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Factors affecting the survival and development rate of upper Columbia River Chinook salmon

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Abstract

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Pacific salmonids are a highly valued resource worldwide, are invaluable to tribal traditions and livelihoods immemorial, and have been a staple of both native and non-native culture and commerce in the Pacific Northwest for nearly 200 years. Concerns regarding salmon population abundance and productivity are nearly as long-standing as their commercial harvest, identifying threats such as overfishing, dam passage, and habitat degradation. The iconic status of salmon is understandable; they are remarkable animals which rear in fresh water but then migrate hundreds or thousands of km to the ocean to feed. They then return years later, often to the location where they themselves emerged from the gravel, where they spawn, bury their eggs, and protect their nest until they die. Even in death, they provide nutrients vital to ongoing ecosystem health. Salmon possess great resilience and flexibility in life-history strategies, as is necessary to survive given unpredictable differences in habitat quality between years or locations. Due to uncertainty, salmon, and perhaps especially Chinook salmon (*Oncorhynchus tshawytscha*), have evolved to distribute risk of mortality across life-stages. For instance, Chinook salmon populations exhibit

both ocean- and stream-type life history strategies. They vary in the duration of freshwater residence, migration timing, age of maturity, return timing, and fecundity. All these traits have been studied in detail by the scientific community, which continues to untangle the complexity of life-history strategies and specific limitations to survival at each stage. Adding to the potential impacts to survival are concerns associated with climate change. Future changes in ocean temperatures may severely impact salmon survival at sea in the coming years, and current survival rates are low. Inland populations, such as Columbia River stocks have the added pressure of passing several hydropower projects as smolts, and then again as adults returning to spawn. Still earlier, survival to the smolt stage relies on the quantity and quality of rearing habitat, food availability, and low predation pressure on juveniles. However, survival in freshwater also entails the incubation stage, when most life-time mortality commonly occurs. Incubating eggs are defenseless against extreme temperatures in the late fall or mid-winter, high flow events that may scour them from the interstitial spaces between the gravel that they occupy, or to subsequent settling of fine sediment which may fill these spaces, lowering oxygen availability at critical developmental stages or entombing fry that would otherwise swim up through and emerge from the gravel. Chinook salmon generally have a higher rate of survival during this early life-stage compared to other Pacific salmonids. However, estimates suggest mortality from egg deposition to emergence to be on the order of 50 to 70 % and as such may represent the largest proportional mortality of offspring per spawning female across all life stages. Therefore, the incubation stage may provide the best opportunity for actions aimed at maintaining listed populations. In addition to surviving the months buried below the surface of the stream, it is important that the juveniles emerge at the optimal time in the spring to take advantage of hatching insects that they prey on, and avoid predatory birds and fishes. Chinook salmon are invaluable to the culture of various Pacific Northwest tribes, are perhaps the most highly valued component of sport fisheries and are essential to commercial fisheries. Therefore, understanding not only the factors that limit their survival, but also their spatial and temporal influence on specific populations is necessary to prevent the extirpation of listed populations in response to a continually and rapidly changing environments. This work directly addresses the need for greater clarity in spatial and temporal limitations to Chinook salmon and in the methods used to assess these processes. Chapter one describes field studies to improve estimates of Chinook salmon egg-to-fry survival, providing spatially explicit estimates of survival and limiting environmental factors for four upper Columbia River Chinook salmon populations, three of which are ESA listed as Endangered. The second chapter highlights variability in thermal conditions within incubation environments and management practices leading to differences in timing of juvenile emergence in the spring, which may affect subsequent growth and survival. Lastly, we highlight the need for improved estimators of the relationship between temperature and developmental rate of embryos in the absence of empirical data, to better guide life-history models, themselves necessary to identify life-stage specific environmental changes that may be made to reduce negative impacts to already threatened or endangered populations.

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This thesis almost didn't happen.

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CHAPTER 1.

Factors affecting the survival of Chinook salmon (*Oncorhynchus tshawytscha*) embryos in upper and middle Columbia River watersheds, Washington State, USA.

