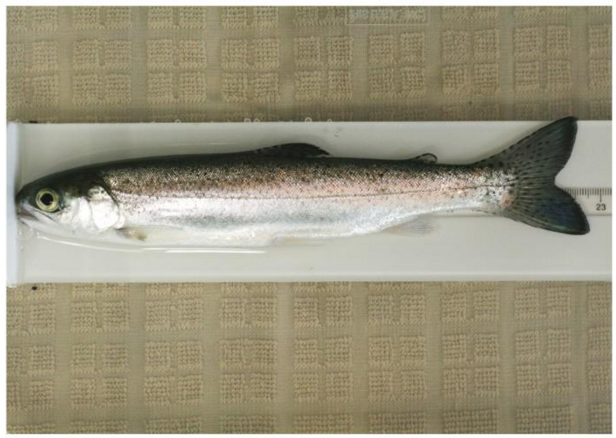
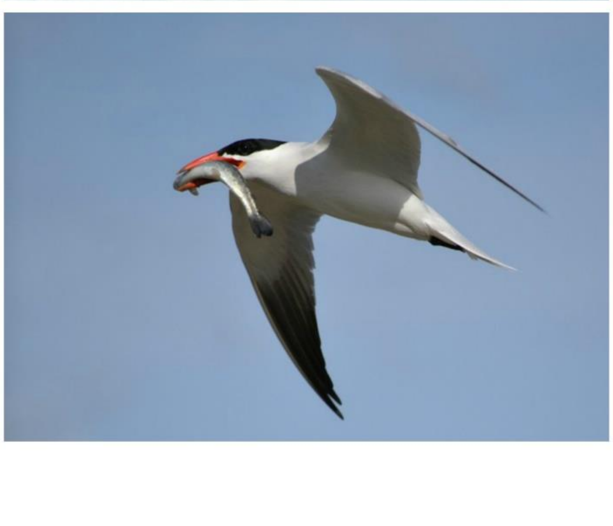
FINAL TECHNICAL REPORT

Effects of Biotic and Abiotic Factors on Juvenile Steelhead Survival in the Middle Columbia River, 2008-2015





FINAL TECHNICAL REPORT

Effects of Biotic and Abiotic Factors on Juvenile Steelhead Survival in the Middle Columbia River, 2008-2015

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SUMMARY
Identifying factors that affect survival probabilities of juvenile steelhead *Oncorhynchus mykiss* listed under the Endangered Species Act (ESA) is paramount to develop effective plans for recovery. To evaluate which factors best explained steelhead survival in the middle Columbia River during 2008-2015, we compared and contrasted survival models that incorporated various biotic and abiotic factors experienced by smolts during outmigration. Biotic factors investigated included (1) predation by colonial waterbirds, (2) the relative abundance of steelhead in the river, (3) fish travel times, and (4) individual fish characteristics or traits (condition, size, and rear-type). Abiotic factors investigated included (1) river temperatures, (2) river flows, (3) water transit times, and (4) dam operations (percent spill, powerhouse indices). Two independent release groups of fish were included in survival models, with the suite of biotic and abiotic factors investigated differing based on the data available for each release group. Release groups included double-tagged steelhead (fish tagged with both acoustic telemetry [AT] and passive integrated transponder [PIT] tags) travelling through a 105 river kilometer [Rkm] section of the middle Columbia River (hereafter “Reach 1”) and single-tagged steelhead (PIT tags only) travelling through a 259 Rkm section of the middle and lower Columbia rivers (hereafter “Reach 2”).

Best fitting survival models for steelhead in Reach 1 indicated a strong relationship between avian predation and steelhead survival, with bird predation accounting for 12% to 62% of all mortality sources experienced by steelhead during outmigration. There was an inverse relationship between steelhead survival and the proportion of steelhead migrating through a powerhouse (PH index) compared with other passage routes at Wanapum Dam. The odds of survival through Reach 1 decreased, on average, by a factor of 0.95 for every 0.1 increase in the PH index. There was a direct relationship between survival and the relative abundance of steelhead (STHD index) in the middle Columbia River. On average, for every 1,000-unit increase in the STHD index the odds of survival through Reach 1 increased by a factor of 1.11. Additional models with significant support from the data indicated a relationship between water transit times and survival, with survival increasing as water transit times decreased. A comparison of best fitting survival models for steelhead in the Wanapum and Priest Rapids reservoirs (spatial subsets within Reach 1) further confirmed the importance of avian predation, steelhead abundance, and water transit times. Additionally, reservoir-specific models provided evidence of an inverse relationship between water temperature and survival.

Best fitting survival models for steelhead in Reach 2, which investigated biotic factors only, indicated that avian predation, fish size (fork length), external condition (body injuries, descaling, fin damage and/or disease), and rearing-type (hatchery, wild) were all significantly related to survival. Bird predation accounted for between 31% and 83% of all smolt mortality sources. Survival was directly related to fish size, with each 10 mm increase in fork length associated with 2% greater odds of surviving Reach 2. Compromised fish (i.e., fish with signs of external damage or disease), which were disproportionately hatchery-reared, had 62% lesser odds of surviving Reach 2 compared with uncompromised fish (i.e., fish with little to no signs of external damage or disease). Wild fish, which were generally uncompromised, had 144% greater odds of surviving Reach 2 compared with hatchery-reared fish.

Collectively, results indicated that a combination of biotic and abiotic factors were associated with variation in steelhead survival in the middle Columbia River; demonstrating the complexity and inter-related nature of factors that regulate smolt survival during outmigration. Results suggest that management plans aimed at reducing avian predation, coupled with dam operations that minimize powerhouse passage, increase water transit times, and minimize passage-related injuries to juvenile

steelhead are the most likely to increase steelhead survival in the middle Columbia River. Releases of uncompromised hatchery-reared steelhead during the peak outmigration period may also increase survival rates by increasing steelhead abundance, abundance that is likely associated with a predator swamping effect. Additional research to understand the association between these various biotic and abiotic factors on survival at larger spatial and temporal scales may be warranted to evaluate if survival gains in the middle Columbia River are additive throughout the entire smolt life history.

INTRODUCTION

Steelhead trout *Oncorhynchus mykiss* originating from the upper Columbia River are listed as threatened under the Endangered Species Act (ESA) and during their seaward migration must pass up to eight hydroelectric dams. The National Oceanic and Atmospheric Administration (NOAA), the agency responsible for ESA-listed steelhead recovery, has established survival standards for juvenile steelhead passing impounded reaches of the Columbia River. Survival standards for steelhead passing through the Wanapum-Priest Rapids Project (Wanapum and Priest Rapids dams and reservoirs) in the middle Columbia River require 93% fish survival through each development (one dam and reservoir) or 86% survival through the entire Project (NMFS 2004). To evaluate whether these survival standards were being met during 2008-2010 and again during 2014-2015, Public Utility District No. 2 of Grant County (Grant PUD) conducted survival studies using steelhead smolts tagged with acoustic telemetry (AT) tags. These tagged fish, along with a network of telemetry receivers, allowed for spatially- and temporally-explicit measures of survival within the middle Columbia River. Results indicated that steelhead survival varied significantly by year and river reach, and that survival standards were not met in all years and reaches (Skalski et al. 2016).

As part of a study to investigate the influence of colonial waterbird predation on steelhead survival in the middle Columbia River, the U.S. Army Corps of Engineers and Grant PUD implanted and released over 55,000 steelhead smolts with passive integrated transponder (PIT) during 2008-2015. Following release, nearby bird colonies were scanned for PIT tags to determine steelhead predation rates (proportion of available tagged fish consumed by birds). Results indicated that bird predation was a significant source of fish mortality in the middle Columbia River, compromising the majority of all smolt mortality sources in some years (Evans et al. 2013; Evans et al. 2016). Bird predation was likely just one of several mortality factors influencing steelhead survival in middle Columbia River during the study period, however efforts to investigating the relative importance of other, non-avian factors were not explored (Evans et al. 2016).

Multiple biotic and abiotic factors influence steelhead survival during outmigration through the Columbia River basin. Abiotic factors like river flows, river temperature, and hydroelectric dam operations (e.g., spill regimes, powerhouse operations) – factors that influence large aggregates or groups of fish (hereafter “population-level variables”; Juanes et al. 2000) – have all been linked to variation in steelhead survival in the region (Petrosky and Schaller 2010; Haeseker et al. 2012). Biotic factors, like bird predation, the relative abundance or density of smolts, and individual fish characteristics (fish size, condition, and rear-type; hereafter “individual-level variables”; Evans et al. 2014) have also been linked to steelhead survival during outmigration (Zabel et al. 2008; Hostetter et al. 2011; Evans et al. 2014; Hostetter et al. 2015a). Efforts to compare and contrast which of these biotic and abiotic factors best explain variation in steelhead survival, however, are generally lacking but may be paramount to developing recovery plans for ESA-listed steelhead. Thus, the primary goal of this study was to evaluate if biotic and abiotic conditions experienced by steelhead smolts traveling through the middle Columbia River during 2008-2015 were associated with variation in survival at various spatial and temporal scales, and to determine which factor or suite of factors best explained variation in survival.

