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Prespawn mortality of female Chinook Salmon increases with water temperature and percent hatchery origin

Running headline: Willamette River Chinook Salmon prespawn mortality

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Abstract

High rates of prespawn mortality, when adult salmon die after completing migration but prior to spawning, can lead to population declines and can impede recovery of threatened stocks. In this study, annual prespawn mortality of female Chinook Salmon *Oncorhynchus tshawytscha* ranged from 1% to 100% over 14 years in seven study reaches located throughout the upper Willamette

River Basin, Oregon. Prespawn mortality rates were positively correlated with the annual maximum seven-day average maximum stream temperature and the percentage of spawning fish of hatchery origin. Observed prespawn mortality rates varied considerably, but where maximum temperatures exceeded 20°C and the composition of spawning fish was >80% hatchery origin, annual female prespawn mortality rates were consistently >80%. In several spawning tributaries, prespawn mortality rates generally decreased at higher elevations. The proximate cause of prespawn death was not evaluated here and observed patterns likely reflect additional factors that influence mortality either directly or indirectly, including handling, dam passage, fishing pressure, instream habitat, energetic budget, fish density, and pathogen loads.

Introduction

Semelparous species make a single, large reproductive investment, and consequently death before breeding results in zero lifetime fitness. Semelparity in Pacific salmon (*Oncorhynchus* spp.) likely evolved in parallel with anadromy plus long-distance adult migrations that favored large body size (Crespi and Teo 2002). Large eggs and high fecundity allowed many salmon populations to persist despite high mortality, particularly in early life stages (Hilborn et al. 2003; Wilbur and Rudolf 2006). However, excessive mortality of adult salmon during freshwater migration and holding prior to spawning can lead to rapid population decline (Nehlsen et al. 1991; Spromberg and Scholz 2011) and has been a challenge in many salmon management and conservation programs (Cooke et al. 2004; Keefer et al. 2008; Hinch et al. 2012).

Adult mortality has been a persistent issue for threatened spring-run Chinook Salmon (*O. tshawytscha*) in Oregon's upper Willamette River basin (NMFS 1999). Recovery efforts for the

aggregate Willamette River population have been hampered by both adult migration mortality (Keefer et al. 2017) and prespawn mortality (PSM) in tributaries (Keefer et al. 2010; Benda et al. 2015; DeWeber et al. 2017). Prespawn mortality occurs after fish have returned to natal streams but prior to spawning (Hinch et al. 2012; Bowerman et al. 2016). Within the Willamette River basin, considerable variation in PSM rates has been reported among locations and among years at a single location (Sharpe et al. 2013; Benda et al. 2015; DeWeber et al. 2017). In one population from the Middle Fork of the Willamette River, PSM was associated with high water temperatures and poor fish condition (Keefer et al. 2010). A follow-up experiment found that Chinook Salmon held in cool, pathogen-free water had similar pathogen loads but lower PSM than those in the adult trap and haul program (where adult salmon are trapped, transported around barriers, and released upstream) in several Willamette River tributaries (Benda et al. 2015). The experimental results were consistent with the long-standing hypotheses that high water temperatures interact with stress, existing pathogens, and other factors to increase adult salmon mortality (Schreck 1996; Crossin et al. 2008).

Mechanisms driving PSM in Willamette River Chinook Salmon are likely cumulative, given the number and magnitude of various stressors fish encounter during migration and on spawning grounds. Much of the high quality spawning habitat for Chinook Salmon is located in higher-elevation forested parts of the basin, while lower-elevation habitat is often located in urban areas or agricultural land (Hulse et al. 2004). Access to high-quality spawning and rearing habitat is blocked by high-head (> 20 m of hydraulic head) hydroelectric and flood-control dams in many tributaries; providing access to these habitats is now part of salmon recovery planning (ODFW and NMFS 2011). The dams affect flow regimes, water temperatures, and spawning gravel

availability in downstream sections, as well as the distribution of wild- and hatchery-origin salmon throughout much of the upper Willamette River basin. Many adult salmon are collected at trapping facilities, transported, and released at sites above high-head dams (Keefer et al. 2010; DeWeber et al. 2017). Numerous smaller dams (< 20 m) located throughout the basin allow fish passage but may result in migration delays or cause fish to aggregate at high densities. Migration and handling stress, as well as pathogen transmission and other density-dependent effects associated with fish aggregations and trap and haul, all likely contribute to relatively high PSM in some upper Willamette River populations (Keefer et al. 2010; Benda et al. 2015). In this complex fisheries management setting, there is a need for greater understanding of general factors affecting basin-wide PSM, as well as specific evaluation of individual populations. More generally, there is a need to identify factors associated with PSM and potential management actions to minimize the effects of PSM on populations of conservation concern (Bowerman et al. 2016).

