Population-specific migration timing affects en route survival of Chinook salmon through a variable lower-river corridor

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Abstract

Migration timing is an important factor in determining conditions experienced along migratory corridors, as it influences en route survival and latent mortality. This was the case for spring-summer Chinook salmon from the interior Columbia and Snake River basins in 2010–2015, as earlier migrants experienced lower survival from the river mouth to Bonneville Dam (RKm 233). In 2013–2015, survival was especially low for early migrants, corresponding with a period of increased California sea lion presence in the estuary. Chinook salmon populations exhibit a range of migration timings due to their different migration strategies adapted in response to phenology of migration, spawning and juvenile rearing habitat conditions. Therefore, we examined the role of migration timing in determining population- and year-specific survival rates from the mouth of the Columbia River to Bonneville Dam. We estimated population- and year-specific river-entry timing by combining one model of detections of tagged fish that were identifiable to populations of origin at Bonneville Dam, with another model of travel time between the river mouth and the dam. We estimated population- and year-specific survival rates using both a previously developed model of survival as a function of river-entry date and our river-entry timing model. There was considerable variation in population-specific migration timing, with spring-run populations generally migrating earlier than summer-run populations. Early migrating populations experienced a 22% reduction survival in 2013-2015 relative to a baseline period of 1998 to 2012. Survival of later-migrating populations declined by only 4–16%, showing that the trend of decreasing survival disproportionately affected early-migrating populations. Further investigation of the causes of mortality, modeling of predator-prey interactions and dynamics, and life-cycle modeling of salmon populations would help to evaluate the potential impacts of low survival on salmon population viability, and the impact of actions designed to offset these impacts.

Introduction

Conditions experienced within migratory corridors can significantly affect demographic rates for highly migratory species, and effect conservation efforts (Moore et al. 1995, Newton 2006, Bolger et al. 2008, Keefer et al. 2008a, Sawyer et al. 2009, Klaassen et al. 2014). Perceived predation risk and direct attacks can lead to immediate and latent mortality of vulnerable and physiologically stressed animals along migratory corridors and at stopovers (Schmaljohann and Dierschke 2005, Lind and Cresswell 2006, Middleton et al. 2013, Mysterud 2013). For example, migratory elk in the Canadian Rockies had 1.7 times the wolf predation risk during migration than in summer foraging grounds (Hebblewhite and Merrill 2007). Birds are also subject to predation when migrating, both in flight and while replenishing fuel reserves at stopovers (Schmaljohann and Dierschke 2005, Ydenberg et al. 2007, Newton 2010). Sandpipers were subject to increased predation at stopover beaches in British Columbia as peregrine falcon populations recovered from the widespread use of dichlorodiphenyltrichloroethane (DDT), triggering steep population declines (Ydenberg et al. 2004).

Migration timing and rate is an important aspect of the life history of all migratory animals (Scheuerell et al. 2009, Newton 2010). It is controlled by exogenous and endogenous proximate factors such as day length, temperature, precipitation, and development of fat reserves and gonads (Gwinner 1996, Keefer et al. 2004a). Responses to these cues evolve over generations in response to environmental factors that influence survival and reproductive success, ultimately selecting for optimal migration periods (Berthold and Helbig 1992, Quinn and Adams 1996, Hodgson and Quinn 2002, Monteith et al. 2011). Consequently, migration timing can vary considerably even across populations of a single species, if conditions within habitats have different phenologies (Keefer et al. 2004b, Kelly and Hobson 2006). Furthermore, migration timing may be driven by phenology in one habitat, but relatively inflexible to changes within other habitats like portions of migration corridors. The role of migration timing on conditions experienced in seasonally variable migration corridors and the impacts on en route mortality are considerations when attempting to conserve vulnerable highly migratory species (Quinn and Adams 1996, Ydenberg et al. 2007, Sawyer and Kauffman 2011).

Spring-summer Chinook salmon (*Oncorhynchus tshawytscha*) in the interior Columbia and Snake Rivers are composed of multiple populations with unique migration timings that effect their en route mortality rates (Keefer et al. 2004b, Crozier et al. 2008a, Keefer et al. 2012, Rub et al. in prep.). They comprise two evolutionarily significant units (ESUs) listed as threatened under the Endangered Species Act (ESA) due to reductions in their abundance and productivity as a result of large-scale hydropower development, habitat degradation, harvest, and hatchery supplementation to provide harvesting opportunities (Matthews and Waples 1991, National Research Council 1996). Mature adults migrate from their adult rearing grounds in the North Pacific Ocean to the Columbia River, and then hundreds of kilometers upstream to their spawning grounds. The salinity gradient experienced upon river entry is physiologically

stressful, and they are vulnerable to predation and harvest due to their concentration in the estuary at predictable times each year (Clarke 1995, Wright et al. 2007).

A recent study by Rub et al. (in prep.) found that the survival of returning adults transiting from the Columbia River mouth to Bonneville Dam (RKm 233) was remarkably low and decreased substantially between 2010 and 2015. Survival was lowest for fish that arrived earlier in the season, suggesting that stressors and threats within the estuary differentially affected populations with different migration timings. These patterns coincided with the interannual trend and seasonality of the presence of California sea lions (*Zalophus californianus*), which suggested that predation mortality had a significant impact on spring-summer Chinook salmon survival (Brown and Wright in prep, Rub et al. in prep.) Decreased estuarine survival represents an emerging threat and additional insult to which depressed populations may not be resilient. However, different populations appear to have variable survival through the presumed predation gauntlet due to their migration timing, suggesting that there is a gradient of risk (Keefer et al. 2012).

The Upper Columbia and Snake River ESUs are composed of multiple major population groups (MPGs) composed of individual populations, each with unique migration timings. Migration timing is a heritable behavior that has evolved in response to optimal migration conditions, enabling spawning in locations and at times that maximize reproductive success and survival of offspring (Healey et al. 1991, Quinn et al. 2002, Waples et al. 2004, Crozier et al. 2008a). It shifts subtly from year to year in response to environmental conditions within the marine and riverine environments, but the order of populations returning to the river is conserved across years (Keefer et al. 2008b, Anderson and Beer 2009). Populations are categorized into spring or summer runs based on their migration timing, spawning location, and genetics (Matthews and Waples 1991). In general, spring-run populations begin their spawning migrations earlier than summer-run populations, which appears to subject them to lower survival through the hazardous lower section of the Columbia River (Rub et al. in prep.) Given the threatened and endangered status of these populations, this increased estuarial mortality that occurs near the end of the life cycle could significantly affect the viability of these populations.