METHODS

Study Area

We investigated factors that explained variation in juvenile steelhead survival in two river reaches: (1) a 105 river kilometer (Rkm) section of the middle Columbia River between Rkm 729 and Rkm 624 during 2008-2010 and 2014-2015, and (2) a 259 Rkm section of the middle and lower Columbia rivers between Rkm 729 and Rkm 470 during 2008-2015 (*Figure 1*). Survival and avian predation estimates in Reach 1 were based on releases of double-tagged (AT, PIT) steelhead smolts into the tailraces of Rock Island Dam and Wanapum Dam and subsequent live detections of fish passing AT arrays, and dead recoveries of PIT tags on bird colonies. Survival and avian predation estimates in Reach 2 were based on releases of single-tagged (PIT) steelhead smolts into the tailrace of Rock Island Dam and subsequently live detections of fish passing PIT arrays, and dead recoveries of PIT tags on bird colonies (see *Fish Tagging, Recapture, and Recovery* for details).

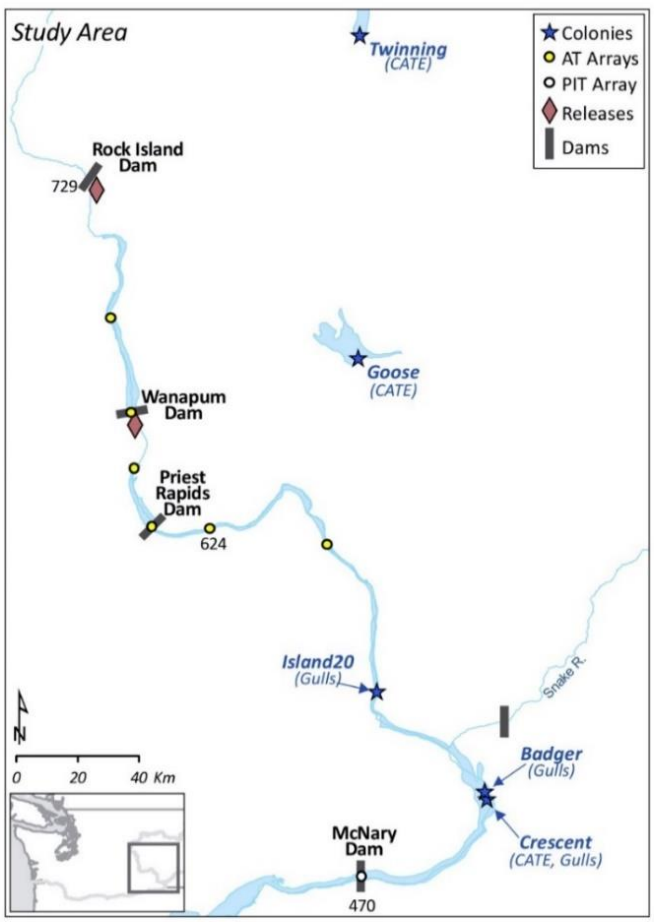

Figure 1. Locations of steelhead smolt release sites (red diamonds), acoustic arrays, (yellow dots), PIT arrays (white dots), hydroelectric dams (grey rectangles) and bird colonies (blue stars; Caspian tern [CATE] and California and ring-billed gulls [Gull]) used to estimate survival and avian predation during 2008-2015. Survival of double-tagged steelhead were evaluated between Rkm 729 and Rkm 624 in the middle Columbia River. Survival of single-tagged steelhead were evaluated between Rkm 729 and Rkm 470 in the middle and lower Columbia rivers.

Fish Tagging, Recapture and Recovery

Detailed methods regarding the capture, tagging and release of double-tagged steelhead used in this study are presented in Timko et al. (2011) and Hatch et al. (2016). In brief, downstream migrating steelhead were collected at Wanapum and Priest Rapids dams by dip-netting smolts from the gatewell slots at each dam. Following established AT-tagging protocols, steelhead were selected for tagging based on their weight (15–89 g) and external condition (no signs of disease; ≤ 20% descaling; no open wounds, hemorrhaging, or deformities). Fish were anesthetized, implanted with an AT tag (*Hydroacoustic Technology* Model 795 during 2008-2010 or *Lotek* Model L-AMT during 2014-2015) and a PIT tag (*Biomark* Model SST12 during 2008-2010 or *Biomark* Model HPT12 during 2014-2015), and held in a recovery tank for 18 to 24 hrs. Following recovery, fish were released via helicopter at release sites in the tailraces of Rock Island Dam and Wanapum Dam (*Figure 1*). Approximately equal numbers of steelhead were released daily between late April and late May each study year.

Detailed methods regarding the capture, tagging and release of singled-tagged steelhead used in this study are presented in Evans et al. (2014) and BRNW (2016). In brief, steelhead smolts were captured at the Rock Island Dam fish trap, PIT-tagged (*Biomark* Model SST12 during 2008-2013 or *Biomark* Model HPT12 during 2014-2015), and released into the tailrace of Rock Island Dam. Steelhead smolts selected for PIT-tagging were randomly selected for tagging (i.e., tagged regardless of size, condition or rearing-type; see *Covariate Modeling* of single-tagged fish for additional details) and were tagged in relative proportion to the number of smolts passing Rock Island Dam. PIT-tagged steelhead were released daily into the tailrace of Rock Island Dam between early April and early June each study year.

Following release, double-tagged fish in Reach 1 were detected alive (hereafter "recapture event") when passing each downstream AT array (a series of receivers placed in lines perpendicular to the shore; see Timko et al. 2011 and Hatch et al. 2016). The AT array located at Rkm 624 (*Figure 1*), 15 Rkm downstream of Priest Rapids Dam, was the boundary or exit array for survival estimates within Reach 1. It is important to note that the total length of Reach 1 (105 Rkm) was 15 Rkm longer than the section of river comprising the Wanapum-Priest Rapids Project (90 Rkm) and for this, and other reasons (see *Covariate Modeling*), survival estimates generated herein are not directly comparable to those of Skalski et al. (2016). The furthest downstream AT array used in this study was at Rkm 593 (*Figure 1*), an array used to estimate detection probabilities of AT-tagged smolts passing the exit array at Rkm 624. Following release, single-tagged steelhead smolts were recaptured alive at PIT arrays located at or below McNary Dam. PIT arrays below McNary Dam included the array at John Day Dam (Rkm 370), Bonneville Dam (Rkm 235), and a pair-trawl in the Columbia River estuary (Rkm 75). The PIT array at McNary Dam was the exit array used in survival estimates within Reach 2. Detections of PIT-tagged fish passing arrays below McNary Dam were used to estimate detection probabilities of smolts passing McNary Dam.

Tags from both release groups (single- and double-tagged) were recovered dead (hereafter "recovery event") at multiple bird colonies located both upstream and downstream of Reaches 1 and 2. Dead recoveries were used to estimate predation probabilities and to provide an additional source of information regarding the final fate of each study fish (see *Simultaneous Survival and Avian Predation Modeling*). Detailed methods regarding the recovery of PIT tags on bird colonies, including a description of methods used to estimate tag detection and deposition probabilities, are provided in Hostetter et al. (2015b) and Evans et al. (2016). In brief, each colony was scanned for tags after the nesting season (August-September) using hand-held PIT tag antennas. The number of tags recovered on each colony was adjusted/corrected for tag loss or non-detection due to the fraction of consumed tags deposited by birds off-colony (at loafing, roosting, or off-colony areas) or deposited by birds on-colony but not detected by researchers following each nesting season.

Survival of Double-tagged Fish

We performed three analyses to estimate survival using double-tagged fish traveling through Reach 1. First, we employed an adaptation of the Cormack-Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) mark-recapture model to incorporate recoveries of tags on bird colonies to estimate both survival and avian mortality rates simultaneously (Barker 1997; Evans et al. 2016). Second, these estimates of survival and predation were employed in a covariate analysis that explored the association between various biotic and abiotic factors on steelhead survival in Reach 1 and separately within the Wanapum and Priest Rapids reservoirs. Third, we used differences in detection times at adjacent AT arrays to evaluate the relationship between smolt migration speed (km/hr) and survival in the Wanapum and Priest Rapids reservoirs. Each of these three analyses are described in more detail below.

Simultaneous survival and avian predation modeling – A detailed description of our joint survival and avian predation model is provided in *Appendix A* (see also Evans et al. 2016). In brief, we developed a model that allows for the concurrent estimation of survival and mortality due to colonial waterbird predation using a Bayesian analytical framework. The main impetus behind this approach was to provide a more holistic view of the fates encountered by steelhead during outmigration in middle Columbia River. Similar recapture/recovery methods have been shown to result in survival and predation estimates that are more precise, with reduced bias relative to standard CJS capture/recapture models (Hostetter et al. *in-review*). While the recapture and recovery opportunities varied by year, depending on array configuration and scanning efforts at bird colonies, the resulting survival and avian predation estimates used in covariate models were calculated such that they would be comparable across years. Estimates were calculated specific to cohorts of fish grouped by release day and release location (Rock Island Dam tailrace, Wanapum Dam tailrace).

