 21.0 | 0.00 |
| ρ(.) ϕ(.) | 2.0 | 95.1 | 31.0 | 0.00 |

| Intermediate-term Survival | | | | |
|---|---|---|---|---|
| Model | pV | DIC | Δ DIC | ω DIC |
| ρ(y) ϕ(.) | 3.9 | 90.1 | 0.0 | 0.58 |
| ρ(i) ϕ(.) | 7.0 | 92.2 | 2.1 | 0.20 |
| ρ(y) ϕ(y) | 5.3 | 93.2 | 3.1 | 0.12 |
| ρ(y) ϕ(i) | 7.2 | 95.3 | 5.2 | 0.04 |
| ρ(i) ϕ(y) | 8.4 | 95.4 | 5.3 | 0.04 |
| ρ(i) ϕ(i) | 10.2 | 98.8 | 8.7 | 0.01 |
| ρ(.) ϕ(.) | 1.9 | 102.4 | 12.3 | 0.00 |
| ρ(.) ϕ(y) | 3.3 | 104.9 | 14.8 | 0.00 |
| ρ(.) ϕ(i) | 5.5 | 106.8 | 16.7 | 0.00 |

A total of 749, 989, and 516 adults were PIT tagged and detected above BON in 2011, 2012, and 2013, respectively. Of these 740, 983, and 509 were also detected at BON. The annual PIT tag detection probabilities at BON, estimated using equation 4, were similar across years based on contingency table analysis (PMI =0.91, BF=10). The pooled detection estimate was 99.0% (95% CI: 98.6%-99.4%) which indicated very strong support based on the contingency table analysis.

Rawding et al. (2014b) reported that of 130 PIT tagged steelhead and held at Skamania Hatchery, one fish was recorded as a tag loss and two were reported as tagging mortalities. The combined tag retention and survival from this study was 97.5% (95% CI: 94.0%-99.3%). Based on the adjusted survival method, the short-term survival by gear type was similar to the estimates from the R2R model (Table 7, Figure 4a). The median survival estimates ranged from 92.5% to 99.0%. The median estimate for the pooled survival was 96.8 (95% CI: 94.6%-100.6%). For adult steelhead previously tagged at BON as adults (N=6) and subsequently caught in the fishery, all survived and were detected at BON a second time.

Log linear models were used to determine associations between detection (D), gear (G), and year (Y) from Table 8. Analysis of residuals and the Bayesian p-value did not indicate any lack of fit. The inclusion probability for DY, DG, GY, and DGY were 0.09, 0.95, 1.00, and 0.00. The posterior model probabilities were 0.87, 0.08, and 0.05 for DG+GY, DY+DG+DY, and GY models, respectively. The BF of 10.9 provided strong support for the DG+GY model. Using the best model, the odds ratio (OR) for detection in the years of 11+12, 11+13, 12+13 were 0.96 (95%CI: 0.57-1.53), 2.11 (95% CI: 1.31-3.28), and 2.25 (95% CI: 1.47-3.33). Since the first OR included 1, the recovery rates were similar in 2011 and 2012. However, the remaining OR were greater than 2 and 95% CI did not include 1, which provides support that there were higher recoveries in 2011 and 2012 compared to 2013 (Table 8, Figure 4a). Thus “adjusted survival” model selection based on BF and OR indicates a similar survival of ~98% for 2011 and 2012 and a lower survival of 93% for 2013.

Table 8. Summer steelhead survival estimates based on the adjusted survival method for gear type by year, steelhead previously tagged as juveniles (Juv), and the pooled estimate for all years and gear types (Pooled). The observed survival is adjusted by PIT tag loss, tagging effects, and detection at BON. Survival estimates are the median point estimates and 95% CI of the posterior distribution.

| Year | Gear | Released | Recaptured | Survival | 95% CI |
|---|---|---|---|---|---|
| 2011 | Purse | 316 | 300 | 98.3% | (94.8%-102.5%) |
| 2011 | Beach | 231 | 219 | 98.2% | (94.2%-102.5%) |
| 2012 | Purse | 460 | 440 | 99.0% | (96.1%-103.1%) |
| 2012 | Beach | 371 | 351 | 98.0% | (94.7%-102.2%) |
| 2013 | Purse | 269 | 245 | 94.3% | (90.0%-99.0%) |
| 2013 | Beach | 352 | 314 | 92.5% | (88.3%-96.9%) |
| Juv | Seine | 40 | 39 | 98.0% | (89.9%-100.8%) |
| | | | | | |
| Pooled | Seine | 1999 | 1869 | 96.8% | (94.6%-100.6%) |

An analysis to examine the sensitivity of the posterior probabilities for the R2R model to different priors indicated that the posterior distribution of the annual estimates of survival was slightly sensitive to a range of prior distributions that were considered (Appendix). However, since the data were partially or completely pooled across years and gear types, the resultant survival estimates were not sensitive to the priors. See the Appendix for more details on the sensitivity analysis.

*Factors Affecting Recovery*

Based on a logistic regression model for detection at BON, the posterior inclusion probabilities for location was 0.04 with other covariates less than 0.01 (Table 9). However, the inclusion probability for the random effect of year was 1.00. This indicated that there was a large year effect; location (control vs. treatment) explained little of the variation, and the other covariates explained almost none of the variation in detection probability at BON. The model posterior probability for intercept and year model was 0.95 and 0.04 for the same model with the addition of location. This equates to a BF of 23.7 compared to the second best model, which is interpreted as strong support for the intercept and year random effect model. Support for the year effect was also found using model selection for the R2R and "adjusted survival" models (Table 7 and 8, Figure 4). The data from the full model were pooled into 10 subgroups for a Bayesian version of the Hosmer-Lemeshow (HL) test. The Bayesian *p*-value for the HL GOF test was 0.41, which indicated adequate model fit. Examination of individual residuals found 165 (5.6%) standardized Pearson residuals with mean values outside of -2 to 2, which is slightly above the expectation of 5% under the normality assumption. The mean of the lowest CPO value of 0.20 was greater than the value of 0.01 used to identify possible outliers. The maximum absolute value from the correlation matrix of covariates was 0.26, which was less than the recommended threshold value of 0.6 for multicollinearity.