The goal of this study was to examine the survival rates of Chinook salmon populations from the mouth of the Columbia River to Bonneville Dam as a function of their migration timing. Extensive data on the migration timing of Chinook salmon in the Columbia and Snake River basins are available due to large-scale tagging of juvenile parr with passive integrated transponder (PIT) tags and the presence of high-efficiency tag detectors within adult fish ladders at Bonneville Dam. We used this data and the recent study of survival through the Columbia River estuary to characterize how migration timing influenced the exposure of different populations to an emerging and temporally variable threat within their migration corridor.

Methods

General approach. We modeled average population- and year-specific survival rates between the Columbia River delta (near Astoria, Oregon) and Bonneville Dam from 2010 to 2015, and retrospectively predicted survival from 1998 to 2009. We developed a model of population- and year-specific migration timing and applied it to model-estimated year-specific daily survival rates. We bootstrapped the data to sample the uncertainty in both models and developed distributions of population- and year-specific survival rates.

Mark-recapture survival model. Survival rates of adult spring-summer Chinook salmon from the Columbia River delta to Bonneville Dam were estimated with a mark-recapture study by Rub et al. (in prep.), who captured fish near the river's mouth, east of Astoria at RKm 44, and implanted them with PIT tags. They used genetic stock identification to isolate fish originating from and presumably returning to habitats upstream of the dam (Teel et al. 2009). Tagged fish originating from populations upstream of Bonneville Dam were interrogated for the presence of tags at the adult fish ladders at the dam (RKm 234), with detection used to infer survival (Rub et al. in prep.).

We used a modified version of the logistic regression model developed by Rub et al. (in prep.) to determine survival rates from the Columbia River mouth to Bonneville Dam (s) based on the 7-day running mean number of California sea lions hauled out near Astoria (CSL) and water temperature in the lower Columbia River (t) on the date of tagging (approximately equivalent to date of river entry). The equation for survival was:

$$logit(s) = 1.416 - 0.553 * CSL + 0.287 * t - 0.376 * clip, \quad (1)$$

where *clip* was a dummy variable to adjust survival downward for adipose fin-clipped fish. Fishery removals comprised a negligible portion of total mortality for natural-origin fish, but likely explained the lower survival rates for adipose fin-clipped fish for which there is a selective fishery. The positive relationship between temperature and survival was likely due to the faster swimming speeds exhibited by salmon at the upper end of the range of temperatures that existed during this period, which likely helped fish escape from pinniped attacks and reduced their overall time of exposure (Salinger and Anderson 2006). We failed to reject the null hypothesis that this model did not fit the data based on a Hosmer-Lemeshow goodness-of-fit test with 10 groups conducted with the *ResourceSelection* package in the statistical software program R ($\hat{C}$ = 6.951, df = 8, p = 0.542; R Core Team 2015 , Lele et al. 2016). We used the *ROCR* package in R to calculate the area under the ROC curve which was 0.682 for this model (Sing et al. 2005).

We retrospectively predicted survival in 1998 and 2000–2009 using the model and a historical record of sea lion counts in Astoria conducted by the Oregon Department of Fish and Wildlife (Brown and Wright in prep, Rub et al. in prep.). We filled Short gaps in the record of sea lion counts by linear interpolation. Water temperature data were obtained from the Columbia River DART (1993) website.

Ashbrook et al. (2009) estimated that post-release survival of Chinook salmon captured in tangle nets in the lower Columbia River to Bonneville Dam was approximately 87.2% in the absence of pinniped predation, suggesting that our modeled survival rates were roughly 12.8%

lower than that of untagged fish. Thus, we view our estimates of population-specific survival as lower bounds of true survival rates. Because we were ultimately interested in how survival rates had changed due to the recent increase in pinniped presence, we examined ratios of survival rates between the baseline period and the 2013–2015 interval when sea lion presence was highest. By examining ratios, we eliminated any bias in survival estimates from handling and tagging effects, which were presumably equal in all years. The exception would be if handling effects had a significant interaction with pinniped presence, which Rub et al. (in prep.) did not believe to be the case.

Migration-timing data and analysis. Given the variability in estuarine survival across cohorts of fish entering the estuary on different days, we characterized the arrival timing of different ESA-listed populations into the estuary to estimate their annual survival rates. To estimate the population- and year-specific arrival timing of adult Chinook salmon in the Lower Columbia River, we fit a linear model of arrival dates at Bonneville Dam based on detections of fish marked with PIT tags as juveniles in their natal habitats. We modeled PIT tag detections from 2001 through 2016, when there were between 130 and 899 detections per year that fit our criteria. Detections of adult Chinook salmon at Bonneville Dam were queried from the PIT Tag Information System database (PTAGIS 2016), and we assigned fish to populations based on their tagging location (Supplementary Table S1). We restricted our analysis to wild ESA-listed populations within the Upper Columbia River spring and Snake River spring-summer Chinook salmon ESUs with > 90 total adult detections. We only used fish released in unambiguous locations within the natal habitat of a single population in the analysis. Populations were designated as spring- or summer-run based on previous work examining their life histories and genetics (Matthews and Waples 1991, PTAGIS 2016). Summer-run Chinook from the Upper Columbia River are not part of that ESU and were therefore not included in the analysis. Fish that returned after only a single year spent in the marine environment, based on the number of years between tagging and subsequent detection as returning adults, were also excluded from the analysis, because nearly all of these fish were male and are generally not included in population-dynamics models (Zabel et al. 2006).