Covariate modeling – We compiled an *a priori* list of biotic and abiotic factors previously identified in the published literature as explaining differences in steelhead survival during outmigration in the Columbia River basin. Variables or covariates were assembled into a framework of credible models to be investigated. The fitness of each set of variables in explaining variation in survival probabilities was accessed using the corrected Akaike Information Criterion (AICc) as calculated from weighted logistic regression models (Burnham and Anderson 2002). The model(s) with the lowest AIC values were considered the best fitting survival models.

Covariates used in survival models included measures of (1) avian predation, (2) steelhead abundance, (3) river discharge, (4) water temperature, (5) percent spill, (6) water transit times, and (7) powerhouse passage index. We approximated relative steelhead abundance by using a running three-day average of the steelhead passage index (hereafter “STHD index”) at Rock Island Dam (FPC 2016). Flow conditions in Reach 1 were represented by average daily measurements of discharge (kilo cubic feet per second [kcfs]) at Rock Island and Wanapum dams and an approximation of water transit time index (hereafter “WT index”) in Wanapum and Priest Rapids reservoirs. WT indices were calculated as the ratio between discharge and reservoir elevation. Water temperature (°C) was measured daily in the forebay of Wanapum Dam and Priest Rapids Dam. Variables related to dam operations included average daily percentage spill and the estimated percentage of fish traveling through the powerhouse (hereafter “PH index”) at Wanapum and Priest Rapids dams. Data relating to temperature, discharge, percentage spill, and elevation were obtained from the Data Access in Real Time website (DART 2016). Passage routes of AT-tagged fish were identified by Blue Leaf Environmental using amplitude changes in the final two minutes of forebay detections during a fish's approach to the dam (see Hatch et. al. 2016 for details). PH index was then defined for each cohort at Wanapum and Priest Rapids dams as the proportion of fish assumed to have passed the powerhouse rather than by an alternative route (i.e., spillway, bypass). Because the number of fish from each release group with accurate passage information was limited, a seven-day running average for PH index at each dam was calculated to increase sample sizes of fish with known passage histories. Finally, avian predation in Reach 1 was attributed to Caspian terns *Hydroprogne caspia* nesting on Twinning Island in Banks Lake and on Goose Island in Potholes Reservoir (*Figure 1*). These two colonies were previously identified as posing the greatest risk to steelhead survival in Wanapum-Priest Rapids Project (Evans et al. 2016). Point estimates of predation probabilities were calculated with the joint survival and avian predation model described above (see *Appendix A*).

As noted above, a list of biologically justifiable models was constructed *a priori* with at most one variable from each of the above listed covariate categories and up to one two-way interaction term between categories. Possible interactions between covariates is useful in explaining variation in survival (Zabel et al. 2002; Hostetter et al. 2012). In order to avoid overfitting models, however, we allowed the inclusion of at most one interaction term among those variables selected.

We evaluated the relationship between estimated daily survival rates and covariates using a weighted logistic regression models. The relationship between the covariates listed above and the daily estimates of survival, $\hat{s}_i$, calculated from the joint survival and avian predation model, can be expressed by the logistic regression equation,

$$logit(\hat{s}_i) = \alpha_y + \vec{\beta}\,\vec{x_i} + \epsilon_i$$

where α_y represents the mean logit survival for year *y*, $\vec{\beta}$ represents the vector of all covariate coefficients as selected from the outlined covariate categories above (i.e., β_1 is the coefficient related to steelhead abundance, etc.), and ϵ_i represents the random variation associated with the i^{th} observation. The precision in the estimates of survival varied by release location, year, and day. This difference in precision was accounted for by inverse variance weighting. That is, each estimate $\hat{s}_i$ was given weight $w_i = 1/var(\hat{s}_i)$. All logistic regression models were run using R (R Core Team 2015). The resulting models were ranked using Akaike's information criterion (AIC) corrected for small sample size (AICc) and compared using the AICc difference (AICc; Burnham and Anderson 2002). The model(s) with the lowest AICc values were considered the best fitting survival models.

Traditional survival estimates in the Wanapum-Priest Rapids Project are based on releases of AT-tagged smolts above and below each reservoir and dam (hereafter "paired-release model"). Paired-release models, through a series of multiplicative corrections between release and recapture sites, can then be used to adjust estimates of survival for delayed handling effects (estimated proportion of fish that die due to the effects of tagging; Skalski et al. 2016). Calculating a handling effect on daily bases, however, would require the use of tenuous assumptions regarding the "paired" nature of each release-recapture group and would introduce extraneous variation in daily survival estimates, potentially confounding the effects of the covariates. Additionally, any attempt to correct daily survival estimates for handling effects would suggest the need to correct predation probabilities in the same manner. However, the initial river segments encountered by paired-release groups are subject to incomparable levels of avian predation. Finally, multiplicative corrections in a paired-release model can result in survival estimates > 1.0 in some river reaches and years (Skalski et al. 2016), estimates that are less than optimal for covariate modeling options (e.g., unfit for logistic regression).

Supplementary migration speed analysis – We investigated the interrelated effects of migration speed and WT index on steelhead survival in Reach 1. The use of AT tags provides precise information relating to the speed or travel times of each fish (an individual-level variable). Estimates of travel times, however, are only available for fish that survived migration through a particular river reach, potentially resulting in a bias by limiting data to the fastest individuals within that reach (Tuomikoski et al. 2013). Such a bias is presumably increased over longer river reaches. An alternative, but indirect, measure of fish travel times is the WT index (a population-level variable). Other studies have implied that metrics of WT can be used as proxies for the average speed of fish through a river reach (Schaller et al. 2007; Petrosky and Schaller 2010). The AT-tagged fish used in this study provide a unique dataset to compare and contrast which metric (actual fish travel times or WT index) best explained variation in steelhead survival. We assessed the association between WT index and the observed average traveling speeds of AT-tagged smolts using descriptive statistics. Assuming travel times through consecutive river segments are highly correlated, we then assessed whether there was a significant association between traveling speed over a river segment and the subsequent detection of that fish at a downstream array. Evidence that travel time and WT index have similar associations with survival in the immediate subsequent river reach further supports the use of WT index, rather than direct measures of steelhead travel times, in our covariate modeling described above. We performed this analysis using all steelhead interrogated at the final arrays in the forebay of Wanapum Dam and the forebay of Priest Rapids Dam (*Figure 1*). For each forebay, we model the apparent survival, $\hat{d}_i$, of a fish *i* through the subsequent river segments using the logistic regression function,

$$logit(\hat{d}_i) = \beta_{year} + \beta_m * ms_i + \beta_w * wt_d + \beta_x * (ms_i * wt_d) + a_{d|y} + \epsilon_i$$

where β_m accounts for the assumed differences among years, β_m is the regression coefficient for migration speed (ms_i), β_w is the regression coefficient for water transit index (wt_d), β_x is the regression coefficient for interaction between migration speed and water transit index, $a_{d|y}$, and ϵ_i are the random effect terms respectively for day within a year and each individual fish arriving. Models including/excluding each of the fixed effects above were run, and compared and contrasted using χ^2 tests for fitness. The evaluation of each model was performed using the *glmer* function of the *lme4* package in R (R Core Team 2015). Covariance matrices were investigated for overdispersion (Hosmer and Lemeshow 2000); none was detected.

Survival of Single-tagged Fish

There were several advantages to using single-tagged fish to estimate survival and to evaluate covariate effects on survival. First, the random tagging of PIT-tagged fish at Rock Island Dam resulted in a more representative sample of upper Columbia River steelhead. Second, detailed data regarding individual fish characteristics were available for each single-tagged fish, providing data to evaluate the relationship between individual-level variables and fish survival. Lastly, survival estimates in Reach 2 were calculated at a much larger spatial scale (259 Rkm) than Reach 1 (105 Rkm) and data from all study years (2008-2015) were available. Two disadvantages to using single-tagged fish were that (1) survival estimates were less precise due to lower detection probabilities of PIT-tagged fish passing dams compared to AT-tagged fish passage arrays (see *Results*) and (2) an investigation of abiotic factors on the survival of single-tagged fish could not be conducted due to concerns that accurate measurements of environmental conditions experienced by smolts were not available in such a large and diverse section of river. For instance, no weekly average measurement of river flow or dam operations exists that could accurately characterize environmental conditions experienced by a smolt traveling through 259 Rkm section of river, a section that includes inputs from the lower Snake River (*Figure 1*). As such, covariate analyses of single-tagged fish focused solely on biotic variables, variables that presumably remained unchanged as tagged smolts migrated from the Rock Island Dam tailrace to McNary Dam. A covariate for avian predation was included on a weekly basis. The additional influence of other abiotic variables on survival in Reach 2 was indirectly accounted for by grouping fish according to their week of release.

Covariate modeling – To model the relationships between steelhead survival and biotic factors we used a covariate mark-recapture-recovery model with two recapture events (an adaptation of the CJS model; Hostetter et al. *in-review*). The first recapture event were detections at the PIT array in the juvenile bypass system at McNary Dam. For the second recapture event we used the combination of all detections from PIT tag arrays located downstream of McNary Dam; at John Day Dam (Rkm 347), Bonneville Dam (Rkm 235), and at the pair-trawl in the Columbia River estuary (Rkm 75). Similar to analyses on double-tagged fish, we also incorporated recoveries of tags on bird colonies known to forage within and downstream of Reach 2 (see *Appendix A* for a list of bird colonies and Evans et al. 2016 for colony-specific foraging ranges).