We explored PSM patterns across a diverse set of spawning reaches located in five major Willamette River tributaries using systematically collected salmon carcass data. The study reaches had varying degrees of hatchery and anthropogenic influence, as well as different thermal and flow regimes. We investigated the relationship between female PSM and: (1) stream temperature; (2) stream discharge; and (3) the percentage of fish spawning in the wild that were of hatchery origin. We hypothesized that PSM would be positively correlated with water temperature (Quinn et al. 2007; Keefer et al. 2010) and negatively correlated with river discharge (Hyatt et al. 2003; Tillotson and Quinn 2017). We also expected that PSM would increase as the percentage of hatchery-origin fish spawning in the wild increased. Hatchery-

origin effects on PSM have been reported in regional Chinook Salmon populations (e.g., Schroeder et al. 2007; Young and Blenden 2011), and may be related to factors such as increased spawner density, greater competition, elevated fishery effort, or phenotypic differences between natural- and hatchery-origin fish.

Methods

Study area.—We evaluated PSM in seven study reaches where Chinook Salmon carcasses were routinely surveyed in the Willamette River Basin by the Oregon Department of Fish and Wildlife (ODFW). The reaches, as delineated in ODFW summary reports, were located in five tributaries containing both low- and high-head dams and a range of spawning habitat quality (Figure 1). The low-head dams (< 20 m) had adult fish passage facilities, while all but one (Clackamas River) high-head dam (> 20 m) did not. In contrast to the trap and haul populations evaluated in the Keefer et al. (2010) and DeWeber et al. (2017) PSM studies, salmon could volitionally reach all study reaches described here.

In general, Chinook Salmon spawning habitat quality in reaches below high-head dams generally lacked complexity due to poor wood and substrate recruitment. Habitat quality was typically higher in the upper watershed reaches, where there was a greater percentage of forested land use and less agriculture and urban development compared with reaches lower in the watershed (NMFS 2008). The highest quality habitat was found in the two reaches that had no (Clackamas) or minimal (upper McKenzie) influence from upstream dams (Figure 1). These two reaches were the least impacted in the study and contained considerable Chinook Salmon spawning habitat (ODFW and NMFS 2011). In contrast, the lower McKenzie River study reach

below the low-head Leaburg Dam had less and relatively poorer quality spawning habitat. The upper and lower North Santiam reaches were located below two high-head dams: the lower reach had relatively lower quality spawning habitat and most spawning took place in the upper study reach. The South Santiam reach was downstream from the high-head Foster Dam, and contained simplified spawning habitat. Very little spawning took place below the low-head dam located in the middle of the South Santiam reach, so the limited carcass data collected in this section was combined with data from the upper portion of the reach in ODFW reports. The Middle Fork Willamette River reach contained limited Chinook Salmon spawning and was located downstream of two high-head dams that altered reach hydrology, thermal regime, and physical structure.

Prespawn mortality estimates.—Estimates of female Chinook Salmon PSM rates in each study reach were calculated annually by the ODFW and published in agency reports (e.g., Schroeder et al. 2007; Sharpe et al. 2013). PSM was estimated from examination of female carcasses recovered in each study reach prior to and during the spawning season, and all estimates of PSM in this study refer to females. All carcasses that could be recovered by hand or with long-handled gaffs, and that were intact enough to determine spawning status, were examined for egg retention. Empirical estimates of the rate of carcass recovery were unavailable, but relative to total run size, <10% of returning spawners were typically recovered. A female carcass was defined as a PSM if it retained more than 50% of the expected number of eggs (as described in DeWeber et al. 2017). Once a carcass was inspected, its tail was removed to ensure that it was not counted in subsequent surveys. The annual reach-specific PSM estimates were calculated as the number of unspawned female carcasses divided by the total number of female carcasses for

which spawning status was determined (i.e., carcasses that were too damaged or decayed to determine spawning status were excluded). Data were summarized by reach and year because data on individual fish were not available, and PSM estimates were presented as percentages for consistency with reports from throughout the basin (Table A.1). To avoid bias from small sample sizes (Bowerman et al. 2016), annual PSM estimates were excluded from our analyses if fewer than 10 female carcasses were collected in a given study reach. As a result, data from several years were excluded from the lower North Santiam reach (Table 1).

We also qualitatively evaluated PSM data collected at the spatial scale of <1 to 18 km within each of the study reaches except the Clackamas River. Covariate data were not collected at this scale, so we did not perform a formal analysis, but we visually examined these data for longitudinal patterns of PSM within each river corridor.

Hatchery-origin spawners.—The percentage of hatchery origin spawners (PHOS) was estimated annually in each study reach by ODFW (Table 1). Within the Willamette River basin, most hatchery spring Chinook Salmon were marked with an adipose fin clip, coded wire tag, or both. Thermal marks were also induced on otoliths of all hatchery-released Chinook Salmon to further help identify hatchery-origin fish that were missing fin clips or coded-wire tags. Otoliths were collected from carcasses recovered on spawning grounds and thermal marks were used to adjust PHOS estimates to account for the proportion of otherwise unmarked fish. The PHOS estimate for each study year and reach was derived from counts of fin-clipped fish (AD) plus unclipped thermally-marked fish (UTM) divided by the total count of fish examined (TOT), where $PHOS = (AD + UTM)/TOT$.