Model of population- and year-specific arrival timing at Bonneville Dam. The population-specific distributions of arrival dates (i.e. PIT tag detection dates) at Bonneville Dam appeared to be log-normally distributed based on visual examination. Therefore, we fit a generalized linear model of the mean natural-log-transformed Julian date of arrival (D) for each population (p) and adult-return year (y), where both year and population were categorical fixed effects. In addition to the mean arrival date for each population and year, we were interested in the variances of arrival dates, which characterized the shapes of arrival-timing distributions. Due to small sample sizes for some populations in some years (Supplementary Table S2), we assumed constant variances within populations across years. Thus, we assumed that each population had an inherent spread of arrival dates, which shifted earlier or later among years

based on environmental conditions in the marine and estuarine environments. The equation of the linear model was:

$$\mathrm{Log}(D_{p,y}) = \beta 1_p + \beta 2_y + e_p, \qquad (2)$$

where $\beta 1_p$ and $\beta 2_y$ were population- and year-specific coefficients, and e_p was a population-specific error term. Model fitting was conducted with the *gls* function in the 'nmle' package in R (Pinheiro et al. 2015). We also fit models with year effects specific to either ESUs, MPGs, populations, or runs types to see if there was increased support for any of these models, which would have indicated that a substantial component of interannual variation in run timing was specific to one or more of these groupings.

We fit a similar model that predicted year effects based on environmental variables to use to predict run timing based on historical data. We based the candidate environmental variables on a set used by Keefer et al. (2008), who established relationships between migration timing and riverine, oceanic, and climatic factors. We tested the North Pacific Index (NPI; Climate Analysis Section et al. 1994) for December–March, and the Pacific Decadal Oscillation (PDO; Mantua and Hare) for January–April. We also tested the monthly averages of the following climatic and riverine variables for January–April: air temperature (C°) at Portland International Airport (~RKm 175; National Weather Service Forecast Office), surface water temperature (C°) above Bonneville Dam (Columbia River DART 1993), and discharge (m^3/s) at Bonneville Dam (Columbia River DART 1993).

In order to select environmental variables for our predictive model of population- and year-specific run timing, we used the *dredge* function in the 'MuMIn' package in R (Barton 2016) to find the best model which contained the population covariate and up to three environmental variables, based on Akaike Information Criterion (AIC). Although so called "data dredging" has the potential to produce models based on spurious relationships (Burnham and Anderson 2002), our set of candidate variables were strategically chosen because they were understood to impact the distribution of salmon in the ocean, their initiation of migration, and their travel time through the estuary (Keefer et al. 2008b). Therefore, we believe that the relationships identified through data dredging represented a reasonable model for predicting migration timing up to three years before the start of our data set of PIT-tag detections. We examined the correlation between candidate variables to ensure that significantly correlated variables were not included in the final model.To predict the proportion of each population arriving at the dam on each date in each year, we used the *dlnorm* function in R to obtain densities of lognormal distributions defined by the means and standard deviations from the model.

Model of river-entry timing. We fit the model of survival as a function of tag date, which corresponded with river-entry date, so we needed to estimate the timing of fish entering the river as a function of their arrival timing at Bonneville Dam. To do so, we developed a model of the number of days between tagging near Astoria and detection at Bonneville Dam, hereafter referred to as travel time. For details of how the travel time data were collected see Rub et al. (in prep.).

We normalized observed travel times with a log transformation and regressed them against environmental variables. To describe interannual variability in travel time, we tested the same environmental variables as used above for modeling arrival timing at the dam, as well as average water temperature, discharge, and spill at the dam over the 15, 20, and 25 days following each river-entry date. The 'dredge' function selected the best model containing up to two explanatory variables based on AIC.

For a given river-entry timing distribution, we used the travel time model to estimate the resulting arrival-timing distribution at Bonneville Dam. Assuming that river-entry timing was log-normally distributed for each population, we iteratively fit distributions of river-entry timing to minimize the differences between the arrival timing distribution at Bonneville Dam that they produced based on the travel time model, and the distributions predicted based on the model fit to detections of PIT-tagged fish that were identifiable to populations of origin.

We estimated arrival timing at Bonneville Dam based on arrival timing in the river as follows. We used the 'predict' function in R to estimate the mean and 95% prediction interval of travel times for each cohort of fish, which entered the river on a given Julian date (c), and year (*y*), and divided half of the prediction interval by 1.96 to obtain the standard deviation of the lognormal distribution of travel times for each cohort. We used the 'dlnorm' function in R to obtain the densities of the travel time distributions (*tt*) for fish from each river-entry cohort that arrived at Bonneville Dam on each date (*b*) in each year. The proportions of a population (*P*) that arrived at Bonneville Dam on each date in a given year was estimated by multiplying *tt* by the proportion of the population in the corresponding cohort and summing across cohorts:

$$p_{P,b,y} = \sum_{c=1}^{b} tt_{b,c,y} * p_{P,c,y} \ . \qquad (3)$$

Population- and year-specific survival. To estimate population- and year-specific survival rates (*S*), we weighted cohort-specific survival rates estimated from the survival model by the proportions of each population in each cohort. We restricted the range of possible river-entry cohorts to be between 20 March and 14 June, the period when the mark-recapture study was conducted, and added the proportions of each population that were predicted to enter the river before or after this interval to the first and last days of the interval. We multiplied the proportions of each population within each cohort by the corresponding survival rates, and summed the products across cohorts:

$$S_{p,y} = \sum_{c=79}^{165} P_{\mathrm{p,y,c}} * S_{c,y} \ . \qquad (4)$$

We characterized model uncertainty and generated distributions of population- and year-specific survivals by bootstrapping the models of arrival timing at Bonneville Dam and survival 1,000 times. For each iteration, the models were refit to random samples of the original data sets, drawn with replacement, of the same lengths of the original data sets.

Results

Population- and year-specific migration timing. In the model of arrival timing at Bonneville Dam, which included covariates for population and year, all coefficients were highly significant ($p < 0.001$). Visual examination of model fits to the observed distributions of population- and year-specific arrival dates at Bonneville Dam suggested that the model accurately described the data. Models that included unique year effects for individual ESUs, MPGs, populations, runs, or origin types received significantly less support based on AIC than the model with common year effects across all populations under study, indicating that annual shifts in migration timing were similar across populations (Supplementary Table S3).