The evaluation of steelhead condition was performed according to the non-invasive examination methods outlined by Hostetter et al. (2011). In brief, data on presence and severity of body injuries, descaling, fin damage, and disease were record on each fish. For the purposes of this analysis, external condition factors were grouped or combined into a single categorical variable indicating fish in a "compromised" condition or "uncompromised" condition. Compromised fish were those that had (1) severe body injuries (defined as deformities, open wounds, or large surface area scarring on the head, trunk, operculum, or eyes), (2) significant descaling (defined as a loss of scales on more than 20% of the body); (3) evidence of disease (defined by any external signs of bacterial, fungal, or viral infections), or (4) severe fin damage (defined as fin wear and damage greater than 50% on three or more fins). Uncompromised fish were those that did not meet any of the criteria listed for compromised fish. Fish size was measured as fork-length (mm) and each fish was classified by rear-type as hatchery or wild (see Hostetter et al. 2011 and Evans et al. 2014 for details).

We model $\hat{s}_{1,i}$, the estimated survival probability of steelhead *i* to McNary Dam (the first recapture event in the CJS framework), using a logistic regression function,

$$logit(\hat{s}_{1,i}) = \mu_y + \beta_{predation}\,\hat{\theta}_{yw}\,\epsilon_{yw} + \vec{\beta}_{covariates} * \vec{z}_i$$

where μ_y is the average logit probability for all steelhead released year *y*, and $\beta_{predation}$ is the linear effect of weekly predation by avian predators, ϵ_{yw} is the week level random error term (~ $normal[0, \tau_y]$) included to account for all additional abiotic factors effects on steelhead released in week *w*, and $\vec{\beta}_{covariates}$ is the parameter vector representing the coefficients effects of the biotic covariates. The $\vec{z}_i$ represents the values of the covariates included in the model and $\hat{\theta}_{yw}$ represents the weekly cumulative estimates of avian predation. These predation estimates were developed through simplified iteration of the combined survival-predation model used in the double-tagged fish analysis. Avian predation associated with Caspian tern colonies on Goose, Twinning and Crescent islands; and gulls on Island 20, Crescent, and Badger Islands, were modelled simultaneously and aggregated, resulting in a single metric of the estimated impact of avian predation on fish in Reach 2. These six colonies were previously identified as posing the greatest risk to steelhead survival for fish passing between Rock Island and McNary dams (Evans et al. 2016).

The fit of models with additional coefficients were evaluated, including coefficients for the average multiplicative difference in the odds of survival between wild and hatchery fish, the expected multiplicative difference in the odds of survival between uncompromised versus compromised fish, and the linear and quadratic effects associated with fork length. We evaluated further models including interaction terms among each of these factors as well as possible interactions between each of these factors and predation.

We let $\hat{p}_{1,y}$ represent the year specific detection at McNary dam. We let $\hat{s}_{2,y} * \hat{p}_{2,y}$ represent the joint survival-to/recapture-at probability for the set of all downstream recapture events. Explicitly, these were modeled as

$$logit(\hat{p}_{1,y}) = \gamma_{year}$$
$$logit(\hat{s}_{2,y} * \hat{p}_{2,y}) = \alpha_{year}$$

Parameter estimates were calculated using a Hamiltonian Monte Carlo (HMC) process implemented via program STAN, accessed via the *rstan* package (Stan Development Team 2015a) available for the statistical software R (R Core Team 2015). Three parallel chains were run for 5,000 iterations after a "warmup" of 1,000 iterations resulting in ~500 effective samples for each parameter. Chain convergence was tested using the Gelman-Rubin statistic ($\hat{R}$; Gelman et al. 2004). We report results as posterior modes along with the Highest Posterior Density (HPD) 95% credibility intervals. The resulting models were ranked by using Akaike's information criterion corrected for small sample size (AICc) and compared using the AICc difference (AICc; Burnham and Anderson 2002). The model(s) with the lowest AIC values were considered to be the best fitting models.

RESULTS

Fish Tagging, Recapture and Recovery

Numbers of double-tagged fish released into the tailrace of Rock Island Dam and Wanapum Dam varied by year and release location, ranging annually from 201 to 794 tagged steelhead (*Table 1*). Recapture probabilities of live fish passing AT arrays within Reach 1 were very high (> 97% per array). A range of 7 to 46 PIT tags were annually recovered on bird colonies foraging within Reach 1, data used to estimate predation probabilities in Reach 1 (see *Survival of Double-tagged Fish* below). A range of 25 to 73 PIT tags were annually recovered on bird colonies foraging downstream of Reach 1, data used to increase the precision of survival estimates in Reach 1.

Numbers of single-tagged fish released into the tailrace of Rock Island Dam also varied by year, ranging from annually 5,893 to 7,756. Recapture probabilities of PIT-tagged fish in Reach 2 were low in comparison to those of AT-tagged fish in Reach 1, with a median of 6% detection probability at McNary Dam (weekly range = < 1% to 19%). A range of 266 to 620 tags were annually recovered on bird colonies foraging within Reach 2, data used to estimate predation probabilities (see *Survival of Single-tagged Fish*). A range of 288 to 640 tags were annually recovered on bird colonies foraging downstream of McNary Dam, fish used to increase the precision of survival estimates in Reach 2.

Table 1. Numbers of double- and single-tagged juvenile steelhead used to estimate daily and weekly survival and avian predation rates in Reach 1 (Rkm 729 to Rkm 624) and Reach 2 (Rkm 729 to Rkm 470), respectively. Double-tagged smolts were released into the tailrace of Rock Island Dam (RIS; Rkm 729) and Wanapum Dam (WAN; Rkm 669). Single-tagged fish were released into the tailrace of Rock Island Dam.

	Double-tagged fish			Single-tagged fish	
Year	RIS	WAN	No. Days	RIS	No. Weeks
2008	201	267	7	7271	10
2009	794	647	20	7114	11
2010	483	477	22	7365	10
2011	-		-	7756	11
2012	-		-	6712	10
2013	-		-	5893	10
2014	399	771	18	7663	9
2015	639	543	21	7069	9

Survival of Double-tagged Fish

Daily survival probabilities of double-tagged steelhead in Reach 1 ranged from 62.0% to 86.6% over the five-year study period (*Figure 2*). Daily predation probabilities by Caspian terns ranged from 2.1% to 16.4% of available fish in Reach 1. Daily Caspian tern predation probabilities accounted for 11.9% to 62.2% of all mortality sources experienced by steelhead migrating through Reach 1 during the study period.

Daily survival probabilities of double-tagged steelhead in the Wanapum Reservoir and Priest Rapids Reservoir (smaller spatial subsets within Reach 1) ranged from 82.5% to 98.4% (depending on the reservoir) during the study period. Daily predation probabilities by Caspian terns ranged from 0.1% to 9.5% (depending on the reservoir) during the study period.