Table 9. Posterior inclusion and model probabilities using Gibbs variable selection (GVS) for regression coefficients ($B_j$) for covariates for detection of PIT tags at BON from the full model. The covariates are the intercept ($B_0$), water temperature ($B_1$), origin ($B_2$), group ($B_3$), location ($B_4$), and the random effect of year ($\varepsilon_y$).

| | Covariates | | | | | | Model | |
|---|---|---|---|---|---|---|---|---|
| Type | B0 | $B_1$ | $B_2$ | $B_3$ | $B_4$ | $\varepsilon_y$ | $B_0+B_5$ | $B_0+B_4+B_5$ |
| Inclusion Probability | NA | 0.00 | 0.00 | 0.01 | 0.05 | 1.00 | 0.95 | 0.04 |
| Mean | 2.86 | 0.16 | 0.11 | 0.36 | -0.59 | 0.21, 0.33, -0.46 | NA | NA |
| Standard Deviation | 0.54 | 0.15 | 0.17 | 0.18 | 0.21 | 0.54 , 0.54, 0.54 | NA | NA |

*Detection by Fish Condition*

A 2x3 way contingency table was used to examine the association between detection (True/False) at BON (D) and injury type (I; wedged/gilled, tangled, not injured) including immediate mortalities. The wedged and gilled categories were pooled due to small sample sizes (N=30). The posterior inclusion and model probability for the two-way interaction term (DI) were both 1.00. Based on the BF, this indicates a decisive support for the model with the association between detection and injury classification. A total of 96.0%, 90.2%, and 56.7% of the PIT tagged fish that were classified as uninjured, tangled, and gilled/wedged were detected at BON, respectively (Figure 5).

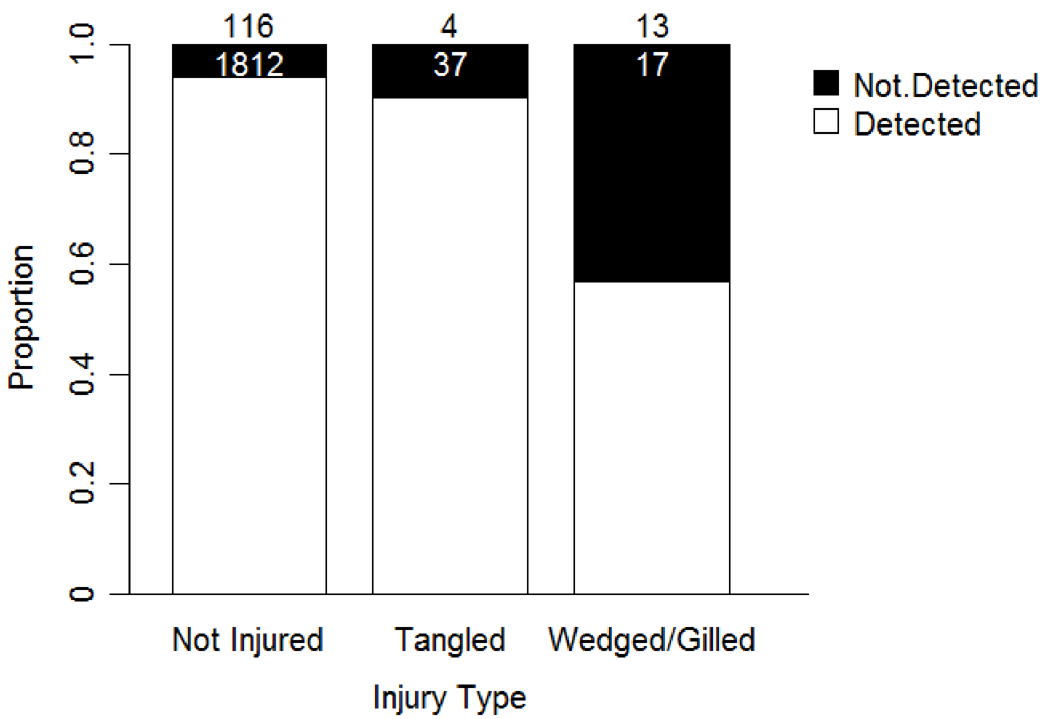


Figure 5. The proportion of fish caught in seines by injury category that were detected and not detected at BON, 2011-2013. The numbers in black are for not detected fish and the white number are for detected fish.

The odds ratio for not detected fish was 1.9, 4.9, and 11.7 for those fish that were classified as tangled, injured (e.g. gilled/wedged/tangled), and wedged/gilled vs. not injured fish, respectively (Figure 6). In addition, wedged/gilled fish were 8.4 times less likely to be recovered than those with tangle injuries. The best model fit was consistent with the data based on the GOF test using the posterior predictive check (Bayesian *p*-value = 0.50) and all standardized Pearson residuals ranged from -0.11 to 0.25.

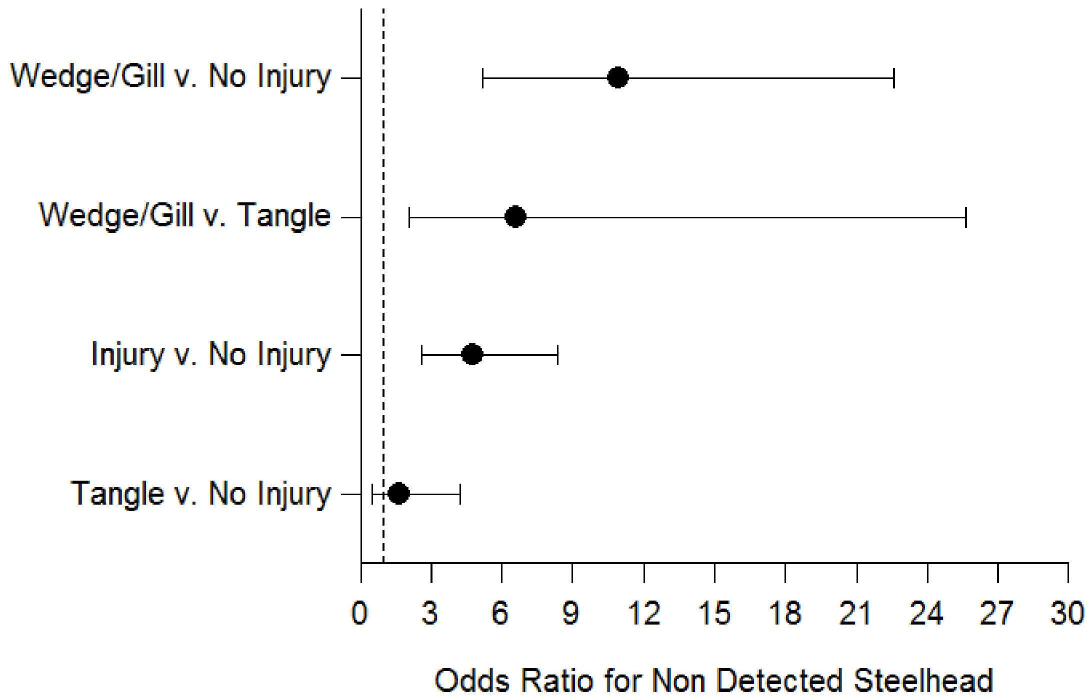


Figure 6. Estimated posterior probability of the median pair-wise odds ratio for PIT tagged steelhead that were not detected at BON by injury (wedged/gilled, tangled, and not injured). Note: Injured is the combination of wedged, gilled, and tangled. When 95% CI for odds ratios overlap with 1 (dashed vertical line), odds ratios are not significantly different.