The highest ranked model of arrival timing at Bonneville Dam contained the environmental variables January PDO (JPDO), March NPI (MNPI), and February Discharge (FD):

$$\text{Log}\,(D_{p,\,y}) = \beta 1_{\text{p}} - 0.0131878\ \ (\text{JPDO}_y) + 0.0014732\ \ (\text{MNPI}_y) + 0.0003270\ \ (\text{FD}_y) + e_p. \quad (5)$$

This model produced very similar predictions to the model that included individual year effects (Equation 1), based on visual examination. We used the environmental-variable model (Equation 5) to generate distributions of arrival timing at Bonneville Dam in the remainder of our analysis, because it could be used to predict historical arrival-timing in years for which there was insufficient PIT tag data to accurately estimate migration timing. However, our results would have been similar using either model for the years when they were both applicable. The earliest modeled average arrival date at Bonneville Dam between 2000 and 2016 occurred in the year 2003 and was approximately ten days earlier than the latest, which occurred in 2000 (Figure 1).

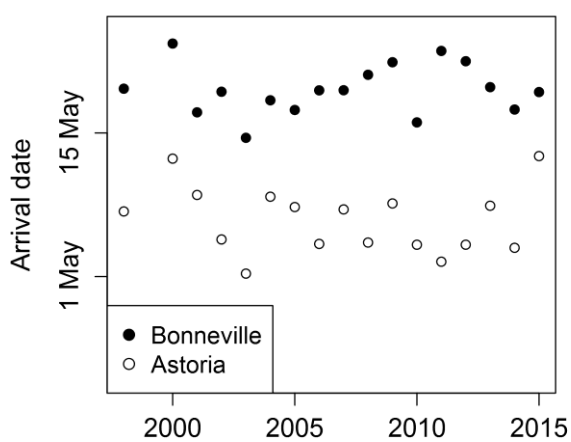

Figure 1. Modeled average arrival date for all populations combined in the river mouth near Astoria and at Bonneville Dam.

There was considerable variability among populations in arrival timing at Bonneville Dam, including within individual MPGs (Figure 2). For example, the Upper Grande Ronde (above the Wallowa River) and Catherine Creek populations, both within the Grande Ronde MPG, migrated earlier than the Lostine River population, also in the Grande Ronde MPG. Across all populations examined, there did not appear to be distinct early- and late-arriving groups, but rather a continuum of run timings. Furthermore, some spring-run populations, such as the Lostine River, had relatively late arrival timings that were closer to summer-run populations. However, summer-run populations did have considerably later migration timings than spring-run populations on average.

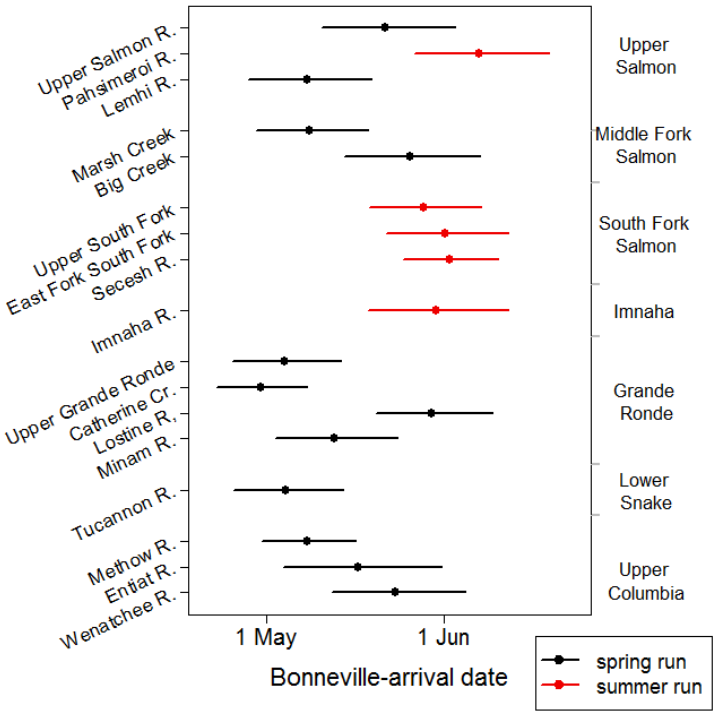

Figure 2. Modeled means (points) and interquartile ranges (lines) of arrival dates at Bonneville Dam for wild spring and summer Chinook salmon populations in 1998–2015. There was considerable variation across populations. Earlier-migrating populations had lower survival than later-migrating populations.

River-entry timing. Travel times between the river mouth and Bonneville Dam decreased from an average of 30–40 days at the beginning of the mark-recapture study in late March to 5–10 days in mid-June (Supplementary Figure S1). The best model of travel times contained terms for average discharge over 20 days following river entry, and average water temperature over 25 days following river entry (Supplementary Table S4). Outflow had a positive relationship with travel times while temperature had a negative relationship with travel times. The modeled travel times and prediction intervals appeared to fit the observed data well (Supplementary Figure S1).

The models of travel time and arrival at Bonneville Dam combined to determine arrival timing in Astoria, which we used to predict survival. Surprisingly, average annual arrival dates at Bonneville for all populations were only moderately correlated with average arrival dates at Astoria from 1998 to 2015 (Pearson correlation = 0.254), with an average travel time of 12.7 days between them (Figure 1). The greatest average travel time within a single year over this period was 20.5 days in 2011, and the shortest was 6.2 days in 2015. The year with the earliest average river-entry date was 2003, and the average river-entry occurred in 2015 (11.5 days later than 2003). The river-entry timing distributions interacted with cohort-specific survival curves to drive population- and year-specific survival-rate distributions (Supplementary Figure S2).

Survival to Bonneville Dam. Timing of river entry had a strong effect on population-specific survival rates, especially in 2013-2015, when survival was very low in the early part of each year (Figures 3–5). The earliest-arriving of the spring-run populations examined—Lemhi River, Marsh Creek, Upper Grande Ronde, Catherine Creek, Tucannon River, and Methow River—had somewhat lower survival rates than other populations in 2010–2012, when annual medians ranged from 69% to 81%, and much lower survival rates in 2013–2014, which had a 50–70% range in annual median survivals. Populations with intermediate run timing such as the Upper Salmon River, Big Creek, Minam River, Entiat River, and Wenatchee River had experienced survival that was somewhat lower in 2013–2015, with annual medians of 67–85% than 2010–2012's 79% to 88%, range. Late-arriving populations—Pahsimeroi River, Upper South Fork Salmon River, East Fork South Fork Salmon River, Secesh River, Imnaha River, and Lostine River—most of which are considered summer-run, had the highest survival rates with the least interannual variability. Unlike early-arriving populations, these fish had similar survival rates in 2010–2012, with annual medians ranging from 84% to 92%, and 2013–2014 (83–92%).