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1.1 ABSTRACT

Understanding the combined effects of environmental factors influencing salmon survival during incubation can aid in the prediction of survival at both local and regional scales. Between 2009 and 2021, four large-scale studies of Chinook salmon egg-to-fry survival were conducted in upper and middle Columbia River tributaries: the Entiat, Methow, Wenatchee, and Yakima River basins. Each study was conducted within known Chinook salmon spawning habitats, over multiple years, and using the same methodology. Together these studies, provided a unique opportunity to assess factors known to influence egg-to-fry survival, such as fine sediment infiltration and substrate scour, while also identifying differences in survival among rivers and study years. We detected prominent negative relationships between Chinook salmon egg-to-fry survival and both substrate scour and fine sediment accumulation across the study design. We identified district differences in survival within and among rivers, and more subtle effects of parentage in the presence of environmental factors. These average survival values, combined with the information on the magnitude and sources of variation, will greatly aid in conservation and restoration planning.

1.2 INTRODUCTION

Embryonic mortality can typically range between 50-90% for many salmonid fishes and may limit freshwater production and recovery in the case of depleted populations (Bradford 1995; Jonsson and Jonsson 2011; Quinn 2018; Smialek et al. 2021). The mortality is not observed directly, as eggs are buried below the surface of the substrate by the female prior to her death (in semelparous species), or abandonment of the nest (in iteroparous species). The mortality apparently results from a combination of density-dependent and independent processes including but not limited to direct disturbance by the digging of other females (Essington et al. 2000; Taniguchi et al. 2000; Murdoch et al. 2005), streambed scour, freezing, low dissolved oxygen, or other abiotic factors (Murray and McPhail 1988; Montgomery et al. 1996; DeVries 1997; Sear et al. 2008; Jensen et al. 2009; Quinn 2018; Smialek et al. 2021). Given the economic, cultural, and ecological value of salmon and the effects of human activities and climate change on many of these processes (NRC 1996), it is important to fully understand the interplay of factors, especially for populations at risk or under special protection.

Estimating embryonic survival of salmonids generally involves employing one of three methods: "capping", escapement estimates, or construction of artificial redds (Rubin 1995). In the first method, individual females are allowed to spawn, their fecundity is estimated from relationships with body length, the redd is "capped" (covered with a net or trap), emerging fry are counted, and survival estimated (e.g., Cederholm et al. 1982; Fast et al. 1991; reviewed by Rubin 1995; see also McMichael et al. 2005). This method works best for species spawning at low to moderate densities in shallow water, as sampling is difficult in large rivers, and disturbance by other females or species complicates analysis (Murdoch et al. 2005). Regardless, such sampling must be carefully replicated and controlled because site-specific features affect the distribution of spawning (Beechie et al. 2008) and embryo survival (Chapman 1988). In the second method, the number of salmonids spawning in a river may be estimated, and the resulting number of surviving fry estimated in the spring, allowing an estimate of survival based on population-wide fecundity estimates (e.g., Hunter 1959; Foerster 1968; Scrivener and Brownlee 1989; Essington et al. 2000). This method is most suitable for species that migrate as fry from the incubation site after emergence from the gravel, notably sockeye (*Oncorhynchus nerka*), chum (*O. keta*), and pink (*O. gorbuscha*) salmon (Quinn 2018). In most salmonids, however, juveniles emerge over a protracted period and feed at or near the site of emergence for months or years. Mortality of early emerging fry is occurring in the stream while those spawned later have yet to emerge, so it is difficult to accurately estimate survival in the embryonic stage. Indeed, for anadromous species, egg to smolt mortality (combined freshwater mortality) is often the primary metric reported (reviewed by Bradford 1995; Quinn 2018). This combined estimate does not allow partitioning into the very different embryonic and free-swimming stages, and stage-specific information may be needed for conservation and restoration planning purposes. As a third approach, fertilized eggs or embryos may be deposited in artificial redds or containers, and the estimated number of emerging fry related to physical variables in laboratory or natural settings (e.g., Reiser and White 1988; Franssen et al. 2012; Johnson et al. 2012). This third approach has the obvious limitation of assuming that artificial redds reliably represent naturally constructed ones, with respect to the environmental factors commonly influencing survival (see Rubin 1995; Johnson et al. 2012). However, this methodology has the advantages of increased replication and often a direct measure of some environmental factors that may influence survival (e.g., in-situ substrate scour and fine sediment infiltration). Historically, studies of this type have generally been conducted over relatively small spatial and temporal scales rather than the broader scales needed to inform salmon recovery efforts (Roni et al. 2016).