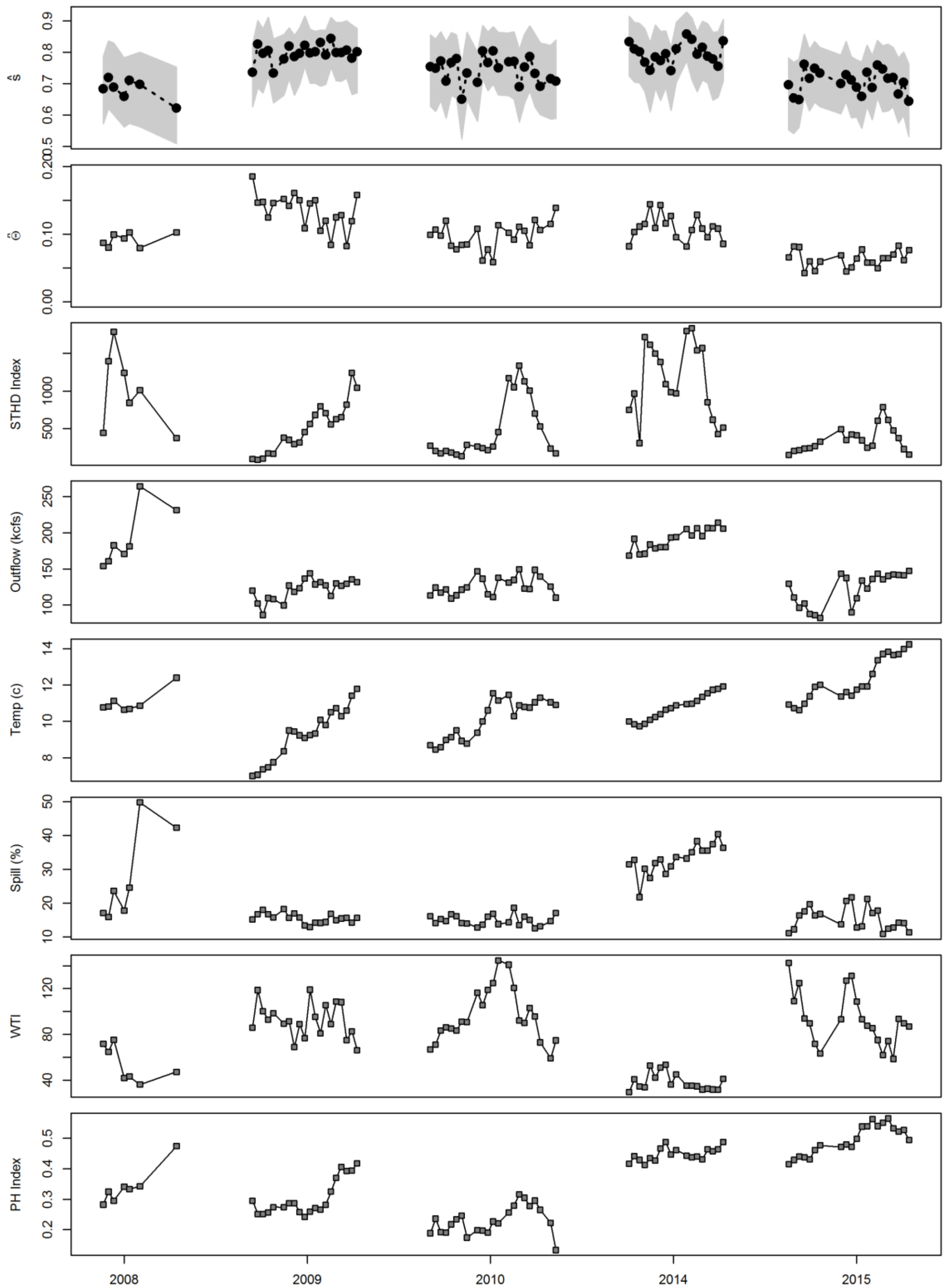

Figure 2. Covariate values related to each release day of double-tagged steelhead passing through Reach 1 (Rkm 729 to Rkm 624) during 2008-2010 and 2014-2015. $\hat{s}$ and $\hat{\Theta}$ represent estimated daily survival and avian predation probabilities. Average steelhead passage index (STHD Index), outflow, water temperature (Temp), spill percentage, water transit index (WTI index), and powerhouse index (PH index) are also provided.

Covariate modeling – The most parsimonious survival model for steelhead passing through Reach 1, based on fish released into the tailrace of Rock Island Dam, included covariates for Caspian tern predation, steelhead abundance (STHD index), the Wanapum Dam (WAN) powerhouse index (PH index), and an interaction between avian predation and the STHD index (*Table 2*). Steelhead survival increases were associated with decreasing avian predation, increasing STHD index, and decreasing WAN PH index (*Table 3*). In general, avian predation was found to be the most prevalent factor in best fitting models. Avian predation decreased the odds of survival by a factor 0.93 (95% CI: 0.92-0.94) for every one percent increase in predation (*Table 3*). Survival increasing by a factor of 1.11 (95% CI: 1.04-1.19) for every 1,000-unit increase in STHD index (*Table 3*). Finally, survival decreasing by a factor of 0.95 (95% CI: 0.90-0.99) for every 0.1 increase in PH index (*Table 3*). The effect of each individual covariate is based on holding all other covariates in the model constant (i.e., multiplicative effects).

Table 2. Best fitting models for the survival of double-tagged steelhead in Reach 1 (Rkm 729 to Rkm 624) during 2008-2010 and 2014-2015. Interactions are denoted by a colon. ΔAICc measures the difference in AICc for each model compared to the most parsimonious model.

Model (Survival in Reach 1)	ΔAICc
CATE predation, STHD index, WAN PH index, and CATE predation: STHD index[a]	--
CATE predation, STHD index, WT index, and CATE predation: WT index	0.45
CATE predation, STHD index, WT index, and CATE predation: STHD index	0.53
CATE predation, STHD index, and WAN PH index	0.85
CATE predation, STHD index, and CATE predation: STHD index	1.33
CATE predation, STHD index, WT index, WAN PH index, and CATE predation: STHD index	1.34
Base Model (includes year)	67.83

[a] *The AICc of the most parsimonious model was -120.60*

Table 3. Estimated multiplicative effects on the odds of double-tagged steelhead survival in Reach 1 (Rkm 729 to Rkm 624) for each variable included in the best fitting model (see Table 2). 95% confidence bounds (CI), model degrees of freedom (df), associated statistical significance test (chi-square), and statistical significance (p-value) are provided. Interactions are denoted by colons.

Variable	Effect	Odds Ratio	95% CI	χ^2 (df)	P
Year	--	--	--	84.81 (4)	< 0.01
CATE predation	1% increase	0.93	(0.92 - 0.95)	72.14 (1)	< 0.01
STHD index	1000 increase	1.11	(1.04 - 1.19)	6.58 (1)	0.01
WAN PH index	0.1 increase	0.95	(0.90 - 0.99)	4.37 (1)	0.04
CATE predation: STHD Index	Unit increase	0.99	(0.99 - 1.00)	3.42 (1)	0.05

An investigation of survival and covariate effects by reservoir (Wanapum, Priest Rapids) indicated that the most parsimonious models included covariates for Caspian tern predation and STHD index in the Wanapum Reservoir and Caspian tern predation, STHD Index, and an interaction between avian predation and the STHD Index in the Priest Rapids Reservoir (*Table 4*). Caspian tern predation impacted survival similarly in both reaches, whereby for every one percent increase in predation there was a decrease in the odds of survival by a factor of 0.88 (95% CI: 0.85-0.90) in the Wanapum Reservoir and a factor of 0.91 (95% CI: 0.87-0.95) in the Priest Rapids Reservoir (Table 5). The effect of the STHD index on survival was also similar in each reservoir; an increase in the STHD index of 1,000 was found to be associated with an increase in the odds of survival by a factor of 1.05 (95% CI: 1.00-1.11) in the Wanapum Reservoir and a factor of 1.17 (95% CI: 1.03-1.34) in the Priest Rapids Reservoir (Table 5). The effect of each individual covariate is based on holding all other covariates in the model constant.

Table 4. Best fitting models for double-tagged steelhead survival in the Wanapum Reservoir (Rkm 729 to Rkm 670) and Priest Rapids Reservoir (Rkm 669 to Rkm 640) during 2008-2010 and 2014-2015. Interactions are denoted by a colon. ΔAICc measures the difference in AICc for each model compared to the most parsimonious model.

Model (Survival in Wanapum Reservoir)	ΔAICc[a]
CATE predation and STHD index	--
CATE predation and WAN WT index	0.27
CATE predation and temperature	0.48
CATE predation, STHD index and CATE predation :STHD index	1.17
Base Model (includes year)	64.12
Model (Survival in Priest Rapids Reservoir)	**ΔAIC_c[b]**
CATE predation, STHD index, and CATE predation: STHD index	--
CATE predation, STHD index, PR WT index, and CATE predation: STHD index	1.07
CATE predation, PR WT index, temperature, and PR WT index: temperature	1.08
CATE predation, STHD index, temperature and CATE predation: STHD index	1.42
Base Model (includes year)	24.47

[a] The AICc of the most parsimonious model was 24.12
[b] The AICc of the most parsimonious model was -3.87

Table 5. Estimated multiplicative effects on the odds of double-tagged steelhead survival (95% confidence bounds[CI]) in the Wanapum Reservoir and Priest Rapids Reservoir for each variable included in the best fitting model (see Table 4). Model degrees of freedom (df) and associated statistical significance test (chi-square) and value (p-values) are provided. Interactions are denoted by colons.

Variable	Effect	Odds Ratio	95% CI	χ^2 (df)	P
Wanapum Reservoir					
Year	--	--	--	86.42 (4)	< 0.01
CATE predation	1% increase	0.88	(0.85, 0.90)	66.30 (1)	< 0.01
STHD index	1000 increase	1.05	(1.00, 1.11)	3.94 (1)	0.04
Priest Rapids Reservoir					
Year	--	--	--	98.46 (4)	< 0.01
CATE predation	1% increase	0.91	(0.87, 0.95)	24.65 (1)	< 0.01
STHD index	1000 increase	1.17	(1.03, 1.34)	3.34 (1)	0.06
CATE predation: STHD index	Unit increase	0.993	(0.99, 1)	3.58	0.05

Supplementary migration speed analysis – The WT index was an imperfect proxy of migration speed in Reach 1, however, both variables were found to be significantly associated with apparent survival on smaller spatial scales (i.e., within the Wanapum and Priest Rapids reservoirs). We observed a correlation between the WT index and average fish travel time in Wanapum Reservoir (r^2=-0.58). After accounting for variation among the year and day of a steelhead's arrival at Wanapum Dam, we found a significant relationship between smolt migration speed in the Wanapum Reservoir and apparent survival through the Priest Rapids Reservoir (*Figure 3*; χ_1=10.78; p<0.01). The relationship between WT index and apparent survival was not found to be significant by itself, however, a model including an interaction term between WT index and migration speed was found to fit the data significantly better than the model accounting for migration speed alone (χ_2=20.55; p <0.01). We estimated that every kph increase in average migration speed through the Wanapum Reservoir was associated with an increase in the probability of survival through the Priest Rapids Reservoir by a factor 2.42 (95% CI: 1.56-3.23). The sign of the interaction coefficient in the full model indicates that the association between migration speed and survival diminishes as water transit time increases (i.e., in a slower moving river environment).