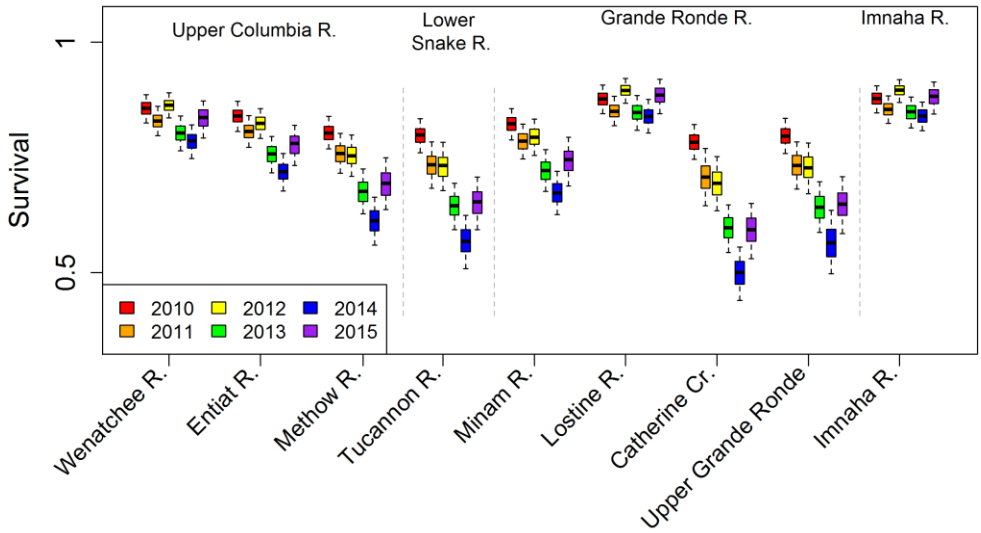

Figure 3. Modeled population- and year-specific survival rates of adult spring Chinook salmon during their migration from the mouth of the Columbia River (near Astoria, OR) to Bonneville Dam. The horizontal black line in the middle of each box represents the median survival estimate, the range of each box represents the interquartile range, and whiskers reach the 5th and

95th percentiles. These survival estimates are likely biased low by approximately 13% due to tagging and handling effects in the mark-recapture study, so we view them as minimum estimates of survival.

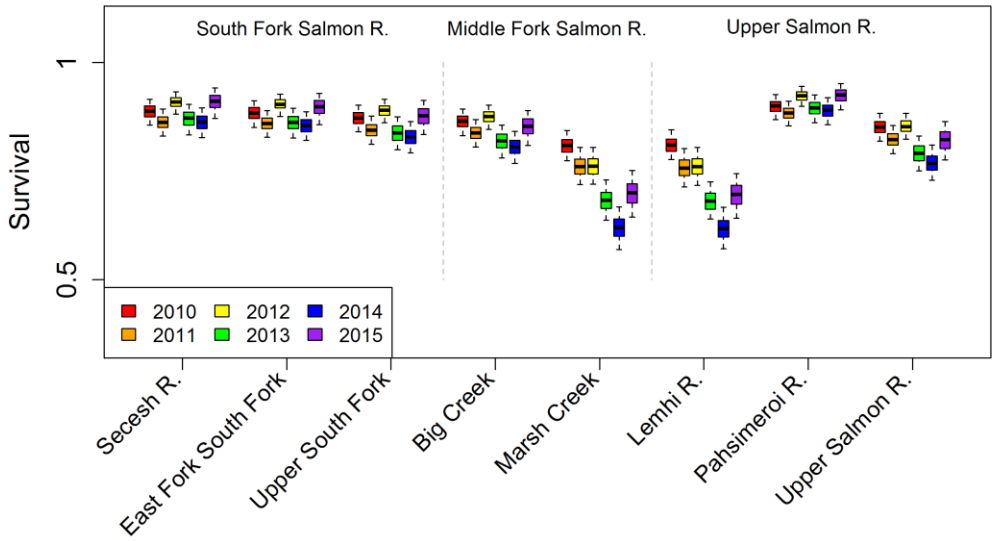

Figure 4. Modeled population- and year-specific survival rates of adult spring Chinook salmon during their migration from the mouth of the Columbia River (near Astoria, OR) to Bonneville Dam. The horizontal black line in the middle of each box represents the median survival estimate, the range of each box represents the interquartile range, and whiskers reach the 5th and 95th percentiles. These survival estimates are likely biased low by approximately 13% due to tagging and handling effects in the mark-recapture study, so we view them as minimum estimates of survival.

Retrospective prediction of average population-specific survival exhibited significant interannual variability between 1998 and 2009, but survival was higher throughout this period than during the 2013–2015 period (Figure 5). Survival rates were relatively low in 2002 and 2003 when fish arrived in the river early and California sea lion presence was slightly elevated in comparison to other years during the 1998–2009 interval. Average survival of the early-migrating populations was 22% lower in the 2013–2015 period than during the 1998–2012 baseline period. Average survival of the populations with intermediate migration timing were reduced by 11%, and survival of the late-migrating populations decreased by only 6% during the increase in sea lion presence in 2013-2015 relative to the baseline period.