In addition to the importance of obtaining comparable and accurate empirical estimates of survival, it is also important to identify the factors which may limit population productivity. The scientific literature has documented the complex effects of environmental factors such as temperature (Heming 1982; Murray and McPhail 1988; Whitney et al. 2013), fine sediment infiltration (Chapman 1988; Reiser 1998; Greig et al. 2005), and mechanical shock on embryo survival. In the latter, gravel bed disturbance reduces survival of embryos and alevins (DeVries 1997, 2008), in part due to the sensitivity of embryos to mechanical shock (Jensen and Alderdice 1989; Johnson et al. 1989). Moreover, gravel scour during floods and subsequent deposition of fine sediment can affect the egg pocket (Montgomery et al. 1996; Peterson and Quinn 1996a; DeVries 1997). In addition to these deterministic environmental factors affecting embryo survival, survival also varies among families owing to genetic and maternal effects (Young et al. 1990; Rubin 1995; Heath 1999; Evans 2010). Failure to consider these effects can weaken study designs if embryos from different parents are used in different treatments (Johnson et al. 2012; Roni et al. 2016).

Understanding the environmental factors affecting embryo survival indicates the relative quality of incubation habitats and informs estimates of subsequent productivity. Such information is especially pressing for Chinook salmon (*O. tshawytscha*). This species achieves the largest body size of the Pacific salmon, typically spawns in larger rivers, in deeper and faster water, and constructs redds that are both larger and deeper than those of smaller-bodied salmonids (Quinn 2018). For example, redd area for this species can approach or exceed 20 m^2 in larger rivers (Chapman et al. 1986; Hughes and Murdoch 2017). This makes studying Chinook survival in the field more difficult than for smaller bodied salmon species. Many Evolutionarily Significant Units (ESUs) of Chinook salmon are listed in the United States under the Endangered Species Act (ESA); thus, the species for which information on embryo survival is most pressing is also the species for which it is most difficult to obtain.

Our study goals were first to document the range and average of Chinook salmon egg-to-fry survival across upper and middle Columbia River watersheds and over multiple years. Second, we wished to identify the factors most influential to embryo survival across our study area. Specifically, we directly measured in-situ egg-to-fry survival at 130 spawning sites at 12 rivers in four large sub-basins of the upper and middle Columbia River basin. We tested the hypothesis that survival of embryos would be negatively associated with greater proportions of accumulated fine sediment and higher rates of substrate scour. We then assessed these variables in combination with temperature accumulation, the duration of incubation, substrate size and embeddedness, and river (categorically) in their ability to predict Chinook salmon egg-to-fry survival. Our hypotheses were tested in a study design that explicitly considered inter-annual and inter-site variation in environmental conditions, and possible parental influences. Together our study objectives are intended to extend and advance the goals of providing useful information and data to guide salmon recovery, reintroduction, habitat restoration and life-cycle modeling efforts in the form of empirical estimates of egg-to-fry survival across basins and in multiple years, as proposed as necessary by Roni et al. (2016).