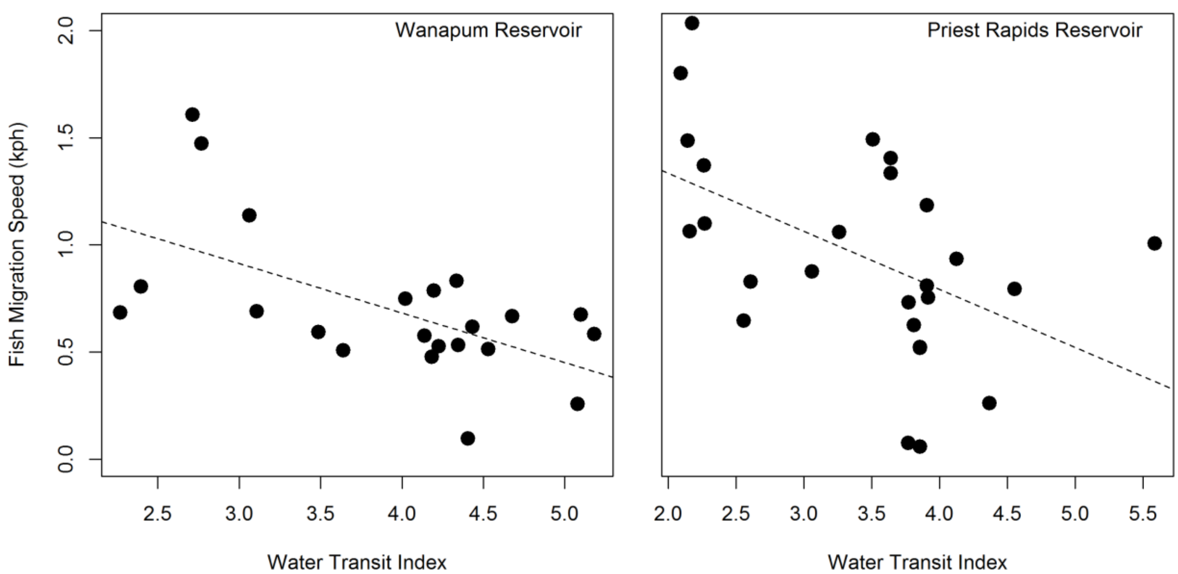

Figure 3. Fish speed (kilometers per hour) and water transit index in the Wanapum Reservoir (Rkm 729 to Rkm 670) and Priest Rapids Reservoir (Rkm 669 to Rkm 639).

We observed a similarly weak correlation between the WT index and average fish travel time in Priest Rapids Reservoir (r^2=-0.57), as was observed in Wanapum Reservoir. After accounting for variation among years and days of a steelhead's arrival at Priest Rapids Dam, we found some evidence of a relationship between smolt migration speed in the latter portion of the Priest Rapids Reservoir and apparent survival through the subsequent congruent study area (*Figure 3*; χ_1=3.00; p=0.083). The relationship between the WT index and apparent survival was found to be significant (χ_1=8.52; p=0.004). A model including an interaction term between the WT index and migration speed was found to fit the data significantly better than the model accounting for the WT index alone (χ_2=5.49; p=0.004). The effect of migration speed through the Priest Rapids Reservoir was estimated to affect subsequent survival less than through the Wanapum Reservoir. We estimated that every kph increase in average migration speed through the Priest Rapids Reservoir was associated with an increase in the probability of survival through the subsequent river reach by a factor of 1.20 (95% CI: 1.03-1.39). Again, the sign of the interaction coefficient in the full model indicates that the association between migration speed and survival diminishes as water transit time increases although to a lesser degree than that observed Wanapum Reservoir.

Survival of Single-tagged Fish

The proportion of single-tagged fish surviving Reach 2 varied weekly from 0.31 to 0.82 (*Figure 4*) and annually from 0.56 to 0.69 (*Table 6*). There was a strong relationship between weekly avian predation and weekly survival, with survival decreasing as predation increased in Reach 2 (*Figure 4*). For instance, weekly survival often greater than 70% when weekly bird predation was less than 15%. Conversely, weekly survival was often less than 50% when weekly bird predation was greater than 25% (*Figure 4*).

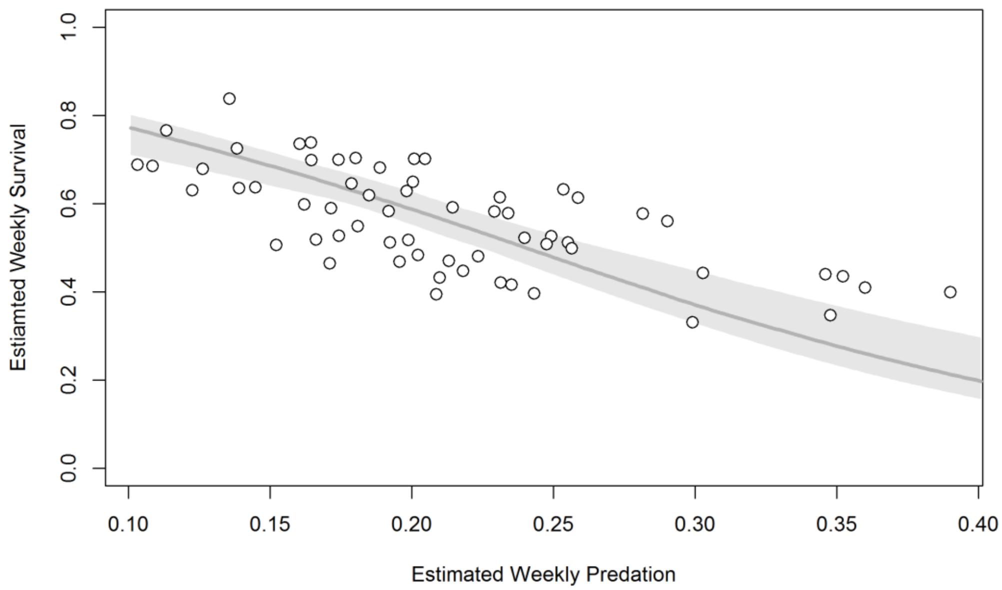

Figure 4. The relationship between weekly median avian predation on weekly median survival (95% confidence intervals) of single-tagged steelhead smolts in Reach 2 (Rkm 729 to Rkm 470) during 2008-2015.

The majority of single-tagged fish released into the tailrace of Rock Island Dam were hatchery-reared, comprising 72.2% to 76.9% of all tagged fish (*Table 6*). The distribution of steelhead sizes was relatively similar among years, with median fork length ranging from 191 to 204 mm. Between 3.6% and 23.1% of each yearly cohort of steelhead were considered to be in a compromised condition, as denoted by severe descaling, bodies injuries, fin damage, and/or signs of disease. The most common condition anomaly was body injuries, which was present, on average, in 5.5% of study fish, followed by severe descaling in 2.5%, disease symptoms in 2.3%, and fin damage in 2.0%.

Table 6. Estimated survival (95% confidence interval [CI]), avian predation (95% CI), and prevalence of individual fish characteristics (rear-type, external condition [uncompromised = uncomp., compromised = comp], and length) of single-tagged steelhead in Reach 2 (Rkm 729 to Rkm 470). Survival and predation estimates are depicted as annual values, but were modelled as weekly values in covariate models.

	Survival	Avian Predation	Rear-type		External Condition		Fork Length mm
Year	(95% CI)	(95% CI)	Hatchery	Wild	Uncomp.	Comp.	(min to max)
2008	0.61 (0.55-0.69)	0.17 (0.14-0.21)	5373	1898	6497	774	193 (88-302)
2009	0.56 (0.49-0.63)	0.31 (0.26-0.39)	5150	1964	6680	434	195 (96-291)
2010	0.59 (0.52-0.66)	0.22 (0.18-0.27)	5387	1978	6750	615	197 (70-297)
2011	0.68 (0.57-0.83)	0.20 (0.16-0.25)	5961	1795	5964	1792	204 (102-320)
2012	0.55 (0.46-0.65)	0.24 (0.19-0.32)	5107	1605	6060	652	196 (92-320)
2013	0.59 (0.48-0.72)	0.23 (0.20-0.29)	4284	1609	5471	422	193 (90-320)
2014	0.63 (0.52-0.77)	0.16 (0.08-0.26)	5686	1977	7387	276	191 (77-308)
2015	0.69 (0.56-0.85)	0.14 (0.10-0.22)	5105	1964	6106	963	193 (86-300)

Covariate modeling – The most parsimonious survival model for steelhead passing through Reach 2included variables for avian predation, fork length, fish condition, and rearing-type (*Table 7*). Of all the individual variables examined, only the quadratic term for fork length was excluded from the most parsimonious model. Each factor had considerable effect on the odds of survival (*Table 8*). Results indicated that for each one percent increase in avian predation, the odds of survival decreased by a factor of 0.91 (95% CI: 0.90-0.94; *Table 8*). For each additional 10 mm in fork length, as measured at Rock Island Dam, there was an increase in the odds of survival by a factor of 1.02 (95% CI: 1.01-1.04; *Table 8*). Steelhead released in compromised condition at Rock Island Dam experienced a reduction in the odds of surviving through Reach 2 by a factor of 0.62 (95% CI: 0.56-0.69; *Table 8*). We estimate the odds of a wild steelhead surviving passage through Reach 2 to be 1.44 times greater than that of hatchery steelhead (95% CI:1.32-1.60; *Table 8* and *Figure 5*). The effect for each individual covariate is based on holding all other covariates in the model constant.