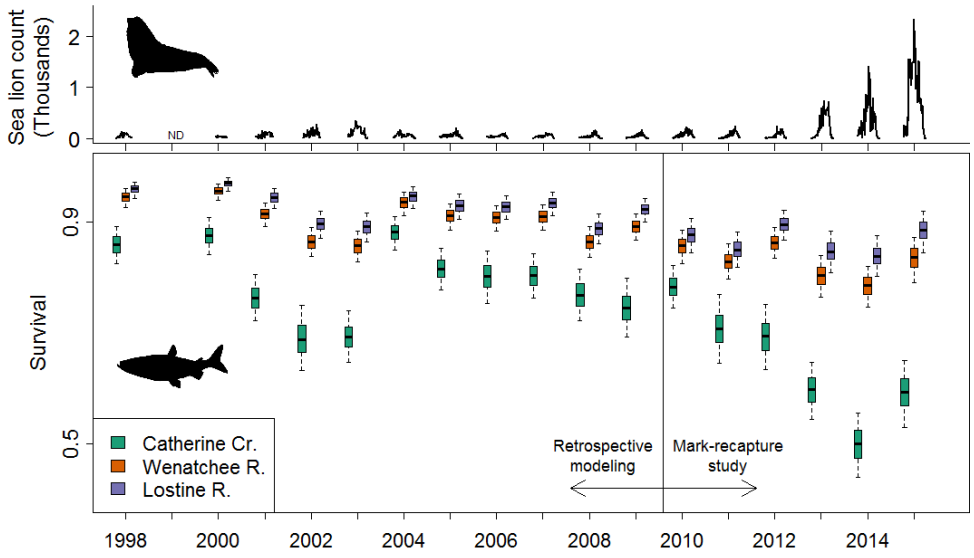

Figure 5. Top Panel: Daily counts of California sea lions hauled out at the East Moring Basin in Astoria from 1 January to 30 June of 1998–2015. Sea lion counts were unavailable for 1999. Bottom Panel: Modeled population- and year-specific survival rates of adult spring-summer Chinook salmon during their migration from the mouth of the Columbia River (near Astoria) to Bonneville Dam. The boxplots represent medians, interquartile ranges, and 5th and 95th percentiles of survival rate estimates. We used the model of survival based on the mark-recapture study conducted in 2010–2015 to retrospectively model survival rates as a function of California sea lion counts. These survival estimates are likely biased low by approximately 13% due to tagging and handling effects in the mark-recapture study, but show the degree that survival decreased in 2013–2015.

Discussion

The overall decrease in survival through the Lower Columbia River in late March through April of 2013–2015 strongly affected the survival rates of earlier-migrating spring-run Chinook salmon populations, whereas it had much less of an effect on later-migrating populations. Our analysis suggested that survival rates of early migrating fish decreased by 22%, which would likely have significant effects on population viability and recovery. The coincident increase in California sea lion presence and decrease in salmon survival suggests that predation by pinnipeds is significantly influencing salmon survival, which presents a management dilemma because both groups of animals are protected by federal statutes. Recovery planning for salmon should consider the impacts of estuarine mortality with population specificity, because of the significant differences owing to their migration timings.

The interannual variation in arrival timing at Bonneville dam had a correlation with oceanic and riverine conditions prior to the peak migration of these fish through the lower river. However, January PDO had a significant positive correlation with river temperatures during the

months of peak migration, and February discharge had a significant positive correlated with river discharge during peak migration, so it is hard to pick out the precise mechanisms controlling migration timing.

Our travel time model had a significant effect on our predictions of river-entry timing and therefore survival. The water temperature and discharge in the lower river when fish were migrating appeared to drive travel time, and there was significant interannual variability in these factors and thus travel times. Arrival timing at Bonneville Dam was not always a good predictor of arrival timing in the river mouth.

Early-migrating Chinook salmon are constrained in their ability to adapt their migration timing to conditions in the Columbia River estuary, because of the timing of conditions upstream of Bonneville Dam that maximize survival and access to spawning habitats (Quinn and Adams 1996). In the Columbia River, average survival of natural-origin Chinook salmon populations through the 236 km of river between Bonneville Dam and McNary Dam ranged between 77% and 97% from 2004 to 2015 (Crozier et al. 2016). Late-migrating populations exhibited lower survival over this period, presumably due in part to warm water temperatures. This suggests that there were survival advantages to late migration from the river mouth to Bonneville Dam, whereas there were advantages to early migration from Bonneville Dam to McNary Dam

To project more accurately the potential future impact of mortality incurred between the river mouth and Bonneville Dam on population viability, we need a better understanding of the underlying mechanisms. Additionally, there is a need to evaluate the effects of conditions in the lower river on subsequent survival through the remainder of their migration and on reproductive success (Naughton et al. 2011). Potential causes of increased mortality include compounding effects of pinniped predation, disease, thermal stress, inadequate energy reserves, fisheries, and other factors (Cooke et al. 2006, Farrell et al. 2008, Miller et al. 2011, Keefer et al. 2012). The coincident increase in California sea lion presence and decrease in estuarine survival implicates them in the observed mortality, and warrants further investigation and potentially management action. The increase in California Sea lions in 2013–2015 coincided with an increase in eulachon and spring Chinook returns to the Columbia River, as well as warmer than usual sea surface temperatures in the northeast Pacific (Di Lorenzo and Mantua 2016, Lee et al. 2016). The smaller increase in sea lion presence that occurred in 2002–2003 also coincided with strong spring runs of anadromous fish, suggesting an aggregatory response of sea lions to eulachon and salmon, although the dynamics of this response are unknown (Womble et al. 2005, Gustafson et al. 2016). The presence of pinnipeds in the Columbia River Estuary in the future will likely have a significant effect on the viability of salmon populations and warrants further investigation into the drivers of their seasonal abundance, and potentially management actions to offset their impacts.

Population-dynamics models that incorporate demographic rates at multiple life stages, such as life-cycle models for salmon, will be valuable for evaluating the effect of en route

mortality on population viability (Kareiva et al. 2000, Zabel et al. 2006). The expected future survival rates of adult Chinook salmon within the Columbia River Estuary could be combined with expected demographic rates at other life stages, based on climate projections and proposed restoration actions, to evaluate overall impacts on viability and improvements from management actions (Crozier and Zabel 2006, Crozier et al. 2008b). Increased mortality of adults could have a strong effect on population dynamics, because there may be limited scope for compensatory survival as they approach the end of their life cycles. Furthermore, many populations are already depressed and may be below the capacity of their spawning and rearing habitats (McClure et al. 2003). The quantitative estimates of population-specific mortality developed in this study will enable modeling to evaluate such hypotheses about the impact of survival in the Lower Columbia River on broader population dynamics. Future modeling should include a range of scenarios of future pinniped presences to examine and compare impacts on population viability, and the ability of different hypothetical management actions to reduce or offset the negative impacts of pinniped predation. Detailed viability analyses will be especially important because one federally protected species poses a threat to another federally protected species (Redpath et al. 2013).