1.3 METHODS

We measured egg-to-fry survival and collected associated environmental data in the Methow, Entiat, Wenatchee, and Yakima river basins in Washington State, USA from 2009 to 2022. In total, the study area represents 380 river kilometers (rkm) of Chinook salmon spawning habitat in the middle and upper Columbia River system. Our study focused on spring Chinook salmon populations, i.e., those returning in the spring of the year, but spawning in the late summer and early fall. Our overall approach was as follows: We selected study sites representing the spatial range of spawning in each river system, fertilized eggs on-site, placed them in egg boxes, and buried them in areas routinely used by naturally spawning Chinook salmon at each study location. We measured substrate scour, fine sediment infiltration, substrate size and embeddedness, and temperature accumulation through the period of incubation at each site, and integrated parentage (i.e., sire and dam) into the study design. Below we provide a brief overview of the field methods but refer to Johnson et al. (2012) for details on the methodology.

Acknowledgement of data use

A portion of the data used in this study, collected in the Yakima River basin in years 2009 to 2012, has been previously published with respect to the methodology, and in assessing interannual variability in factors affecting Chinook salmon egg-to-fry survival (Johnson et al. 2012; Roni et al. 2016).

Study area and site selection

Study basins together drain approximately 13,515 km^2 of the upper and middle Columbia River basin. The Methow River basin lies in the northernmost portion of the upper Columbia River basin, draining an area of approximately 4730 km^2 (NPCC 2005) in north-central

Washington State (Figure 1.1). In this basin, the Methow River receives approximately 54% of the returning adult Chinook salmon, the Chewuch River 26%, and the Twisp River 20%, averaging just under 650 redds annually (Snow et al. 2019). The Entiat River, situated just south along the Columbia River, drains an area of 1,210 km^2 (NPCC 2005), and averages 156 spring Chinook salmon redds annually within survey sections comprising the majority of available Entiat river spawning habitat (Fraser et al. 2018). Moving south, the Wenatchee River Basin drains an area of approximately 3,450 km^2 and has about 635 spring Chinook salmon redds each year. Spawning is primarily in the Chiwawa River (69%), but also in Nason Creek (15%), and the White (7%), Wenatchee (5%), and Little Wenatchee (4%) rivers (three-year average, WDFW unpublished data). Farthest south, the upper Yakima River basin drains approximately 5,537 km^2 (USGS 2019). Approximately 1016 spring Chinook salmon spawn in the upper Yakima River basin annually, primarily in the Yakima River (84%), and to a lesser extent in its two primary tributaries, the Cle Elum River (12%) and the Teanaway River (4%); (Yakima–Klickitat Fisheries Project [YKFP] redd counts 2010–2020, unpublished data).

The Chinook salmon spawning range was first determined throughout each of the river systems by reviewing GPS locations of naturally constructed redds observed during spawning surveys conducted in previous years (A. H. Dittman, NOAA, M. S. Hughes, WDFW, G. S. Fraser, USFWS; unpublished data). Study sites were then established at intervals of approximately 2 rkm within the spawning range in each river. With some small exceptions, (see analysis below) study sites were established in areas where spawning surveys indicated the greatest probability of use by Chinook salmon over multiple years, and in areas that could be accessed for stocking live eggs and subsequent sampling.

Artificial redds and gamete collection

Egg boxes were installed over a 3-d period for each weekly stocking event. Artificial redds were constructed on the first day, eggs and milt collected on the second day, and fertilization and stocking was completed on the third. This progression allowed all sites to be stocked on the same day, given the number of replicates at each site and travel distance among sites. Artificial redds were dug by shovel to 30 cm, an estimate of average Chinook salmon egg pocket depth, following review of Healey (1991) and DeVries (1997). A covered bottomless bucket was then inserted to prevent backfilling until fertilized eggs could be stocked. Temperature loggers were deployed in the water column at each site near the redds.