Temperature and streamflow data.—Water temperature and discharge data from U.S. Geological Survey (USGS) gaging stations were used to characterize annual river conditions within each stream reach (Figure 1; Table 1). When temperature data were missing (4 y of data were missing for each of the lower McKenzie and lower North Santiam reaches, and 3 y were missing for the Clackamas reach), we estimated temperatures based on a linear relationship between hourly water temperature at the gage of interest and the next closest gage within the same stream. We summarized annual water temperatures as the warmest seven day average of the daily maximum water temperatures ($^{\circ}\text{C}$, 7DADM; U.S. EPA 2003) within each stream reach during the migration through spawning period. The maximum 7DADM usually occurred in late July through mid-August, when most salmon were holding near spawning grounds. We defined low flow frequency (LowQ) as the number of days during the migration through spawning period when daily discharge was among the lowest 10% of flows in each reach for the study period (2002-2015). With the exception of just a few observations, days that fell below this low flow threshold were consecutive; thus, this metric represented the duration of low flow during the season. Discharge data were missing for the lower North Santiam study reach, so this reach was omitted from initial statistical models that included LowQ. The migration through spawning period was defined as 15 April through 15 October based on typical spring Chinook Salmon run timing in the Willamette River main stem and the end of spawning in tributaries (Keefer et al. 2015; DeWeber et al. 2017).

Data analyses.—We evaluated the relationship between annual reach-specific PSM (expressed as a proportion calculated from the number of PSMs divided by the total number of carcasses found) and predictor variables using Generalized Linear Mixed models (GLMM) assuming a

binomial error structure and modeled with a logit link, implemented with the lme4 package (Bates et al. 2015) in R 3.3.2 (R Core Team 2016). Fixed effects included PHOS, 7DADM, LowQ, and all two-way interactions. There was no significant correlation between any of the fixed effects. Stream reach ($n = 7$) and study year ($n = 14$) were modeled as crossed random effects to account for the repeated measurements within each study reach and correlation within years (Bolker et al. 2009; Zuur et al. 2009). Likelihood ratio tests (LRT) were used to evaluate the contribution of the random effects in the global model (i.e., including all fixed effects), and results of these tests indicated that there was strong support for retaining both year and study reach as random effects (all LRT $P < 0.001$; Bolker et al. 2009).

Preliminary analyses showed that the PSM data were overdispersed. Investigation into the typical causes of overdispersion (e.g., missing covariates, outliers, non-linear effects) did not alleviate the problem, so an observation-level random intercept was included to address the extrabinomial variation (Browne et al. 2005; Harrison 2014). The full model took the form:

$$\begin{aligned} \log\left(\frac{P_{ijk}}{1 - P_{ijk}}\right) &= \beta_0 + \beta_1 \cdot 7DADM + \beta_2 \cdot PHOS + \beta_3 \cdot LowQ + \beta_4 \cdot PHOS \cdot 7DADM + \beta_5 \\ &\cdot PHOS \cdot LowQ + \beta_6 \cdot 7DADM \cdot LowQ + a_i + b_j + \varepsilon_k, \\ \log\left(\frac{P_{ijk}}{1 - P_{ijk}}\right) &\sim Bin(P_{ijk}, N_{ijk}); a_i \sim N(0, \sigma_i^2); b_j \sim N(0, \sigma_j^2); \varepsilon_k \sim N(0, \sigma_k^2), \end{aligned}$$

(1)

where P_{ijk} is the probability of PSM for the k th observation in year j in study reach i . The fixed effects portion of the model was reduced in a backward stepwise manner; fixed effects that did not differ significantly from zero ($\alpha = 0.01$; Zuur et al. 2009) based on Wald tests were eliminated (Bolker et al. 2009). We evaluated model fit using residual diagnostic plots and goodness-of-fit tests in the R package DHARMA (Hartig 2017). To better understand the amount of variance in the data explained by the final model, we calculated marginal and conditional R^2 values as described by Nakagawa and Schielzeth (2013).

As noted above, PSM data were collected at finer spatial scales (<1 to 18 km, 2-8 sites per reach) than covariate data within each study reach. At the finer scale, we calculated the mean and interquartile range of annual PSM rates and used boxplots to qualitatively assess within-tributary patterns.

Results

The mean Chinook Salmon PSM rate across all reaches and years was 38% (SE = 4%; $n = 84$ reach \times year estimates). Annual PSM estimates varied substantially both within and among the seven study reaches, ranging from 1% to 100%, with reach-specific means that varied from 6% to 90% (Table 1). Overall, PSM was lowest in the upper McKenzie and Clackamas reaches, which also had relatively cool water temperatures and low PHOS (Table 1; Figure 2). The highest PSM estimates were in the Middle Fork Willamette and lower North Santiam reaches, both of which had some of the highest 7DADM temperatures and generally high PHOS. The four study reaches with the highest values of 7DADM also had PHOS rates >40% (Figure 2). However, there was a considerable range of values at all sites and the two variables had a low

correlation coefficient ($r = 0.26$), allowing both to be included in statistical models. Some temporal synchrony in PSM was evident across study reaches. For example, some of the highest PSM rates occurred in 2003 and 2004, and PSM rates were lower than average for all reaches in 2006 and 2008 (Table A.1). Notably, PSM exceeded 50% at least once during the study period in five of the seven reaches and was $> 75\%$ in most years in the Middle Fork Willamette and lower North Santiam.