For fish capture and release conditions, bleeding vigorous, bleeding lethargic, not bleeding vigorous, not bleeding vigorous, and moribund were combined into two classes, vigorous and lethargic, due to the small sample sizes for bleeding fish (N=14 at the time of capture). Fish classified as vigorous had higher recovery probabilities compared to those classified as lethargic (Figure 7). A 2x2x2 contingency table was created with detection (D), fish condition (C; lethargic/moribund vs. vigorous), and sampling event (E; capture vs. release) including immediate mortalities. There was a strong correlation between capture and release condition (0.85). Based on contingency tables, the posterior inclusion and model probability for the (DC) interaction were 0.99 and 0.81, respectively. Based on the BF, these provide substantial support that detection was associated with fish condition. The posterior probability for the interaction between detection and event (capture vs release) was 0.10, which lead to some support of the (DE+DC) model, which had a posterior model probability = 0.09. Based on the best model with the single two way interaction (DC), the odds ratio for a fish not being detected was 2.3 (95% CI: 1.5-3.2) for a fish in lethargic condition compared to fish in a vigorous condition. Model fit was consistent with the data based on GOF test using the posterior predictive check (Bayesian p-value = 0.50) and the standardized Pearson residual, which ranged from -0.95 to 0.98.

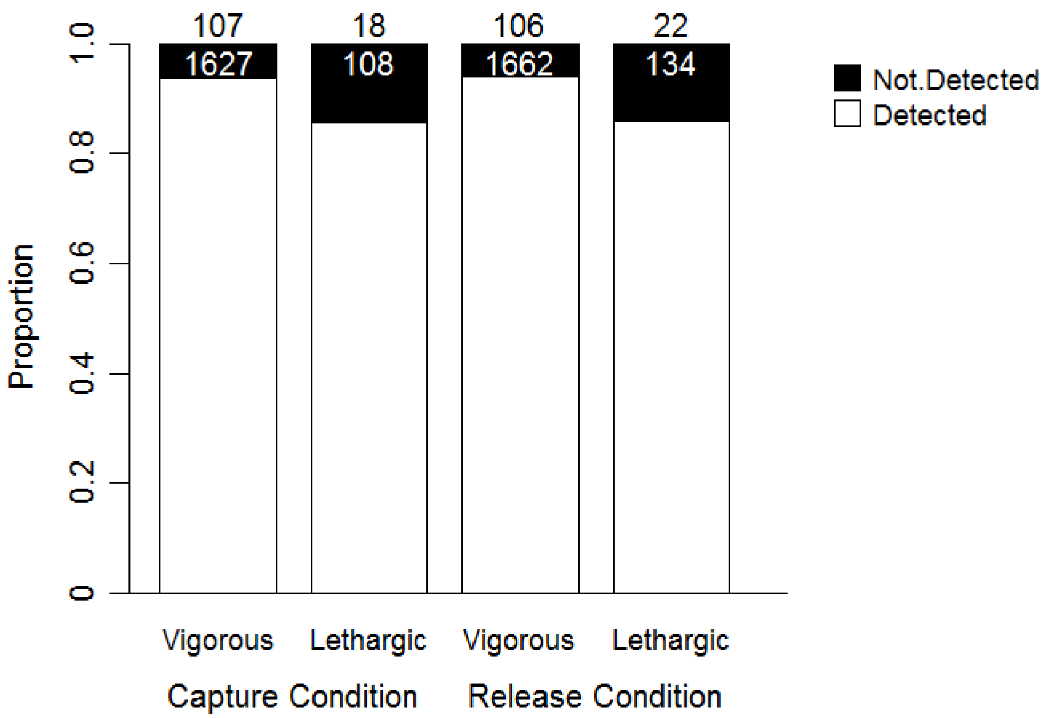


Figure 7. The proportion of fish caught in seines by fish condition category that were detected and not detected at BON, 2011-2013. The numbers in black are for not detected fish and the white number are for detected fish.

# Discussion

The point estimates of short-term survival using the R2R with fish tagged in the study, the R2R based on previously tagged juveniles, and the adjusted survival method were 97.8%, 97.1%, and 96.8%, respectively. The weight of evidence from three different analyses provides very strong support that the short-term survival of steelhead was greater than 96% (Table 4). The intermediate-term survival from BON to MCN, including fisheries and tributary recoveries, approached 100%. Therefore almost all mortality in the study occurred from the fishery to BON, which is an average distance of 21 km with a median travel time of 1.9 days for seined fish and almost no mortality in the next 237 km with a median travel time of 10.7 days. The estimate of cumulative survival obtained using the product method, based on adult fish tagged in the study, was 97.5%. However, when the cumulative survival was directly estimated from the fishery to MCN using the R2R model the estimates of cumulative survival exceed the estimates of short-term survival, which is not biologically plausible. We believe this occurred because survival estimates from the fishery were very high, there was negligible intermediate-term mortality, and we lacked the power to detect small changes in the cumulative survival from the fishery to MCN compared to the product method.

*Survival Model Assumptions*

The reported survival estimates are only valid if the assumptions of the survival models used in the analysis are met. These assumptions of the R2R model are: 1) control and treatment fish have the same tagging and handling mortality, 2) control fish have no or negligible mortality caused by the downstream transport from BON AFF to the release sites, 3) the control and treatment fish are subject to the same additional mortality (e.g., marine mammals, harvest) between the point of release and BON and between BON to MCN, including fisheries and tributary detections, 4) control and treatment fish have the same probability of tag loss, 5) control and treatment survivors have the same probability of detection following release, and 6) the fate of each fish is independent.

The first assumption addresses mortality due to handling and tagging, which was minimized through the use of standardized and proper handling and tagging techniques for control and treatment fish. Handling and tagging procedures implemented in this study were based on Columbia Basin protocols for PIT tagging (CBFWA 1999) and followed those implemented in a recent adult summer steelhead PIT tag detection and mortality study (Rawding et al. 2014b). Due to the use of standardized handling and tagging methods for both control and treatment groups, we believe this assumption was met. Handling and tagging effects for adult summer steelhead in the present study were assumed to be minimal based on a previous study that demonstrated a 32-day survival rate of 98% for PIT tagged summer steelhead held in a hatchery environment (Rawding et al. 2014b). For the R2R model, we conducted separate survival estimates for adults captured that were previously tagged as juveniles, which eliminated the assumption of tag loss and tag induced mortality. We found that the survival estimates were similar using either the R2R method, providing additional evidence that this assumption was met (Figure 4).

The second assumption addresses mortality of the control fish due to downstream transportation. After tagging, the control fish were placed in a holding tank for transport, with time to recover before being released, which is a standard handling procedure at the AFF (Keefer et al. 2004a). Although we did not directly test mortality of control fish due to transport, no direct mortalities of control summer steelhead were observed. Furthermore, a previous study with spring Chinook salmon using the same R2R study design at the same locations found minimal difference in survival estimates (~1%) using control fish captured and released from the AFF versus those captured at the AFF and released at rkm 225 (Ashbrook 2008).