Table 7. Best fitting models for predicting survival of single-tagged steelhead in Reach 2 (Rkm 729 to Rkm 470) based on individual fish characteristics during 2008-2015. ΔAIC_c measures the difference in AIC_c for each model compared to the most parsimonious model.

Model (Survival in Reach 2)	ΔAIC_c [a]
Predation, length, condition, and rearing	--
Predation, length, condition, rearing, and predation: condition	1.77
Base model (with year, week, and predation)	150.33

[a] *The AICc of the most parsimonious model was -103,743.75*

Table 8. Estimated multiplicative effects on the odds of single-tagged steelhead survival (95% confidence bounds[CI]) in Reach 2 for each variable included in the best fitting model (see Table 7). Model degrees of freedom (Df) and associated statistical significance test (chi-square) and value (p-values) are provided.

Variable	Effect	Odds Ratio	95% CI	χ^2 (df)	P
Year/Week	--	--	--	254.64 (15)	< 0.01
Predation	1% increase	0.91	0.90-0.94	424.74 (1)	< 0.01
Length	1 cm increase	1.02	1.01-1.04	10.79 (1)	< 0.01
Condition	Poor Condition	0.62	0.56-0.69	76.82 (1)	< 0.01
Rearing	Wild Raised	1.44	1.32-1.60	60.53 (1)	< 0.01

Hatchery steelhead observed at Rock Island Dam were more likely to be in a compromised condition as compared to wild fish, but were greater in length. Hatchery steelhead were 2.88 times more likely to arrive at Rock Island Dam in compromised condition as compared to their wild counterparts (95% CI: 2.76-3.01). However, hatchery steelhead arrived at Rock Island Dam with fork lengths 23 mm greater, on average, than wild fish (95%CI: 22.8-23.2). Even after accounting for the differences in condition and size of hatchery and wild fish, hatchery fish had lower survival as compared to wild fish (*Figure 5*).

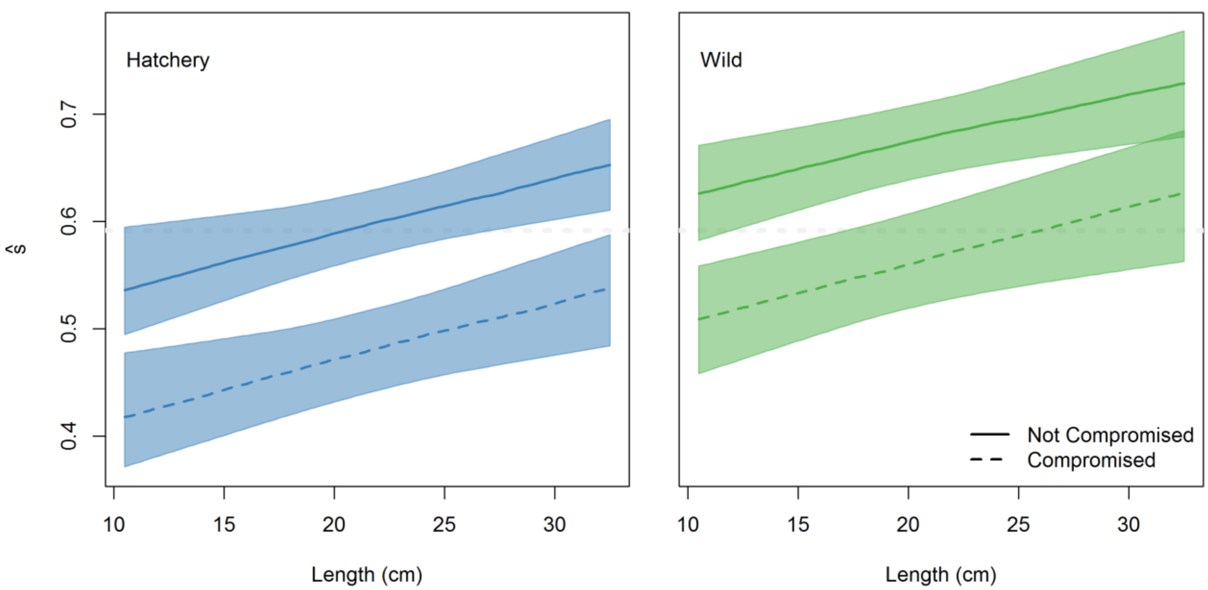

Figure 5. Effects of length on median survival (95% confidence intervals) of single-tagged steelhead in Reach 2 (Rkm 729 to Rkm 470) for hatchery and wild smolts during 2008-2015. Effects hold avian predation constant at its median level. Solid lines are the associated estimate for those fish in an uncompromised condition; dotted lines are associated with fish in compromised condition.

DISCUSSION

This retrospective study is among the first to provide a comprehensive, multi-year evaluation of factors that influence juvenile steelhead survival in the middle Columbia River. Analyses of double-tagged smolts, which focused on population-level variables in the Wanapum-Priest Rapids Project, indicated that Caspian tern predation, steelhead abundance, and powerhouse operations at Wanapum Dam best explained variation in juvenile steelhead survival. There was also evidence that water transit times and temperature were associated with survival. Interaction terms between avian predation and steelhead abundance and avian predation and water transit times were also observed in the most parsimonious models, demonstrating the complexity and inter-related nature of factors that regulate steelhead survival in the middle Columbia River. Analyses of single-tagged fish, which focused on individual-level variables, indicated that avian predation and the intrinsic characteristics of fish size, condition, and rearing-type were all important factors explaining variation in steelhead survival. Collectively, results indicate that multiple factors, at both population- and individual-levels, explained variation in steelhead survival during outmigration during 2008-2015.

Very similar suites of covariates were detected in competing survival models (those within 2 AICc units of the most parsimonious model), indicating that factors associated with variation in steelhead survival were consistent across spatial scales and release groups. For instances, the most parsimonious survival models in the Wanapum Reservoir and Priest Rapids Reservoir contained the same four covariate variables of avian predation, steelhead abundance, water transit times, and temperate. Differences amongst competing models were often related to the inclusion of interactions terms involving the same exact suite of covariates. Although this level of corroboration among competing models was encouraging, it does not necessarily mean that factors excluded from the most parsimonious models were irrelevant to survival. For instance, factors that remained relatively constant during the period of smolt releases were more likely to be excluded from the most parsimonious models as compared to factors that varied greatly on a daily or weekly basis. As an example, spill percentages presumably impacted smolt migration routes at the dams and, therefore, survival. However, spill in general did not vary greatly on daily or weekly bases (within each year) during the study period.

The most parsimonious survival models included avian predation as a key factor explaining variation in steelhead survival. Survival models indicated that Caspian tern predation alone accounted for 12% to 62% of all smolt mortality sources in Reach 1 during the study period. Avian predation (Caspian terns and gulls) was also a dominate factor regulating steelhead survival in Reach 2, with predation accounting for 33% to 63% of all smolt mortality sources. Numerous other studies have documented high levels of bird predation on steelhead smolts in middle Columbia River (Antolos et al. 2005; Evans et al. 2012; Hostetter et al. 2015b; Evans et al. 2016). The novel finding in the present study was not that bird predation was a significant source of steelhead mortality *per se* but rather that variation in steelhead survival was largely explained by variation in avian predation in multiple river reaches, and at multiple temporal scales (daily, weekly, annual). For instance, a strong relationship was observed between weekly survival rates and weekly avian predation rates in Reach 2.

Results of this study indicate that effects of avian predation were related to both the number of smolts in-river and the environmental conditions experienced by those smolts during outmigration. The most parsimonious survival models contained interaction terms between steelhead abundance and avian predation, and water transit times and avian predation. Hostetter et al. (2012) attributed the relationship between smolt abundance and avian predation rates to predator swamping (Ims 1990), whereby an individual fish's probability of being consumed by a predator decreases as the number of fish (prey) available to them increases. As water transit times decreased (i.e., a faster river environment), Caspian predation rates also decreased. Hostetter et al. (2012) also observed a relationship between increases in discharge in the lower Snake River and decreases in Caspian tern predation in McNary Reservoir. Petrosky and Schaller (2010) found that juvenile-to-adult steelhead survival was associated with water velocities, whereby return rates were highest for groups of fish migrating during high flow events. Haeseker et al. (2012) also found that survival rates were associated with water transit times and spill patterns experienced by juvenile Snake River steelhead.

There was some evidence in reservoir-specific survival models of a relationship between increased water temperature and decreased steelhead survival. Previous research has demonstrated that increases in water temperatures were associated with a greater incidence of fish disease, reduced or impaired growth rates, increased measures of stress and other physiological challenges that reduced survival (Brett et al. 1952; Arkoosh et al. 2004; Beamish et al. 2004). Increases in water temperature have also been linked to an over-all decrease in fish condition (Roegner and Teel 2014) and fish in compromised condition may be more susceptible to bird predation compared with uncompromised fish (Hostetter et al. 2012; this study). As such, several direct and indirect factors may be associated with the observed relationship between water temperature and survival during outmigration through the middle Columbia River.