Initial GLMM model selection indicated that LowQ was not a significant predictor of PSM, and none of the interactions were significant. Subsequent models were therefore fit with the entire dataset, including the lower North Santiam study reach. The most parsimonious model included 7DADM temperature and PHOS, both of which were positively related to PSM (Table 2). At the mean observed PHOS value (64%), predicted PSM probabilities increased over the range of temperatures, reaching a mean predicted probability of 0.80 at 22°C 7DADM (Figure 3A). At the highest observed PHOS (97%), the mean predicted PSM probability at 22°C was 0.91; at the lowest observed PHOS (15%), predicted PSM probabilities never rose above 0.50 at any temperature (Figure 3B). Confidence intervals around predicted PSM probabilities were wide, reflecting the considerable variability in PSM at a given temperature or PHOS value, even after accounting for correlations among years and study reaches. The proportion of variance explained by the fixed effects (marginal R^2) was 0.24 and the proportion explained by both fixed and random factors (conditional R^2) was 0.41, indicating that considerable heterogeneity in PSM rates was not explained by the factors included in the final model.

At the finer spatial scale of individual sites within study reaches, we observed a systematic pattern of higher PSM at downstream sites and lower PSM at upstream sites (Figure 4). No covariate data were available at this scale, but a longitudinal pattern of PSM decreasing in an upstream direction was evident in the upper and lower North Santiam, the South Santiam, and the lower McKenzie reaches. This pattern was also apparent when comparing the upper and lower reaches of the McKenzie and North Santiam rivers.

Discussion

Effects of River Environment and PHOS

The results of this study add to the growing body of research indicating that high water temperatures contribute to mortality of adult salmon during freshwater migration and on spawning grounds (Crossin et al. 2008; Keefer et al. 2008; Hinch et al. 2012). We observed an increase in PSM with water temperature across reaches using a metric of annual maximum peak daily temperature (7DADM). High temperatures have been associated with PSM in other spring Chinook Salmon populations in the Willamette River basin (Keefer et al. 2010; Benda et al. 2015), but this is the first study to evaluate PSM across multiple populations with a range of habitats and management practices. Data from multiple study reaches allowed us to evaluate how PSM varied across temperature regimes and to develop a predictive relationship between 7DADM temperature and PSM rates.

Elevated water temperatures have been linked to PSM in populations of Fraser River Sockeye Salmon *O. nerka* (Gilhousen et al. 1990; Hinch et al. 2012), and Chinook Salmon in

Idaho (Young and Blenden 2011) and eastern Oregon (CTUIR and ODFW 2007). However, the relationship between short- and longer-term metrics of thermal regime and PSM remains an important uncertainty. Prolonged exposure (>7 days) at 21-22°C can directly result in adult salmon mortality (McCullough et al. 2001), while shorter-term exposure to temperatures above 20°C can cause physiological stress (Richter and Kolmes 2005) and changes in energy requirements for basal metabolic activity (McCullough et al. 2001). In our data, at maximum 7DADM temperatures between 18 and 20°C, there was considerable variation in PSM rates, which ranged between 16% and 100%, but above 20°C 7DADM, nearly all observations of PSM were > 80%.

Although direct mortality through temperature exposure was possible in this study, elevated water temperatures likely had indirect effects on salmon mortality, and the proximate causes of mortality remain uncertain. Cumulative stresses from elevated water temperatures, handling, transport, dam passage, and angling pressure may put fish at greater risk of premature mortality via interacting mechanisms. Elevated temperature, for example, can increase pathogen prevalence, virulence, and transmission rates (Karvonen et al. 2010). These factors increase energetic demands and may lead to prespawn mortality from energetic depletion (Rand et al. 2006; Bowerman et al. 2017). Our results indicate that in populations subject to additional stressors, PSM rates in some populations were considerable even when maximum temperatures remained below 20°C.

It is likely that elevated stream temperature was not the sole driver of PSM; rather, temperature may serve as a proxy for other habitat conditions that affect PSM, and which may be

influenced by landscape-scale factors. Our observations of lower PSM at upstream sites aligned with a general pattern of decreasing temperature with increasing elevation (e.g., Isaak and Rieman 2013), but a number of other factors may similarly vary predictably from upstream to downstream, such as land use patterns that influence water or habitat quality. In the studied Willamette River tributaries, as in many other stream systems, agricultural and urban land use tended to decrease with elevation (Hulse et al. 2004). The effect of land use on PSM is exemplified by several Coho Salmon (*O. kisutch*) studies, which found that PSM was caused by toxic urban runoff (Scholz et al. 2011; Spromberg et al. 2015), and was thus strongly correlated with the amount of impervious surface within a watershed (Feist et al. 2011). The longitudinal pattern of PSM we observed highlights the importance of protecting upstream habitat and maintaining passage to those areas where PSM rates were the lowest.