The third assumption addresses mortality of the control and treatment groups following release due to additional factors (e.g., marine mammals, harvest). In order to meet this assumption, control fish were released at the upstream end of the fishery area (Figure 2). Selection of these release sites helped ensure that both groups were exposed to similar mortality risks between the fishery and BON (Figure 2). Within this reach, both control and release groups experienced the same exposure to sport and commercial fisheries, marine mammals, and the same challenges locating the entrance to the BON fish ladders and successfully passing the dam. A similar but small proportion of control and treatment fish (<0.3%) were recaptured in the commercial fishery, which supports the releasing of control fish into the fishery area.

The fourth assumption addresses tag loss, which is assumed to be similar between control and treatment groups. The most likely reason that tag loss might differ between the two groups is that individual taggers have different success rates. In order to minimize any tagger effects, staff were trained prior to the season on hatchery summer steelhead following established and standardized protocols (Rawding et al. 2014b). Tag loss was assumed to be minimal based on a previous study that demonstrated a 32-day retention rate of 99% for PIT tagged summer steelhead held in a hatchery environment (Rawding et al. 2014b). In addition, taggers were rotated between the AFF, the beach seines, and the purse seines in an attempt to randomize tagger differences among the release groups. Although the ideal study implementation would have equalized tagging efforts among taggers and groups, logistical constraints prevented complete equalization of effort. Based on the standardization of protocols, training, and rotation of taggers, the assumption that tag loss was similar between groups is likely to have been met in this study.

The fifth assumption of the R2R model addresses the probability of recovery following release which must be similar for control and treatment groups. This assumption is contingent on the control and treatment groups being composed of the same populations such that similar proportions of each group are destined for spawning areas upstream of BON. However, fish captured in the fishery have the potential to be a combination of stocks originating from above and below BON. The fish from the control group had already demonstrated a high propensity for migration above BON because they were intercepted at the BON AFF and likely originated from steelhead populations above BON. We used multiple methods to examine this key assumption. First, the results of contingency table analysis of origin (natural vs. hatchery) and group (A vs. B) supported that there was no association with tagging location (control vs. treatments). Second, a total of 97% of Skamania Hatchery summer steelhead, which have similar timing as other summer steelhead populations below BON, passed Willamette Falls by August 20th, which was the earliest date of the seine study (Figure 8). Because of the low abundance of steelhead returning to areas below BON compared to areas above BON and the difference in timing between the two groups, it is likely that few below BON steelhead would be captured in this study. Third, we used an alternate approach to test the hypothesis of no difference in survival rates to BON of adult steelhead tagged in our study, which could be a mixture of below and above BON populations, compared to adults we captured that were previously tagged as juveniles that originated above BON.  Based on overlap of the 95% CI the survival rates for both groups were similar (Tables 5-7, Figure 4).

The sixth assumption of the R2R model is that individual fates are independent, which cannot be tested.  However, if this assumption is violated, survival model parameter estimates are generally expected to remain unbiased or minimally biased.  The larger impact of violating the individual fate assumption is that the variance may be underestimated (Williams et al. 2002, Abadi et al. 2013).

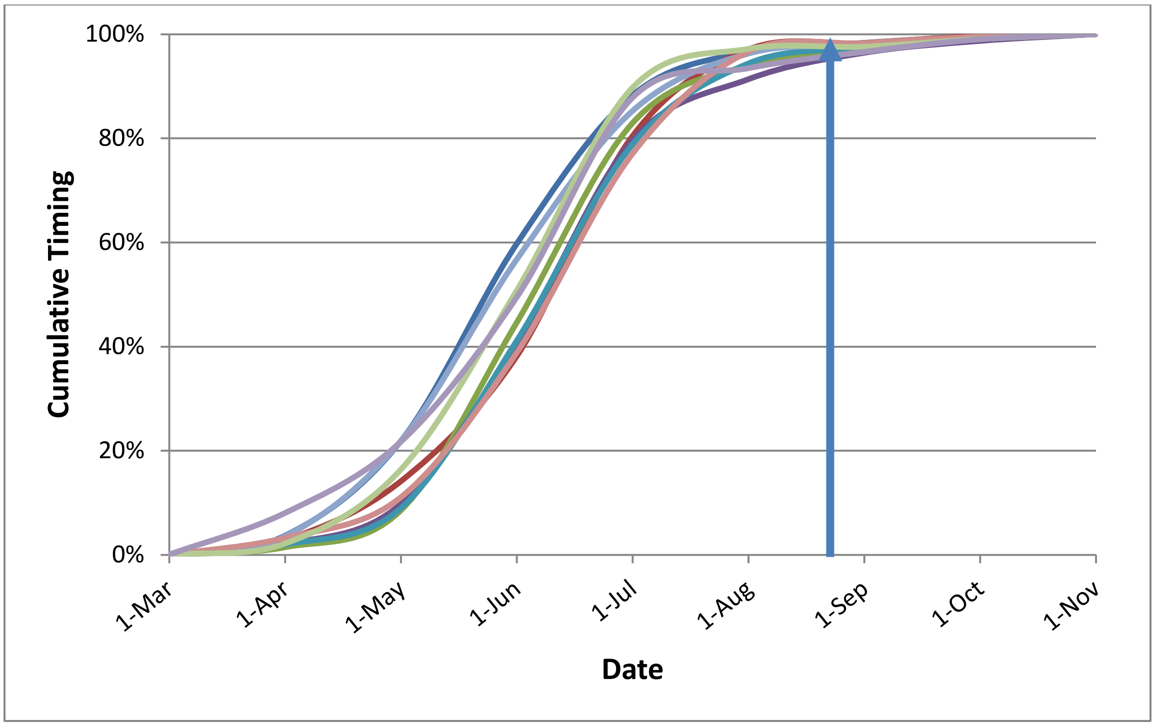


Figure 8.  Return timing of hatchery summer steelhead at Willamette Falls, 2004-2013. Vertical line is August 21st which was the approximate start date of the seine fisheries each year. Data downloaded from the Oregon Department of Fish and Wildlife website (*http://www.dfw.state.or.us/fish/fish_counts/willamette%20falls.asp*).

*Factors Affecting Survival*
We found the immediate survival of steelhead captured in seines was greater than 99.9%. This is higher than the immediate survival of 95.7% to 99.1% observed for spring Chinook salmon captured in the same Columbia River location using tangle and gill nets (Vander Haegen et al. 2004, Ashbrook et al. 2008). We found that 94% of the fish caught in seines were classified as vigorous at the time of capture and release. After accounting for an immediate mortality of 0.09 to 4.3%, Vander Haegen et al. (2004) classified 94%, 86%, and 71% of fish caught in 8.8, 11.3, and 13.8 cm tangle nets as vigorous, respectively. In their study, fish caught in smaller mesh were more likely to be classified as vigorous. Using log linear models we found that lethargic fish were 2.3 times less likely to be recovered at BON than those classified as vigorous. We also reported that there was no difference in the association of detection based on classification of capture or release event. These findings suggest that the qualitative assessment of fish condition is associated with non-recovery (e.g. mortality) of steelhead released from seines. This is consistent with recent research that suggests qualitative measures of fish condition are useful in predicting post-release mortality of Pacific salmon (Donaldson et al. 2012, Raby et al. 2012, 2013, 2015). The classification of fish condition as lethargic or vigorous that was developed by Vander Haegen et al. (2004) is an earlier simplified variation of the recently popularized reflex action mortality predictors (RAMP) procedure using a composite score based in the reflex of tail grab, body flex, head complex, orientation, and vestibular–ocular response (Davis 2010).