Migrations in general, and especially reproductive migrations, represent inherently stressful events in animals' life histories. Migratory populations often travel long distances during which they are vulnerable to predators, disease, starvation, and adverse weather (Cooke et al. 2006), while habitat modifications by anthropogenic activities and climate change are likely to alter conditions experienced along migration corridors and may affect migration timing (Marra et al. 2005, Crozier et al. 2008a, Mysterud 2013). We must consider these factors in order to conserve highly migratory populations, especially when they are already depressed due to insults to their primary habitats. Mortality during migrations appears to have significant affects on the viability of certain populations, and we must monitor and potentially mitigated for it to prevent extinctions. In this instance, early migrating populations are at the highest risk from mortality mechanisms during their upstream migration through the estuary as adults.

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Supplementary Tables

Table S1. List of release sites for PIT tagged fish included in each population. Only release sites located within the natal habitat of a single population were included in the data set.

ESU	MPG	Run	Population	Release Site	Latitude	Longitude
Snake	Grande Ronde / Imnaha	Spring	Catherine Creek	Catherine Creek	45.20966612	-117.8878496
			Upper Grande Ronde	Grande Ronde River - Wallowa River to headwaters (km 131–325)	45.3256363	-117.9205262
			Lookingglass Creek	Lookingglass Creek	45.75719905	-117.9600117
			Lostine River	Lostine River	45.37281443	-117.4235889
			Minam River	Minam River	45.33887738	-117.6001786
		Summer	Imnaha River	Imnaha River	45.39694069	-116.7918754
				Imnaha River Weir	45.19427639	-116.8686635
				Imnaha Trap	45.7637	-116.7:2148
	Lower Snake	Spring	Tucannon River	Tucannon River	46.39571678	-117.7112008
	Middle Fork Salmon	Spring	Big Creek	Big Creek, Middle Fork Salmon River	45.15775882	-115.12014
			Marsh Creek	Capehorn Creek	44.35682643	-115.2196822
				Lower Marsh Creek Trap at RKm 8	44.4084466	-115.1816474
				Marsh Creek	44.39025653	-115.1632599
				Marsh Creek Trap	44.39383164	-115.1673549
	South Fork Salmon	Spring	Rapid River Hatchery	Rapid River Hatchery	45.35368101	-116.394575
		Summer	East Fork South Fork Salmon	Johnson Creek	44.73392789	-115.5486019
				Johnson Creek Trap	44.91761448	-115.4833437
			McCall Hatchery	Johnson Creek	44.73392789	-115.5486019
				Knox Bridge, South Fork (SF) Salmon River	44.65551546	-115.7023954
			Secesh River	Lake Creek	45.32905869	-115.9492036
				Secesh River	45.15195322	-115.796847
				Secesh River Screw Trap	45.05943169	-115.7566901
				Summit Creek, Secesh River Basin	45.20762581	-115.9454983
			Upper South Fork Salmon River	Knox Bridge, South Fork Salmon River	44.65551546	-115.7023954
				Lower South Fork Salmon River Trap at RKm 61	45.01468201	-115.715024
				SF Salmon River Trap (Archaic, replaced with SALRSF or KNOXB)	44.65551546	-115.7023954

	Upper Salmon	Spring	Lemhi River	Big Springs Creek, Lemhi River Basin	44.70845448	-113.4056972
				Hayden Creek, Lemhi River Basin	44.75276564	-113.7129834
				Lemhi River	44.9105456	-113.6250366
				Lemhi River Weir	44.86596003	-113.624721
			Sawtooth Hatchery	Sawtooth Hatchery	44.150681	-114.883659
				Sawtooth Trap	44.148	-114.8837
				Yankee Fork Salmon River	44.4121693	-114.6361472
			Upper Salmon River	Sawtooth Trap	44.148	-114.8837
		Summer	Pahsimeroi River	Pahsimeroi River Trap	44.684528	-114.040438
Upper Columbia	Entiat	Spring	Entiat River	Entiat River	47.91097008	-120.4903306
				Mad River (Entiat River watershed)	47.82092948	-120.5161779
	Methow	Spring	Methow River	Chewuch River	48.75050678	-120.1371161
				Methow River	48.35359525	-120.1092355
				Methow Smolt Trap at McFarland Creek Road Bridge	48.15108488	-120.0565842
				Twisp River	48.35388354	-120.3650912
	Wenatchee	Spring	Leavenworth National Fish Hatchery	Leavenworth National Fish Hatchery	47.558898	-120.674835
			Wenatchee River	Chiwawa River	47.9506332	-120.7768394
				Chiwawa River Trap, 0.5 km below CHIP acclimation pond	47.78812112	-120.6511455
				Lower Wenatchee trap, 2.8 km below Mission Creek	47.51193198	-120.4482675
				Nason Creek (tributary to Wenatchee River)	47.7819426	-120.8776371
				Peshastin River	47.45684205	-120.6588198
				Upper Wenatchee smolt trap just below Lake Wenatchee	47.80976111	-120.7156389
				Upper Wenatchee trap, 4 km above Chiwawa River	47.79787109	-120.6661512
				Wenatchee River	47.58484333	-120.6773509
				Wenatchee River trap at West Monitor Bridge	47.5007	-120.4257
				White River, Wenatchee River Basin	47.92390792	-120.9041708

Table S2. Sample sizes of adult Chinook salmon that were PIT tagged as juvenile in their natal basin and subsequently detected as adults at Bonneville Dam, by population and year of detection.