The observed spatial differences in PSM rate within tributaries may also have been influenced by demographic factors and/or individual fish characteristics. The upper and lower reaches within the McKenzie and North Santiam rivers were treated independently in our analysis because of considerable differences in habitat quality and management. However, surveyed populations in these tributaries were not fully independent because migrating adult salmon that spawned in the upper reaches were exposed to conditions in the lower reaches during migration. Mortality in lower reaches by adults attempting to return to upper reaches may have contributed to the observed longitudinal differences in PSM (e.g., exposure to higher temperatures or other stressors within the migration corridor may have led to mortality in lower reaches prior to reaching natal spawning areas). Disentangling the effect of such *en route* mortality (e.g., Keefer et al. 2017) attributed to PSM would require information on the

natal reach of individual adults and environmental conditions during migration. Additionally, there may be differences in fish attributes, such as size, condition, or energy remaining after migration, that are correlated with both prespawn survival and spawning location within a watershed. For example, salmon that arrive in spawning tributaries in better condition may swim farther upstream in search of suitable habitat. Importantly, such spatial patterns could affect estimation of the relationship between temperature and PSM, particularly if *en route* mortality is attributed to PSM in lower (warmer) reaches.

After accounting for the effect of temperature, we also found that PSM increased as the percentage of hatchery-origin spawners (PHOS) increased, a relationship that has not been thoroughly explored previously. Understanding the link between PSM and hatchery fish is of particular importance in places like the Willamette River basin, where populations are largely sustained by hatcheries, but wild fish are of high conservation value. One possible explanation for the observed correlation between PHOS and Chinook Salmon PSM is simply that hatchery fish are more susceptible to PSM than natural-origin fish. In some hatchery populations, phenotypic traits can rapidly diverge from wild genetic stock (Weber and Fausch 2003; Knudsen et al. 2006), potentially resulting in trait differences that could lead to higher mortality of hatchery fish. Hatchery salmon that return at a smaller size or after fewer years in the ocean (Knudsen et al. 2006; Williamson et al. 2010) and begin migration with less total energy or are less energy efficient (Weber and Fausch 2003), may be more susceptible to PSM than wild fish in the same system. If data on individual salmon were available (i.e., origin and fate of each fish), a similar analysis conducted at the individual scale could more directly address the issue of hatchery origin, as well as explore the effect of variations in phenotypic traits.

An alternative, or additional, possible explanation for the observed relationship between PHOS and salmon mortality is that PHOS covaries with other factors that affect PSM, such as habitat quality or conspecific density. At a large scale, reaches with lower quality habitat in this study also had the highest PHOS levels, and the observed relationship could reflect habitat quality. For example, hatchery-origin adults have been known to hold and spawn in lower areas of a watershed than many natural-origin fish (Hoffnagle et al. 2008; Williamson et al. 2010; Hughes and Murdoch 2017), where habitat is often more degraded. Use of suboptimal habitat by hatchery origin spawners may contribute to the longitudinal pattern of PSM we observed.

At a finer spatial scale, the relationship between PSM and high PHOS values may reflect the influence of unusually high fish densities. In years and locations with large hatchery returns, fish often congregate in high densities below dams, at collection facilities, or near juvenile release sites. High fish densities can increase the likelihood of disease transmission and increase stress, leading to greater energy expenditure and disease susceptibility (Ogut and Reno 2004). Additionally, in 5 of the 7 study reaches (where data were available), PHOS was strongly associated with reported harvest. High fishing pressure in locations and years with abundant hatchery returns may lead to delayed mortality via increased stress or fishing-related injuries (Baker and Schindler 2009). Future studies should aim to separate the effects of PHOS and density. As in many salmon streams, the only consistent density data available in our study reaches were in the form of redd counts. Ancillary analyses of six reaches showed that PSM was negatively correlated with redd density ($r = 0.62$), suggesting that spawner densities were higher in reaches with lower PSM. This relationship presumably reflects a predictable pattern of higher spawner densities in higher quality spawning habitat in this system. Metrics that measure

aggregations of fish, rather than spawning densities, may show a different pattern, particularly near hatchery release and adult collection locations. Insights into interactions among factors related to habitat quality, density, and hatchery origin will help manage PSM in populations comprised of both hatchery and wild spawners. Density-dependent effects may manifest in populations that currently have lower levels of PHOS if planned reintroduction efforts above several high-head dams in the Willamette Basin result in densities of natural-origin adults that are similar to or greater than what we observed in hatchery-origin fish.

We found no evidence of a link between PSM and low river discharge, consistent with results of Gilhousen (1990). Given the large volume of most Willamette Basin tributaries, low flows may not have been sufficient to lead to stranding, substantially affect fish movement to spawning habitats, or result in the types of densities that have been linked to hypoxia in small streams (Sergeant et al. 2017; Tillotson and Quinn 2017). Overall, the associations reported here imply direct and indirect effects of temperature on PSM, and multiple potential contributing mechanisms related to PHOS that should be examined in future studies. Specific research needs include the potential role of pathogen transmission in fish aggregations, and interactions among temperature, habitat, density, and pathogenesis in congregation sites, including below collection facilities.

Implications for PSM Evaluations

Even after accounting for correlations among study reaches and years with a GLMM, our final model explained only 41% of the variance in the observed PSM rates. Considerable inter-annual variability in PSM has been reported in other Pacific salmon populations (Hinch et al.