Our results are similar to other work on Pacific salmon that have demonstrated that post-release mortality is associated with injury (Vander Haegen et al. 2004, Raby et al. 2015). Vander Haegen et al. (2004) reported that nearly every adult Chinook salmon captured in a 20 cm gill net had net marks around the body in front of the dorsal fin or around the gills (e.g. wedged and gilled), and every adult captured in the 11.3 and 13.8 cm tangle nets had net marks around the snout (e.g. tangled). For steelhead captured in seines, only 71 (3.5%) had net marks, which indicated seine fish were less injured than fish caught in gill or tangle nets, which had almost a 100% net mark rate. In our study, we found that fish that had been wedged or gilled in the seines were 8.4 times less likely to be detected at BON compared to those exhibiting a tangle net injury. Vander Haegen et al. (2004) reported post-release recovery from gill nets was approximately seven times less than for fish released from tangle nets, which is consistent with our estimate of 8.4. In addition, our odd ratio for tangled, injured, and wedged/gilled vs. non-injured fish were 1.9, 4.9, and 11.7, respectively.

Using logistic regression, we found that the random effect of year was the most important variable in influencing the detection of fish caught and released from the fishery. This is supported by R2R model selections, which favored models with a year effect for capture probability (Table 7 and 9, Figure 4) and odds ratio for the alternative survival method, which supported a year effect (Figure 4). The next most important factor influencing detection at BON was the treatment group (control vs. seine) but this was smaller than the year effect. Logistic regression analysis indicated that water temperature, origin, and group (A vs. B) did not explain the variability in recovery rates. In modeling detection probability below BON, we considered other covariates such as capture date which highly correlated with water temperature. Since multicollinearity can lead to biased results in regression (Quinn and Keogh 2002), we included the more biologically relevant covariates of temperature in the regression analysis to BON. The year effect was observed in the R2R analysis, adjusted survival analysis, and the logistic regression. The year effect lowered survival estimates in 2013 for the adjusted survival but not the R2R (Figure 4), which highlights the importance of control/treatment designs to estimate survival across years.

Our study did not identify water temperature as an important variable in predicting steelhead detection. The mean water temperature during our study was 19.5°C (range 14.1 – 22.4 °C). However, Rawding and Bentley (*in review*) did identify water temperature as an important factor in the survival of steelhead released from recreational fisheries. Based on limited data, they noted mortality for fish hooked in non-critical locations increased rapidly above 19°C for coastal steelhead. Pacific salmon, *Oncorhynchus spp.*, have species and population specific tolerances with respect to metabolic capacity (Eliason et al. 2011) and capture stressors (Donaldson et al. 2012) across a range of temperatures. Pacific salmon adults have high fidelity to natal spawning areas, which has resulted in genetically distinct populations with specific physiological adaptations resulting in local adaptation to the thermal regimes (Lee et al.2003, Eliason et al. 2011). In resident *O. mykiss*, thermal adaptation has been observed in transplanted strains and supported by genetic evidence (Narum et al. 2010, 2013, Chen et al. 2015). Thermal tolerance for resident (rainbow trout) and anadromous (steelhead) forms of *O. mykiss* based on field observations in California, Oregon, and Idaho ranged from 29 to 32°C (Li et al. 1994, Nielsen et al. 1994, Rodnick et al. 2004, Zoellick 1999, Werner et al. 2005). This is a similar thermal tolerance for resident *O. mykiss* acclimated at temperatures above 15°C in laboratory experiments (Sloat and Osterback 2013). Nielsen et al. (1994) observed that the majority of adult and juvenile steelhead migrated to cool water at temperatures above 23°C. Brewitt and Danner (2014) observed that all juvenile steelhead moved into thermal refuge when temperatures reached 25°C. The mode temperature on the date of peak passage of Columbia River steelhead at BON since 1997 was 22°C (Figure 9). This suggests that while *O. mykiss* may tolerate water temperatures above 29°C, they are likely experiencing thermal stress at water temperatures above 23-25°C, which is above the temperature we observed in our seining study.

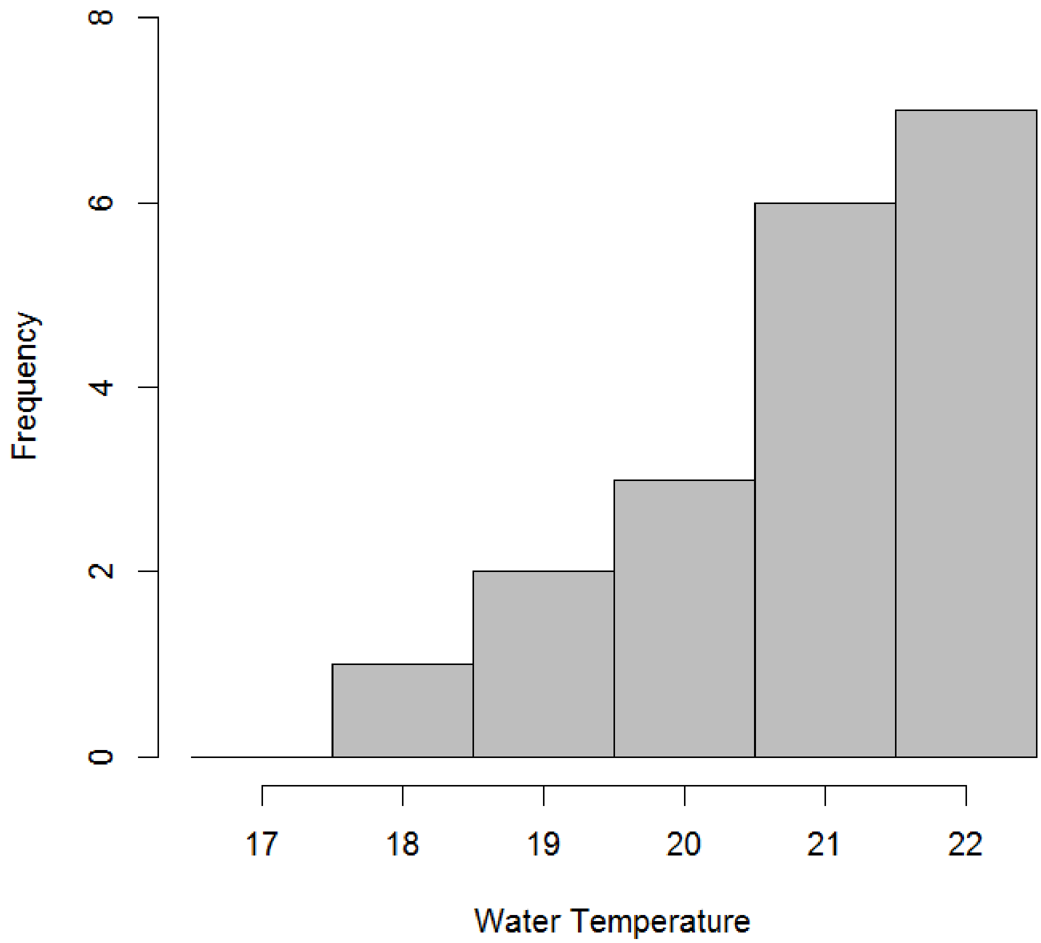


Figure 9. Frequency of annual steelhead peak passage at Bonneville Dam by daily scroll case water temperature (°C) from 1997 to 2015. Data was obtained from Corps of Engineers (COE) Annual Fish Passage Reports.