Analyses of single-tagged fish, which focused on biotic factors alone, provided strong support for survival models with variables for avian predation, fish condition, fish size, and rearing-type. Even after accounting for avian predation, individual fish characteristics were significant factors in explaining variation in survival in Reach 2. External maladies identified in this study (i.e., body injuries, descaling, fin damage, and/or disease) have all been linked to multiple health and survival performance metrics in juvenile salmonids (Zabel et al. 2008, Hostetter et al. 2011; Evans et al. 2015; Hostetter et al. 2015a). Results from this study indicated that after accounting for differences in avian predation, smaller fish, compromised fish, and fish reared in hatcheries were less likely to survive from Rock Island Dam to McNary Dam as compared to larger fish, uncompromised fish, and fish not raised in hatcheries. Newman (1997) found that hatchery juvenile steelhead from the Columbia River basin were significantly less likely to survive out-migration as compared to wild fish. Evans et al. (2014) found that after accounting for differences in fish size and fish condition, wild Snake River and Upper Columbia River steelhead were significant more likely to survive to adulthood than their hatchery counterparts. These findings suggest that large-scale survival studies should include both hatchery and wild fish and fish in compromised condition, otherwise survival estimates may differ from those of the population at-large (Evans et al. 2014).

From a management perspective, results from this study support on-going efforts to reduce the number of Caspian terns nesting in the region (USACE 2014). In fact, recent reductions in the number of Caspian terns nesting on Goose Island and Crescent Island have been linked to increases in steelhead survival in the middle Columbia River (BRNW 2016). The interactions between Caspian tern predation, fish abundance, and survival also suggests that any actions taken to mitigate the impacts of a factor found detrimental to fish survival may have compounding effects. For example, if decreases in avian predation result in increased survival, this also increases smolt abundance, which would further increase survival. Efforts to decrease fish travel times by increasing water transit times may also increase survival, due in part to reducing the time that fish are exposed to point source predation within a given river reach. Results of this study also suggest that efforts to minimize the proportion of fish diverted into powerhouses will increase smolt survival. Grant PUD and other hydroelectric dam operators in the region (U.S. Army Corps of Engineers, Chelan County PUD, and others) have made substantial modifications to their dams in recent years to address concerns of turbine passage, including installation of fish bypass systems at both Wanapum and Priest Rapids dams (GPUD 2016). Finally, increasing the size and over-all health of steelhead smolts may increase survival rates by making fish less susceptible to avian predation (Hostetter et al. 2012; this study), less likely to transmit disease (Arkoosh et al. 2004), and generally more fit to navigate the hydrosystem (Evans et al. 2015; Hostetter et al. 2015a)

Despite the significant and consistent suite of biotic and abiotic factors associated with variation in steelhead survival identified in the present study, data gaps and critical uncertainties remain. Our ability to compare and contrast factors that influence variation in survival depend on the collection of accurate and complete data regarding these factors. For example, piscine predation or predation by non-colonial waterbirds could not be evaluated in the present study due to the lack of data collected regarding these sources of mortality during our study period (Evans et al. 2016). Spatially- and temporally-explicit measures of environmental conditions experienced by smolts traveling through Reach 2, a large and diverse section of the middle and lower Columbia rivers, were also not available or suitable for analyses. Finally, considerable uncertainty remains with respect to the relationship between long-term survival and the various sources of mortality evaluate herein. For instance, whether an increase in smolt survival in one river reach or during one life stage (smolt) is entirely additive to survival in subsequent river reaches or subsequent life stages (adult) is largely unknown. Full life stage models, facilitated by the simultaneous modeling of survival and the various sources of mortality developed herein, may prove useful in analyzing the broader additive effects of specific mortality factors over multiple spatial and temporal scales.

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APPENDIX A: JOINT SURVIVAL AND PREDATION ESTIMATION

The model developed herein synthesize all available data with respect to survival and avian predation using a Bayesian analytical framework. We model survival over sequential river segments using non-physical recapture events (live detections) and physical recapture events (dead recoveries) in order better to estimate recapture probabilities and thus infer survival. Live recapture events were those at acoustic telemetry arrays in Reach 1 (*Figure 1*) and/or those at dams with adequate PIT interrogation capabilities at McNary Dam (*Figure 1*), John Day Dam, Bonneville Dam, and a pair-trawl in the Columbia River estuary. Dead recapture events were those at colonial waterbird nesting sites, which included Caspian terns nesting on Twinning Island, Goose Island, Crescent Island (Rkm 510), Blalock Island (Rkm 440) and East Sand Island (Rkm 8). California gulls *Larus californicus* and ring-billed gulls *L. delawarensis* nesting on Island 20, Crescent Island, Blalock Island, and Miller Rocks Island (Rkm 331). Double-crested cormorants *Phalacrocorax auritus* nesting on East Sand Island (see Evans et al. 2016 for additional details regarding these bird colonies and their respective foraging ranges relative to Reach 1 and 2). Combining these two sources of information (live recapture events and dead recovery events) resulted in higher precision with respect to all the parameters involved (i.e., survival and predation probabilities, as well as recapture and recovery probabilities).

We let Z_{ij} be an indicator variable representing the survival of fish *i* through segment *j.* We let ω_{wj} be the probability of survival by a tagged fish from through the j^{th} segment in day *w.* We let $\boldsymbol{D}_{ij}$ = [D_{ij1}, D_{ij2}, … , $D_{ijother}$] be a (*C*+1) x 1 indicator vector representing the cause of mortality for a fish which does not survive through segment *j*. Each element D_{ijc} indicates whether fish *i* was depredated by piscivorous waterbirds colony *c* of the *C* known breeding colonies within segment *j*. $D_{ijother}$ represents the mortality of a fish from any other cause in segment *j*.

We further let $\boldsymbol{\theta}_{wj}$ = [$\theta_{wj1,}$ θ_{wj2}, … $\theta_{wjother}$] where θ_{wjc} is the probability of predation by colony *c* in the j^{th} segment associated with the tagged smolts released on day *w* and $\theta_{wjother}$ represents the probability of mortality by any other cause with respect to the same release day and segment. Therefore

$$[Z_{ij}\ , \boldsymbol{D}_{ij}] \sim \text{Multinomial}\ (Z_{i(j-1)}, [\omega_{\mathrm{rwj}}, \boldsymbol{\theta}_{rwj}]).$$

We let Y_{ij} be the indicator variable of whether fish *i* is detected at the downstream interrogation array associated with segment j^{th}. We let δ_{rwj} be the probability a surviving fish, released in day *w*, is detected at this array. Therefore

$$Y_{ij} \sim \text{Bernoulli}\ (\delta_{wj} * Z_{i(j-1)}).$$

We hold δ_{rwj} constant for across weeks for each acoustic array within each year. Downstream recapture probabilities are assumed to vary over the course of the year.

Causes of mortality within each river segment were informed with supplementary information. In this study, information regarding mortality was derived using the number of PIT tags found on a given bird colony, with a correction to account for the probabilistic process of consumed tags being deposited by birds on their nesting colony (hereafter “deposition probability”) and the imperfect detected of these tags by researchers following the nesting season (hereafter “detection probability”). Complete details concerning these two processes can be found in Hostetter et al. (2015b) and Evans et al. (2016). The model then calculates not only the abundance of tags being removed but the probable location of their removal as well.

We let R_{ic} be the vector indicating whether the tag associated with the fish *i* was recovered on colony *c*. We let $\phi_c$represent the probability that a tag consumed by a bird from colony *c* is deposited on the colony. We let ψ_{cw} represent the probability a tag deposited on colony *c* in week *w* is detected at the end of the nesting season. Therefore

$$R_{ic} \sim \text{Bernoulli}\ (\phi_c * \psi_{cw} * \textstyle\sum_j D_{ijc}).$$

To independently measure detection efficiency at each bird colony, PIT tags are intentionally sown on multiple days over the course of the breeding season. We let f_{cw} represent the number of PIT tags found of the n_{cw} intentionally sown on colony *c* on day w. We let ψ_{cw} represent the probability that a tag deposited on colony *c* in day *w* is detected. Therefore

$$f_{ic} \sim \text{Binomial}\ (n_{cw},\ \psi_{cw}).$$

Each ψ_{cw} is assumed to be a logistic function of day:

$$\psi_{cw} = \beta_{0c} + \beta_{1c} * (w - m_c),$$

where m_c represents the median day of the breeding season at colony *c*.

Estimates were calculated using a Hamiltonian Monte Carlo (HMC) process implemented through the use of the program STAN (Sampling Through Adaptive Neighborhoods), accessed via the **rstan** package (Stan Development Team 2015a) available for the statistical software R (R Core Team 2015). This requires the above state-space model to be written as recursive formulas (Stan Development Team 2015b). Three parallel chains were run for 5,000 iterations after a “warmup” of 1,000 iterations resulting in ~500 effective samples for each parameter. Chain convergence was tested using the Gelman-Rubin statistic ($\hat{R}$; Gelman et al. 2004). We report survival and predation results as posterior modes along with the Highest Posterior Density (HPD) 95% credibility intervals (95% CI).