2012; Bowerman et al. 2016; DeWeber et al. 2017), so natural variability may be common. However, we suspect that some of the greater than expected variance in our dataset (resulting in overdispersion) could be addressed by accounting for variations in sampling methodology and inclusion of some of the additional predictor variables described above. Given the potential for sampling methods and unobserved factors to affect PSM estimates, we recommend that the results presented here serve as a qualitative indication of the relationship between PSM and both 7DADM temperature and PHOS.

At least four types of information could potentially be used to improve upon future data collection and analyses, the scope of inference from associations among factors, and ultimately, our understanding of mechanisms driving PSM. First, PSM rates could be influenced by additional environmental and demographic variables that were not included in this analysis, such as fish densities at specific aggregation locations, as discussed above. Habitat variables, such as availability of thermal refuges in holding areas and suitable spawning habitat, or measures of water quality (e.g, DO in high density locations; Tillotson and Quinn 2017), may also influence PSM rates and could be included as independent variables in analyses.

Second, management actions that may affect fish survival vary annually and across streams, and include both operations that alter the river environment (e.g., reservoir water releases that influence downstream water temperature), as well as fish handling and transport protocols. Analyses that include factors related to management actions could potentially improve inference from PSM studies.

Third, we did not account for individual fish characteristics in this study. Individual salmon condition and experience during migration and prespawn holding can have considerable effects on the likelihood of successful reproduction. Fish with higher gross somatic energy at the start of migration may be more likely to survive to spawn (Cooke et al. 2006b; Crossin et al. 2009), while those that are injured or infected may be less likely to do so (Baker and Schindler 2009; Keefer et al. 2010). Physiological responses (Cooke et al. 2006a; Cooke et al. 2006b; Crossin et al. 2009) and even particular gene expressions (potentially as a response to viral infection; Miller et al. 2011) differ among individual salmon and have been associated with mortality during migration and on spawning grounds. Thermal experience also varies among individuals during migration (Keefer et al. 2015) and total thermal and disease exposure likely interact to affect PSM risk (Benda et al. 2015). Studies using individually-marked fish can provide insight into how individual traits or behaviors may influence mortality.

Finally, data collection and reporting techniques can also influence PSM estimates, and standardization of these methods or inclusion of known variability in analyses could improve inference from this type of research. In carcass-based PSM evaluations, variation in sampling methods, including timing of and conditions during surveys, can influence PSM estimates (Bowerman et al. 2016; DeWeber et al. 2017). As one example, PSM rates tend to decrease throughout the spawning season in some spring Chinook Salmon populations, and surveys that begin later in the season may miss a substantial proportion of annual PSM (Bowerman et al. 2016). In the Middle Fork Willamette River and several other study reaches, carcass surveys began later than usual in 2006 (Schroeder et al. 2007), a year when PSM estimates were some of the lowest in our time series. Future studies would benefit from more standardized data

collection, improved methods for estimating PSM rates (e.g., DeWeber et al. 2017), and from including known sampling variation in analyses (e.g., accounting for carcass survey start date).

Summary

Chinook Salmon PSM is widespread and rates vary considerably among watersheds. Rates of PSM in the Willamette River Basin are higher than most other locations where PSM is regularly reported (Bowerman et al. 2016) and may be high enough to constrain recovery of these populations. The associations reported here could not be used to determine causation, although direct and indirect effects of temperature on salmon mortality are likely. The causal factors generating the association with PHOS remain more speculative. If the association between PSM and PHOS is largely an expression of fish density, independent of whether those fish are of hatchery or natural origin, then anticipated large returns of natural-origin fish from above-dam production in Willamette River tributaries may precipitate high PSM in the future. The relationships discussed here can serve as a starting point for future mechanistic research aimed at understanding the causes of PSM and devising management actions to mitigate it. Regardless of the mechanism(s) of mortality, the association with increasing river temperatures suggests that alterations affecting thermal experience, including climatic change, are likely to exacerbate existing stressors and thus increase PSM rates.

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Appendix: Detailed Data

Table A.1. Annual female prespawn mortality estimates (%) for each study reach and year. The total numbers of female carcasses examined are given in parentheses.

Year	Clackamas	Lower North Santiam	Upper North Santiam	South Santiam	Lower McKenzie	Upper McKenzie	Middle Fork Willamette
2002		78.6 (42)	55.6 (169)	19.8 (1047)	16.4 (116)	5.3 (395)	83.5 (158)
2003	21.9 (96)	99.4 (155)	64.3 (585)	28.3 (660)	52.2 (46)	16.1 (316)	100.0 (49)
2004	8.7 (149)	94.4 (36)	74.9 (251)	71.6 (557)	60.5 (43)	11.3 (301)	98.7 (76)
2005	26.4 (125)	74.3 (35)	45.7 (138)	31.6 (358)	40.0 (20)	15.8 (190)	93.5 (31)
2006	5.1 (39)		16.2 (105)	12.4 (202)	9.5 (21)	1.2 (170)	29.4 (17)
2007	4.2 (72)		40.0 (125)	8.2 (255)	37.1 (35)	5.1 (274)	95.2 (21)
2008	14.1 (85)		30.0 (20)	7.8 (51)	9.1 (55)	1.1 (91)	17.4 (23)