*Comparison of Survival Estimates*

The cumulative survival estimates for steelhead associated with the seine fishing gear in the lower Columbia River are high compared to estimates reported for other types of commercial fishing gear (Chopin and Arimoto 1995). However, gear related mortality can vary widely based on many variables including the way the gear is operated (Buchanan et al. 2002), the way the fish are handled (Dunning et al. 1989), the time of year the gear is operated (Gallinat et al. 1997), the extent of injury during capture (Baker and Schindler 2009), and water temperatures during capture (Murphy et al. 1995). Our post-release survival estimate for steelhead was 97%, which was similar to the estimate of 96% survival of seine caught steelhead on the Rogue River (Everest 1973). Griffith et al. (2009) estimated a 77% survival rate to BON for Columbia River winter steelhead caught, radio tagged, and released with tangle nets in the same area during the spring season. However, this result should be interpreted cautiously because their sample size was small (N=13). The reported survival of Columbia River spring Chinook salmon caught in tangle nets (11.3 cm mesh) in the same area as our study were 93%, 69%, and 87% for three different studies (Vander Haegen et al. 2004, Ashbrook 2008, and Ashbrook et al. 2008). The survival of spring Chinook salmon released from gill nets (20 cm mesh) in this same area was 51% (Vander Haegen et al. 2004).

We also compared our estimate to the limited studies of post-release survival estimate of Pacific salmon caught in seines in marine waters. The short-term survival of coho salmon caught in southern British Columbia in purse seines was estimated to range from 71 to 76% (Kelly and Hop Wu 1998). Raby et al. (2015) reported survival of coho salmon caught and released from purse seines in southern British Columbia based on 24 hour net pen holding and an acoustic telemetry study was ~80%, but longer term survival based on acoustic tags was 53%. Candy et al. (1996) found the survival of Chinook salmon caught and released from purse seine vessels in southern British Columbia to be 77%, based on the sonic tracking of these fish in saltwater for a single day. In southeast Alaska, Chinook salmon were caught using purse seines and released into net pens (Ruggerone and June 1996). The fish were held for two days and their survival was 98%. Mathews (2012) cited that Van Alen and Seibel (1986, 1987) estimated the survival of immature Chinook salmon (<53 cm) ranged from 25 to 73% for fish caught in purse seines targeting pink, sockeye and chum salmon.

Our steelhead seine survival estimate of 97% is much higher than previously reported seine survival estimates of adult salmon, except for the 98% survival reported by Ruggerone and June (1996). Mathews (2012), in a review of Chinook and coho salmon caught in Puget Sound chum fisheries, reported that the survival of bycatch is low when the purse seine mesh is large enough to act as a gill net on immature salmon because the majority are moribund when handled. We observed only 1.6% of the steelhead catch as being gilled or wedged and those fish had a low (56.7%) probability of being detected upstream (Figures 5 and 6). The purse seine gear between Puget Sound and the Columbia River is similar except a “top strip” of 12.5 cm mesh is built into Puget Sound nets to allow immature Chinook salmon to swim through this area. The cause of the survival difference for this study compared to others is unknown but is likely due to a combination of factors including: 1) environment (marine vs. freshwater), 2) species behavior, or 3) small size of immature Chinook relative to the purse seine mesh size. A second condition in which low survival has been observed occurs when the few non-target species get “lost” among the thousands of targeted salmon on the seiner deck but this can be reduced by requiring fish to be released into a holding tank (Raby et al. 2015). Mathews (2012) and Raby et al. (2015) noted that when seine catches are high fish may become compacted, crushed, and/or injured in the bottom of the brail as they are lifted from the water. The conditions in our study allowed for the non-targeted steelhead to be identified and removed quickly by dip netting one or two individuals from the pursed area. This practice avoided fish being "lost" on the deck or inflicting internal and external damage through compression or crushing. Our handing procedure also minimized air exposure, which can lead to decreased survival (Cook et al. 2015). We believe the low number of steelhead (mean=1.24) and salmon (mean=11.49) caught per set, short set times, and the strict fish handling guidelines contributed to the high survival rates observed in our study.

*Monitoring of Steelhead Catch*

The steelhead catch per seine set was consistent with the negative binomial distribution (Figure 3). There were many instances where the steelhead catch per set was zero but there were few instances of over 20 steelhead caught in a set. Based on this data structure, Hilborn and Mangel (1997) reported that higher observation levels are needed to obtain a reliable estimate of incidental catch. Alternatively, sampling programs could explore the relationship between retained salmon catch and steelhead released (McHugh and Holowatz 2013). This approach may be more cost effective since commercial fisheries below BON are required to report salmon catch.

## Conclusions

In this report, we provide the results of a study to estimate the survival of summer steelhead released from purse and beach seines in the area below BON on the Columbia River from 2011 to 2013. We conducted a robust analysis including model selection, assumption testing, and using alternative models when available to compare survival estimates. Model selection and overlapping 95% CI based on the R2R model suggest similar survival estimates between the two gear types (beach and purse seines), and among years (2011, 2012, 2013). Our median estimates of short-term survival (fishery to BON) using three different approaches were greater than 96% for summer steelhead. For intermediate-term survival (BON to MCN) our estimates approached 100%. The cumulative survival estimates (fishery to MCN) were above 97%. These results indicate a very high post-release survival for summer steelhead caught and released in the late summer and fall Columbia River experimental seine fishery. Our results suggest that purse and beach seines are an important gear type to consider when developing fisheries to harvest salmon populations while minimizing impacts to non-target steelhead populations. Given our review of the wide range of post-release survival of Pacific salmon released from seines and the multiple factors that affect survival rates, we recommend caution in the application of our Columbia River seine mortality estimates to other fisheries. We believe our high survival were likely positively influenced by species, local adaptation, fishing regulations and handling techniques, environmental conditions, catch per set, and fishing locations.