Eggs and milt were collected the following day from one of four hatcheries specific to each population: the Cle Elum Supplementation and Research Facility (Yakima River Basin), Eastbank Fish Hatchery (Wenatchee River Basin), and the Methow or Winthrop National Fish Hatcheries (Methow and Entiat River Basins). Eggs from a given female were divided into lots of 100, and milt into quantities of approximately 0.3 ml (sufficient to fully fertilize the eggs). Average egg mass was estimated from a separate sample of 100-200 eggs from each female. Egg lots and milt were placed in oxygenated air-tight bags, held overnight in an ice-filled cooler, and transported to study sites the next morning. We used modified Whitlock-Vibert egg boxes (see Johnson et al. 2012) to retain post-hatch alevins and allow an estimate of fine sediment infiltration during incubation (Wesche et al. 1989; Garrett and Bennett 1996). Eggs were fertilized on-site and introduced to the egg box (submerged in a small tote) containing washed gravels from the location of the artificial redd. The egg box, still submerged, was then transported to the pre-constructed redd, and transferred to the egg pocket. The egg box was held at the bottom of the egg pocket while the previously excavated and cleaned gravels were backfilled to the top of the bucket. The bucket was then removed, and the area then excavated or backfilled as necessary to resemble the pit and tail-spill of a naturally constructed redd. Unique sire-dam matings were represented equally across each river during each weekly spawning event. That is, eggs from each female were fertilized with milt from only one male, and the resulting embryos placed in egg boxes at each of the study sites. In cases where the number of replicates exceeded the number of eggs available for a given female, egg boxes with a given mating were distributed equally throughout the study (e.g., a specific mating in every third site).

Egg boxes were recovered after 900 - 1000 accumulated thermal units (ATU), a sum of daily mean water temperatures experienced since deployment (Alderdice and Velsen 1978; McMichael et al. 2005; Geist et al. 2006), when median emergence from the gravel was projected. Egg boxes were carefully excavated and placed in a high-sided tote while still submerged, to prevent the loss of accumulated fine sediment. Sediment was retained for later processing (described below). Fry counts made in the field were later verified in the lab. Further details on the methodology were provided in Johnson et al. (2012).

Upper Columbia River collections of ESA listed Chinook salmon fry for this study were approved by the National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS), under Scientific Research Permit 16979 issued to the Washington Department of Fish and Wildlife (WDFW) under the authority of Section 10(a)(1)(A) of the Endangered Species Act. Collection of Yakima River Chinook salmon fry was permitted under research and monitoring activities described in Section 1.2.4 of the National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS) biological opinion under Endangered Species Act (ESA) Section 7(a)(2). Permissions for in-river excavation were obtained through WDFW’s Hydraulic Project Approval Process (RCW

77.55.021). All work met the requirements of the University of Washington (UW) Animal Use Laws and Regulations, and the UW Institutional Animal Care and Use Committee (IACUC).

Habitat Metrics

Wolman (1954) pebble counts characterized the surface gravel size distribution at each site; metrics consisting of median particle size (D_{50}), and the sizes at which 84% and 16% of the particles were smaller (D_{84}) and (D_{16}), respectively (Kondolf et al. 2008). Substrate embeddedness was quantified as a binary measure during pebble counts; embedded particles could not be readily lifted from the surrounding substrate (Chadd 2007). To estimate fine sediment infiltration, the sediment accumulated in the egg boxes was collected, dried, sieved into 13 size categories from 0 to 6.30 cm, and then weighed to the nearest 0.01 g. The metric of "percent fines" was calculated as the percent of the sample by weight ≤ 2 mm in diameter (Lisle 1989; Fudge et al. 2008). We assumed that the proportion of fines lost during the excavation process was minimal based on previous work (Johnson et al. 2012) and was further reduced here because the high-sided tote retained fines from the egg box.

Scour chains approximating the design of Nawa and Frissell (1993) were installed at each artificial redd location to detect bed load movement, and evidence of likely displacement if the egg box could not be found. Scour chains were placed approximately 0.5 m behind each egg pocket prior to egg box placement and driven into the substrate until flush with the streambed. As scour occurred, beads were exposed to the current and moved to the end of the cable. Scour depth was then calculated by multiplying the bead diameter by the number of exposed beads at the time of recovery.