2009	33.3 (9)		29.8 (47)	11.2 (285)	22.1 (68)	0.7 (153)	100.0 (23)
2010	6.0 (50)	92.9 (14)	34.1 (126)	25.0 (799)	22.7 (119)	10.0 (80)	99.5 (186)
2011		97.6 (42)	26.6 (458)	14.8 (519)	27.9 (136)	4.9 (223)	60.2 (93)
2012			30.3 (89)	28.4 (345)	26.3 (285)	1.1 (95)	57.1 (21)
2013			20.5 (78)	22.3 (206)	37.5 (16)	3.1 (65)	88.7 (53)
2014			29.6 (125)	16.5 (224)	28.6 (98)	1.2 (82)	100.0 (33)
2015			64.5 (93)	12.5 (289)	38.1 (42)	4.1 (196)	98.9 (95)

Table 1. Summary of data used to evaluate female Chinook Salmon prespawn mortality (PSM) in seven Willamette River basin study reaches, showing the number of years, and the mean and range (in parentheses) of: female prespawn mortality (PSM), percentage of spawners that were of hatchery origin (PHOS), the maximum seven-day average daily maximum stream temperature (7DADM), and the number of days when daily discharge in each reach was among the lowest 10% of flows for the study period (LowQ).

Survey Reach	N _{years}	PSM (%)	PHOS (%)	7DADM (°C)	LowQ
Clackamas	8	15 (4, 33)	25 (20, 38)	16.5 (15.3, 17.4)	34 (0, 77)
Lower North Santiam	6	90 (74, 99)	82 (46, 96)	19.6 (18.5, 21.3)	
Upper North Santiam	14	40 (16, 75)	75 (43, 97)	18.4 (16.5, 20.5)	34 (0, 56)
South Santiam	14	22 (8, 72)	73 (38, 96)	13.8 (12.7, 16.8)	31 (0, 93)
Lower McKenzie	14	31 (9, 60)	77 (50, 94)	17.8 (16.0, 19.2)	25 (0, 88)
Upper McKenzie	14	6 (1, 17)	27 (15, 45)	16.2 (14.8, 17.17)	25 (0, 112)
Middle Fork Willamette	14	80 (17, 100)	81 (57, 96)	19.2 (17.4, 22.3)	13 (0, 93)

Table 2. Results of the final generalized linear mixed effects model (GLMM) to estimate the probability of annual prespawn mortality (PSM) in Willamette River basin spring Chinook Salmon populations. Coefficient estimates for the intercept, seven-day average daily maximum stream temperature (7DADM), percent hatchery origin spawners (PHOS), standard errors (SE), and *P*-values are reported for fixed effects; standard deviations (SD) are reported for random effects.

Fixed effect	Coefficient estimate	SE	<i>P</i>	Random intercept	SD
Intercept	-9.053	2.101	<0.0001	Study reach	0.969
7DADM	0.387	0.108	0.0003	Year	0.428
PHOS	0.029	0.009	0.0009	Observation-level	0.845

Figure 1. Map of the Willamette River basin, Oregon, showing study reaches (thicker stream lines), high head (●) and low head (⊙) dams adjacent to study reaches, and U.S. Geological Survey (USGS) gages (B) where discharge and water temperature were recorded. In streams with two reaches, letters denote the lower (L) and upper (U) reaches. Unless otherwise noted, USGS gages were the same for discharge and temperature in the Clackamas (discharge 14209500; temperature 14209710), lower North Santiam (14184100), upper North Santiam (14183000; temperature 2010-2015: 14183010), South Santiam (14187200), lower McKenzie (14163900), upper McKenzie (1416500), and Middle Fork of the Willamette (14152000) study reaches.

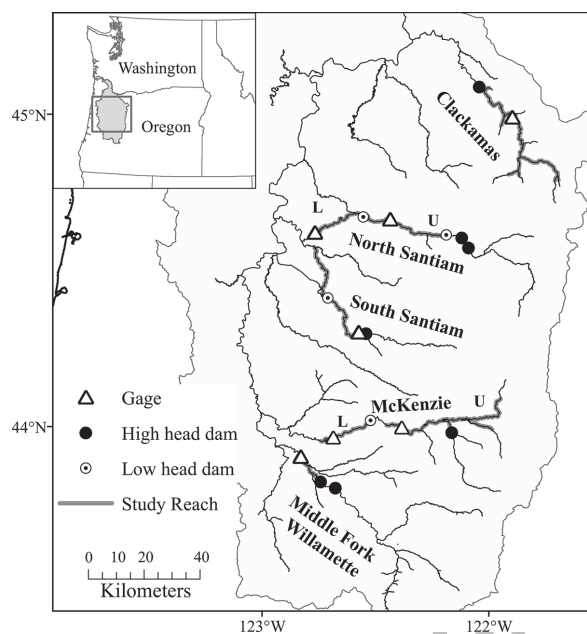


Figure 2. Mean annual estimates (location of points) of maximum seven-day average daily maximum stream temperature (7DADM) and percent hatchery origin spawners (PHOS) in the Clackamas (×), lower North Santiam (●), upper North Santiam (○), South Santiam (+), lower McKenzie (▲), upper McKenzie (▽), and Middle Fork Willamette (□) study reaches; lines depict maximum and minimum of observed values.