## Acknowledgements

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# Appendix

*Sensitivity of Survival Estimates*

In this study, we reported survival based on the median value of the posterior distribution. The mode, median, and mean are commonly reported measures of central tendency for a posterior distribution, which are reported in the form of point estimates. The mode is the most frequent value in the dataset, the median is the middle ranked value of the data, and the mean is the sum of the numbers in the dataset divided by the numbers in the dataset. When the data are symmetrically distributed, these measures of central tendency are the same. For asymmetric distributions, such as those observed in our results, measures of central tendency differ and it is not always clear on which measure to report. The mode can be a poor choice when it is distant to the middle of the distribution. The mean may also be a poor choice with asymmetric distributions as this measure is heavily influenced by extreme values (Carlin and Louis 2009). Given the left skew in our data, annual survival estimates based on the mean of the posterior distribution were slightly lower than those estimated by the median of the posterior distribution. Survival estimates based on the mode of the posterior distribution were slightly higher than those estimated by the median value. However, the posterior distribution of the pooled survival estimate was approximately normally distributed; thus all measures of central tendency were similar for pooled data.

We explored the sensitivity of our results to the three commonly used reference priors described in the paper. It is important to note that our reported estimates based on the different reference priors were used to estimate both the survival and probability of capture although we only report their sensitivity for survival. For annual steelhead seine survival estimates, our results were slightly sensitive to the choice in priors due to the number of observations in our dataset for steelhead (Figure A1). The upper 95% CI estimate for survival was not sensitive to choice in prior but the lower 95% CI estimate was slightly sensitive to choice in prior, with lowest and highest bound corresponding to the uniform and Haldane priors, respectively. Our annual median estimates of short-term survival using the uniform prior were approximately 1% less than those with Jeffreys priors, while estimates with the Haldane priors were approximately 1% greater (Figure A1, upper panel). In contrast, the annual intermediate-term steelhead survival estimates with the uniform prior were approximately 2% less than the Jeffreys prior and the estimates with the Haldane prior were approximately 2% greater (Figure A1, middle panel). The cumulative survival estimates followed the same pattern as the intermediate-term survival estimates. Due to the small sample size, the survival estimates of previously tagged juveniles were most sensitive to the priors. However, our pooled estimates of short-term, intermediate-term, and cumulative survival (All) were not sensitive to the priors, which is consistent with the Berstien Von Mises Theorem.

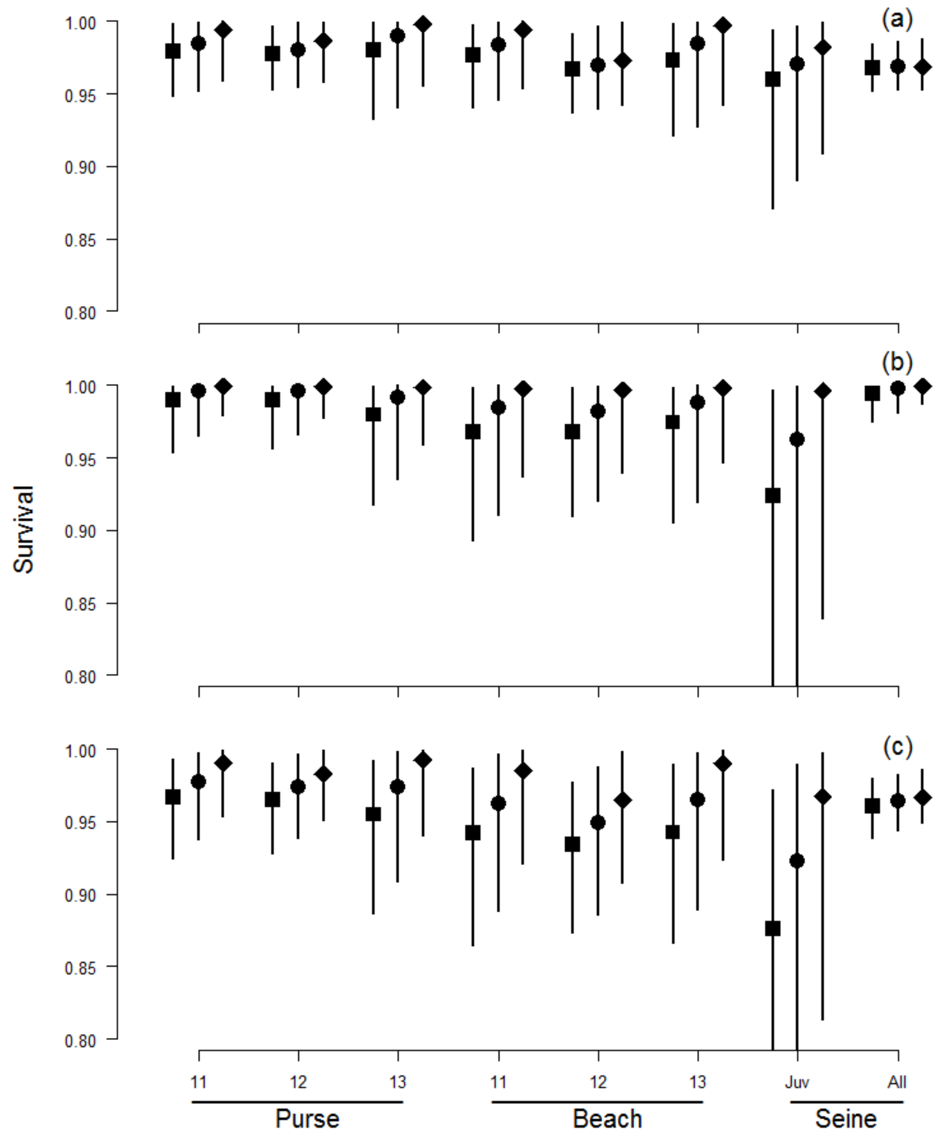


Figure A1. Sensitivity of short-term (panel a), intermediate-term (panel b) and cumulative (panel c) median survival estimates and 95% CI of Columbia River summer steelhead released from seines using the Ricker-Two-Release model . Sensitivity of short-term (panel a), intermediate-term (panel b) and cumulative (panel c) median survival estimates and 95% CI of Columbia River summer steelhead released from seines using the Ricker-Two-Release model. The lower 95% CI are truncated at 0.80. The uniform, Jeffreys, and Haldane priors are displayed by a black square, black circle, and black diamond, respectively. The first three annual survival estimates are for steelhead released from beach seines for 2011 to 2013, the next three are for fish released from purse seines, the seventh survival estimate is the pooled survival for steelhead tagged as juveniles caught in seines, and the final estimate is the pooled beach and purse seine survival excluding fish tagged as juveniles.

The results of the sensitivity analysis were consistent with previous analyses of binomial data (Kerman 2011, Link and Barker 2010, and Lunn et al. 2013). We note that the posterior distribution of survival estimates with the larger sample size (e.g. pooled survival estimates) was less influenced by the prior distribution (Link and Barker 2010). In addition, the uniform prior, with equal probabilities between 0 and 1, pulls the estimates toward the middle value of the prior (50%), while a Haldane prior, with half of its probability at 0 and 1 and with no probability in between, pulls the survival estimates in this study towards 1. The Jeffreys prior yielded posterior estimates intermediate to the uniform and Haldane priors. Since the Jeffreys prior avoids the extremes of the uniform and Haldane priors it often used as reference priors for binomial distributions (Bernardo 1979, Brown et al. 2001). Tuyl et al. (2008) suggested that using prior information (e.g., previous years of survival estimates) may be a better alternative to reference priors when estimates are near the boundaries. However, this was not pursued since in this study it was appropriate to pool across gear types and years and the survival estimates were not sensitive to the choice of priors.