Analysis

The dataset was arranged such that each egg box was paired with all available variables. Some of the 1,148 replicates were missing values from one or more variables due to either differences in data collection protocol (e.g., a single measure of scour for multiple replicates), or environmental conditions (e.g., percent fines could not be measured for egg boxes lost to scour). Together, the explanatory variables were represented as follows: scour depth: 77% of replicates, fine sediment: 91.2% of replicates, substrate size and embeddedness: 86% of replicates. To maximize the number of replicates available for analysis we used data imputation techniques (McElreath 2020) to estimate variables where field values were missing while also incorporating uncertainty around each estimated value given the data.

Statistical models

We used a Bayesian framework to estimate egg-to-fry survival and associated measures of uncertainty by developing a unique multilevel causal model for each predictive variable. To minimize the potential for confounds (Pearl and Mackenzie 2018; McElreath 2020), we developed a causal diagram using the *dagitty* package (Textor 2016) in R (Figure 1.2). We made the simplifying assumption that effects on survival through oxygen availability were attributable to fine sediment accumulation and temperature because flow rates mediate oxygen delivery (Silver et al. 1963; Greig et al. 2007). Hypoxic ground water can also adversely affect survival (Greig et al. 2007; Malcolm et al 2012) but such influences were beyond the scope of our study.

We investigated direct causal relationships between survival and predictive variables: scour depth, parentage, and egg weight; and total effects (those inclusive of mediating variables) between survival and predictive variables: percent fines and the number of incubation days. We interpreted coefficient estimates with posterior probability mass (i.e., the probability distribution of the coefficient estimate considering both our prior and the data) entirely above or below zero on the log odds scale as an indicator of relation between variables listed above and embryo survival.

Graphical relationships between continuous variables and survival were presented on the odds scale where the expected change in the odds of survival for a given unit of measure is defined by the odds ratio (e^{x}), where x is the variable's coefficient value. When the desired units for graphing differed from those passed to the model (e.g., a proportion vs. a percentage) the odds ratio was scaled by raising it to the n power, where n represents the desired number of units over which to calculate the change in odds (e^{xn}) (see Katz 2011).

We developed single intercept multilevel models to compare out-of-sample prediction (i.e. the model's ability to predict the outcome variable using new data). Due to model flexibility when also generating imputed data values, we chose K-fold cross-validation (K = 10) for model comparison, using the loo package in R (Vehtari et al. 2022). All comparisons were made among models fit over the same data, and with the same K-fold data subsets, except for models using substrate size or embeddedness as predictive variables. Due to missing substrate size and embeddedness variables within the Chiwawa River data, a separate group of model comparisons were conducted over the subset of data within which those variables were present (n = 965). We compared selected models from our initial cross-validation, refit to the available data, to models using substrate size metrics and embeddedness as predictive variables using the same data, and with the same K-fold data subsets. We considered a quotient of elpd_diff by se_diff > 2, and a confidence interval exclusive of zero, as evidence supporting a difference expected predictive ability between candidate models.

Models were generated with Markov chain Monte Carlo techniques using the probabilistic programming language Stan (Stan Development Team 2021). Model scripts were written using CmdStanR or Rstan packages in R (Gabry and Cešnovar 2022; Stan Development Team 2023). We used a non-centered model parameterization to optimize convergence issues common to multilevel model structures (McElreath 2020).

General model structure:

$$S_i \sim Binomial(N, p_i)$$

$$logit(p_i) = \overline{\alpha} + \mathrm{Z}_{eggbox[i]}\sigma_\alpha + \gamma_{Var_1[i]}\sigma_\gamma + \beta_{Var_2 \ldots [i]}$$

$$(\gamma, \beta) \sim Normal(0,1)$$

$$\overline{\alpha} \sim Normal(0,1)$$

$$\left(\sigma_\alpha, \sigma_\beta\right) \sim Exponential(1)$$

All models were fit with 2000 warm-up and 5000 sampling iterations for each of four chains. Chain convergence was checked visually using trace plots generated in the bayesplot R package (Gabry and Mahr 2022), and through inspection of $\hat{R}$ and effective sample size metrics for each model parameter (< 1.05, and greater than 100/chain respectively). Overall diagnostics included checks for divergent transitions, saturated max treedepth, and low BFMI values).