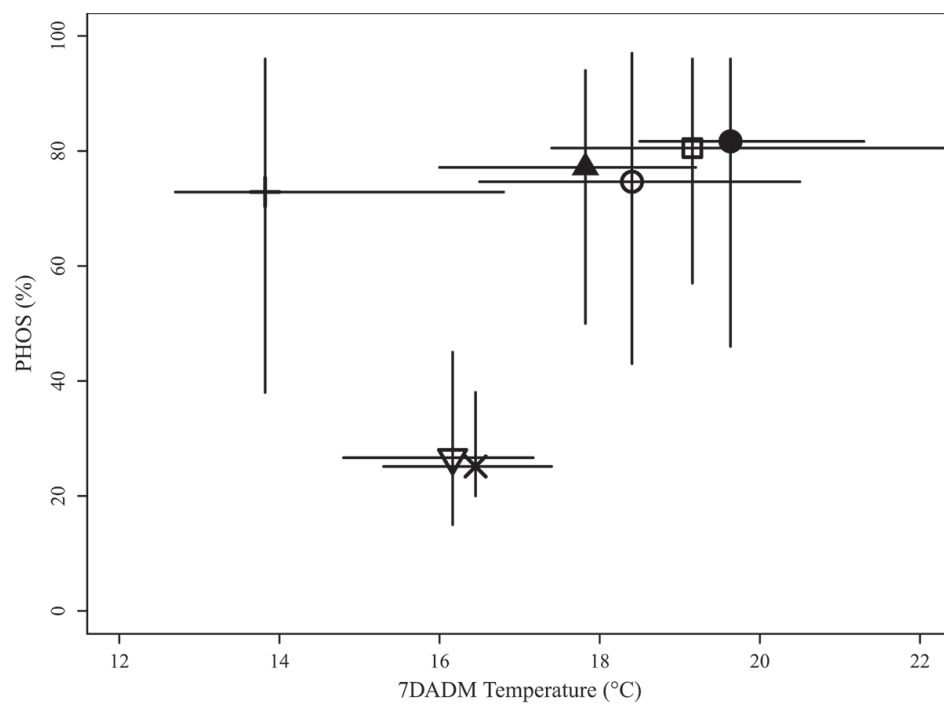


Figure 3. (A) Observed annual female prespawn mortality (PSM) rate (shown as a proportion) of spring Chinook Salmon relative to the annual maximum observed seven day average daily maximum stream temperature (7DADM) in the Clackamas (×), lower North Santiam (●), upper North Santiam (○), South Santiam (+), lower McKenzie (▲), upper McKenzie (▽), and Middle Fork Willamette (□) study reaches. Model-predicted PSM probability (black line) and 95% confidence intervals (shaded area) are shown at the (A) average observed level (64%) of percent hatchery origin spawners (PHOS), and (B) at the highest (97%) and lowest (15%) observed PHOS.

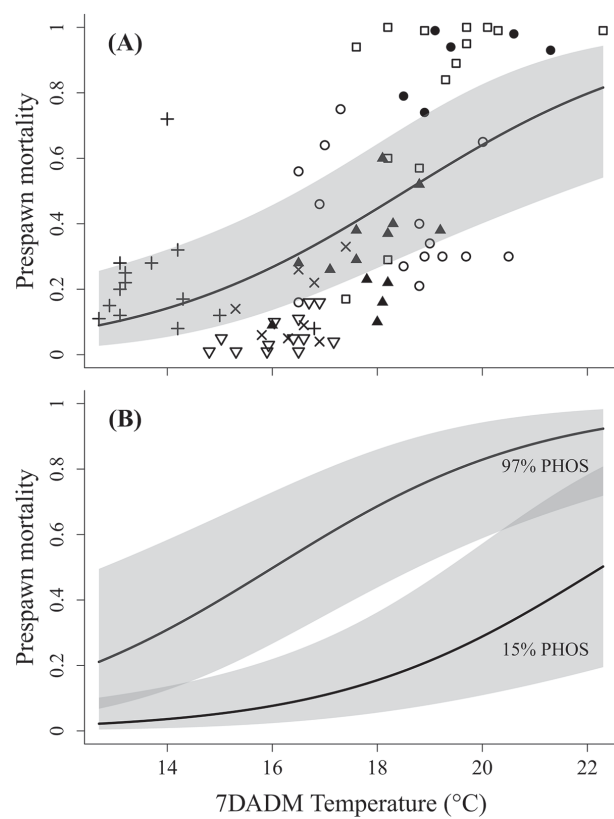


Figure 4. Observed site-specific female prespawn mortality rates (%) of spring Chinook Salmon from 2002 through 2015 ordered by approximate river kilometer from the main stem Willamette River. Solid vertical lines represent the location of high-head (>20 m hydraulic head) and dashed vertical lines indicate low-head (<20 m) dams. Boxplots show medians, quartiles, 10th and 90th percentiles, and outliers. Distances are not to scale.