	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	Total
Big Creek	2	1	3	3	2	0	0	1	21	76	76	35	29	23	26	17	315
Catherine Creek	1	3	7	4	2	3	2	6	6	9	23	13	13	8	5	6	112
East Fork South Fork Salmon	25	29	40	31	6	8	11	39	15	37	39	35	27	30	13	8	393
Entiat River	0	0	0	0	2	4	6	8	9	77	78	53	31	42	52	47	409
Imnaha River	48	110	103	50	30	38	25	25	79	173	198	93	39	78	62	50	1208
Lemhi River	8	9	11	6	2	3	4	6	27	35	40	15	35	53	67	28	349
Lostine River	7	14	15	10	4	5	5	9	14	17	35	15	11	19	22	13	216
Marsh Creek	1	12	14	9	3	0	1	1	17	69	55	27	29	33	26	16	314
Methow River	0	0	0	0	0	0	1	3	8	30	23	6	7	17	20	19	134
Minam River	1	2	6	5	2	2	2	4	9	28	14	9	3	20	11	7	125
Pahsimeroi River	6	6	3	1	0	4	3	5	7	14	11	6	17	19	20	4	126
Secesh River	9	22	33	13	3	2	4	15	69	128	68	36	42	34	25	11	515
Tucannon River	2	0	0	1	2	0	0	1	10	31	29	7	15	18	32	10	158
Upper Grande Ronde	1	3	5	0	4	5	2	7	4	16	7	6	12	9	8	3	93
Upper Salmon River	3	5	9	13	8	10	9	21	14	26	27	25	23	22	28	14	257
Upper South Fork Salmon	16	25	56	4	2	4	3	7	21	22	43	56	26	22	11	6	324
Wenatchee River	0	0	0	0	5	3	1	23	35	100	133	78	36	44	63	49	570
Total	130	241	305	150	77	91	79	181	365	888	899	515	395	491	491	308	

Table S3. AIC values for models of log-transformed arrival date at Bonneville Dam for PIT-tagged adult spring-summer Chinook salmon from the Upper Columbia River and Snake River ESUs. In all models, we assumed that variances were constant within populations across years. Pop = population (based on tagging location of juveniles); Yr = year; MPG = major population group; Run = spring or summer run; and ESU = endangered species unit.

Model	AIC	Δ AIC
Pop + Yr	-8,517	0
Pop + Yr: Run	-8,391	127
Pop + Yr: ESU	-8,300	216
Pop + Yr: MPG	-8,284	231
Pop + Yr: Pop	-8,160	354

Table S4 Coefficient estimates for a model of log-transformed travel times between Astoria and Bonneville Dam. Outflow 20 is the average outflow at Bonneville Dam over 20 days following tag date; and Temp 25 is average temperature over 25 days following tagging.

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	4.432514	0.07776	57	<2e-16
Outflow 20	0.001435	0.000133	10.78	<2e-16
Temp 25	-0.17501	0.006039	-28.98	<2e-16

Supplementary Figures

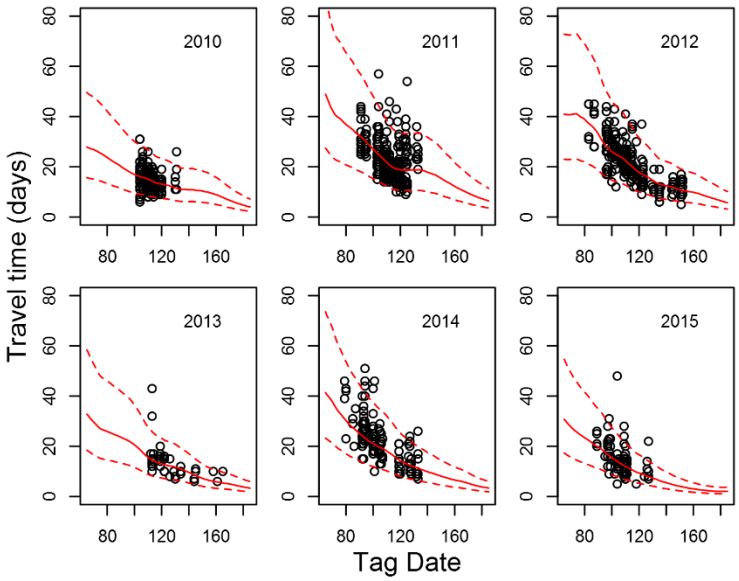

Figure S1. Observed travel times of PIT-tagged fish between Astoria and Bonneville Dam (points) and modeled average travel times and 95% prediction intervals (red lines). We modeled travel times as a function of water temperature and outflow at Bonneville Dam.

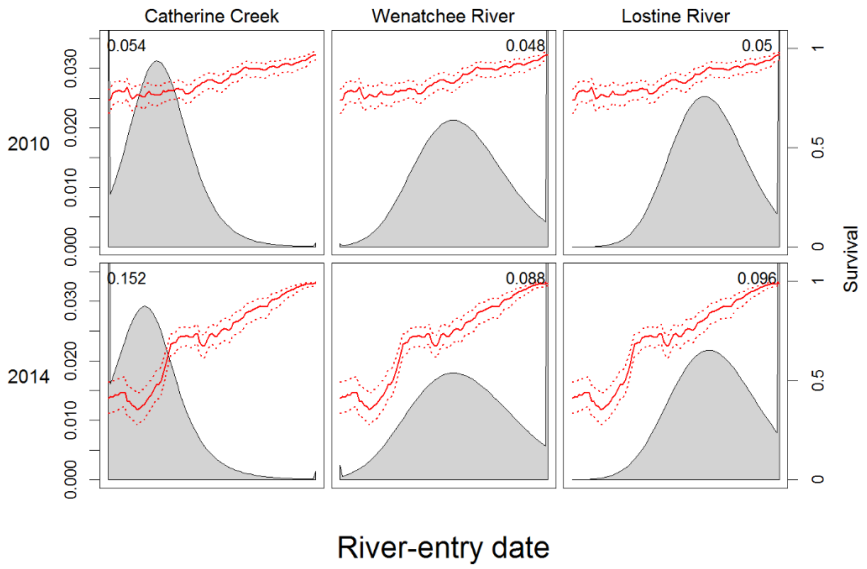

Figure S2. Modeled year-specific river-entry timing distributions of three spring Chinook salmon populations (shaded gray areas, left y-axis). The numbers in the upper corners of the panels represent the proportions of the populations assumed to arrive on the first and last date of the interval, when they are above the range of y-axis. The large proportions of populations arriving at the very beginning and end of the interval of river-entry dates are due to our truncation of the range of possible dates. This was necessary given that survival rates were unknown outside of this range, so it was most appropriate to assign early-arriving fish the survival rates predicted for the beginning of the range of dates of the survival study, and vice versa. Solid red lines represent model-estimated survival for cohorts of fish entering the river on each date, based on the mark-recapture study conducted by Rub et al. (in prep), and dashed-red lines represent 95% confidence intervals around these estimates. We weighted cohort-specific survival rates by the proportions of each population in each cohort in order to estimate population-specific annual survival rates.