*Sensitivity of Model Selection in Logistic Regression*

The covariate inclusion and model probabilities that are known to be sensitive to prior specification of the variance due to the Lindley-Bartlett paradox (Link and Barker 2006, Ntzoufras 2009). With no prior information for logistic regression coefficients ($B_j$) with a normal distribution it is often reasonable to center prior beliefs for the mean at zero if they have been centered and standardized. For the fixed variance ($\Sigma_j$) we used 4 times the sample size (4N), 1,000, and 100 as reference priors. The first prior for the fixed variance is the unit information prior ($\Sigma_j$ =4N), which is equivalent to weighting the prior by one observation (Kass and Wasserman 1995). The results of model selection with this prior are similar to those obtained using Bayesian Information Criteria (Link and Barker 2010). In addition, we included fixed variances of 1,000 and 100, which were recommended as default priors by Dellaportas et al. (2002) and Ntzoufras (2002). These span a sensible range of possible priors (Tenan et al. 2014). (Table A1).

The sensitivity analysis to determine factors that may influence short-term survival of PIT tagged steelhead is presented in Table A1. These steelhead were captured in the seine fishery, PIT tagged, and subsequently detected at BON or captured at the BON AFF and released in the fishery area. All covariates inclusion probabilities were low (<0.04) except for the location (control vs. seine) and the random effect of year. Model selection always favored intercept and random effect of year model regardless of the prior. The BF under the lowest variance ($\Sigma_j$ =100) was 1.8 indicating similar support for the model including location.

Table A1. Posterior interaction inclusion and model probabilities using Gibbs variable selection (GVS) obtained under three different prior sets for regression coefficients (*$B_j$*) for covariates may explain detection of PIT tags at BON from steelhead released in the seine fishery.The covariates are water temperature (*$B_1$*), origin (*$B_2$*), group (*$B_3$*), location (*$B_4$*), and the random effect of year ($\varepsilon$). The first [N(0,4N)] prior was used in the paper and the other priors are part of the sensitivity analysis.

| | Inclusion Probability | | | | | Model Probability | |
|---|---|---|---|---|---|---|---|
| Prior | $B_1$ | $B_2$ | $B_3$ | $B_4$ | $\varepsilon_y$ | $B_0+\varepsilon_y$ | $B_0+B_5+\varepsilon_y$ |
| N(0,4N) | 0.00 | 0.00 | 0.01 | 0.05 | 1.00 | 0.94 | 0.05 |
| N(0,1000) | 0.00 | 0.01 | 0.02 | 0.15 | 1.00 | 0.82 | 0.15 |
| N(0,100) | 0.02 | 0.02 | 0.07 | 0.37 | 1.00 | 0.57 | 0.33 |

For the logistic regression we chose a prior that adds prior information equivalent to one data point in the final analysis. This is based on Zellner's g-prior, which is one of the most common priors in regression model selection. The N(0,4N) prior is supported by the unit information and power priors (Kass and Wasserman 1995, Chen et al. 2000). Setting the mean to zero and adding prior information equivalent to one data point provides support for selecting the most parsimonious model (Ntzoufras 2009). There was strong agreement in model selection between the unit information prior, and the two default priors N(0,1000) and N(0,100) recommended by Ntzoufras (2002). However, when using the N(0,100) the location (control vs. treatment) becomes a more important variable. These priors are likely sufficiently large to avoid bias but not large enough to activate the "Lindley-Bartlett paradox", which support the simplest models (Tenan et al. 2014). Based on Gelman (2006) we used a normal prior for random effects with a uniform distribution (0-2) for the standard deviation. We explored a larger uniform distribution (0-5) with similar results (not shown) and a half Cauchy with a scale of 1 but the models did not meet our convergence criteria.

*Sensitivity for Model Selection in Contingency Tables*

For log linear models with no prior information for regression coefficients (*$B_j$*) with a normal distribution, prior beliefs for the mean were centered at zero with variances of 2 and 10 (Dellaportas et al. 2000, Congdon 2005). To more completely cover the range of possible sensible priors we include a variance of 100. The 2x2 contingency tables had high posterior model probabilities and were not sensitive to priors (results not shown).

A 2x5 contingency table was used to examine the association between the upper most detection Location (L) and Gear (G) where seined fish are from the treatment group and the BON fish are from the control group. The posterior inclusion probability for the two-way interaction term (LG) was 0.00 and the posterior model posterior probability for supporting independence was 1.00 for all models. Thus, the priors had no influence on model selection, which decisively favored the model of independence.

A 2x2x4 contingency table was used to examine the association between detection (True/False) at BON (D) and gear type (G; beach and purse seine), and year (Y: 2011-13). The results of this analysis was used for model selection for the adjusted survival method. Regardless of the priors the inclusion probability for DG and GY exceeded 0.98, for DY was less than 0.17, and DGY was 0.00. The posterior model probabilities for the DG+GY model exceeded 0.80 and BF >5.5, which indicated substantial support for this model. The priors examined had no influence on model selection.

A 2x3 contingency table was used to examine the association between detection (True/False) at BON (D) and injury type (I; wedged/gilled, tangled, not injured) including immediate mortalities. The posterior inclusion and model probability for the two-way interaction term (DI) were both 1.00 for all models regardless of the prior. Based on the BF, this indicates a decisive support for the model with the association between detection and injury classification for all considered priors.

A 2x2x2 contingency table was used to examine the association between detection (D), fish condition (C; lethargic vs. vigorous) and event (E; capture vs. release). The model with a two-way interaction between detection and condition (DC) was favored. Regardless of the prior, the DC interaction term and the model including this term always had the highest probability (Table A2). The interaction between detection and event (DE) and detection and condition (DC) had consistent support based on inclusion probabilities and model probabilities under the first two priors. However, Bayes Factors for inclusion and model probabilities were greater than 5 in favor of the DC model. These results suggest indicator and model selection were not very sensitive to the range of priors explored.

Table A2. Posterior interaction inclusion and model probabilities from the Kuo and Mallick (1998) approach obtained under three different prior sets for regression coefficients ($B_j$). The first [N(0,10)] prior was used in the paper and the other priors are part of the sensitivity analysis.

| | Inclusion Probability | | | | Model Probability | | |
|---|---|---|---|---|---|---|---|
| Prior | DE | DC | EC | DCE | DC | DC+DE | DC+EC |
| N(0,10) | 0.11 | 1.00 | 0.10 | 0 | 0.81 | 0.10 | 0.09 |
| N(0,2) | 0.20 | 1.00 | 0.18 | 0 | 0.66 | 0.16 | 0.14 |
| N(0,100) | 0.04 | 0.99 | 0.04 | 0 | 0.92 | 0.04 | 0.03 |