1.4 RESULTS

Survival by river, site, and year

Egg-to-fry survival averaged 53.5% across rivers and study years (SD: 22.0, range 0 - 87%; Table 1.1). Average survival among rivers ranged between 30.5% (SD: 32.5) in the White River and 82.5% (SD: 21.2) in the Entiat River (Table 1.1). Coefficient estimates indicated lower than average survival in Nason Creek, the main-stem Wenatchee, the Teanaway, and White rivers, and greater than average survival in the Twisp and Cle Elum rivers (Figure 1.3). Site-scale differences in survival were apparent in 21 (16%) of our 130 study sites (Figure 1.4). Mean survival across years within study sites averaged 58.2% (SD: 20.9, range 0 – 93.8). Year coefficients indicated lower than average survival in brood years 2010, 2014, and 2015, and higher than average survival in brood years 2009, 2020, and 2021 (Figure 1.5).

Causal models and group contrasts

Our model indicated a direct negative relationship between scour depth and survival (coefficient: -1.65, q05: -1.91, q95: -1.40), suggesting (on average) a 16.8% decrease in the odds of Chinook salmon survival for every 1-cm increase in substrate scour (Figure 1.6). We also detected a relationship between accumulated fines and survival (coefficient: -1.02, q05: -1.17. q95: -0.86), indicating a 1.0% decrease in the odds of Chinook salmon egg-to-fry survival with each one-unit change in the percentage of fines accumulated throughout the incubation period (e.g., 10% to 11%; Figure 1.7). The proportion of fine sediment at recovery was positively correlated with the depth of scour (correlation coefficient: 0.49, q05: 0.42, q95: 0.56). Coefficient estimates for 8 of the 103 (7.8%) unique matings were above or below zero on the log odds scale. However, all were within the range of coefficient estimates of the total sample (Figure 1.8), indicating at most a weak direct effect of parentage on survival across the design. We did not detect a direct relationship between egg weight (coefficient: 0.03, q05: -0.21, q95:0.27) or the number of incubation days (coefficient: 0.01, q05: -0.16 q95: 0.18) and survival.

Predictive models

K-fold comparisons of 13 fitted models, suggest that a model including the river and percentage of fine sediment was the most parsimonious, and all the top rank models included both variables. Scour depth, temperature accumulation, and incubation period duration were influential when river was not included as a variable. Lastly, knowing even one variable (e.g., river, fines, scour) substantially improved the survival prediction over an intercept-only model (Table 2). We found marginal improvement in the prediction of survival when median substrate size and/or percent embeddedness were included as predictive variables (in addition to river, scour depth, and the percentage of fine sediment) but less evidence of improvement when river was not included (Table 3). Neither d_{16} nor d_{84} improved predictions of survival in the same context.

1.5 DISCUSSION

Our study goals were to 1) document the range of spring Chinook salmon egg-to-fry survival across upper and middle Columbia River watersheds, 2) investigate potential relationships between survival and fine sediment accumulation, scour depth, and other environmental factors in estimating survival, and 3) assess parental effects on survival across the study design. Overall, survival differed among study sites, river systems, and years, tending to be the highest in locations where scour depth and fine sediment infiltration were low and less variable across years (Table 1.1; Figures 1.3 and 1.5). Our results indicated that Chinook salmon survival decreased with greater depth of scour (Figure 1.6) and greater percent of fine sediment infiltration (Figure 1.7). Those two environmental variables, combined with river, temperature accumulation, the duration of incubation, substrate size and embeddedness improved predictive models of survival (Tables 2 and 3). Lastly, parentage (Figure 1.8) and egg size had little or no influence on estimates of survival within our study design.

Our results indicate that mean egg-to-fry survival across our design is consistent with the range of values published in other studies and reviews specific to Chinook salmon (Fast et al. 1991, Healey 1991, Roni et al. 2016; Quinn 2018), averaging 53.5% across rivers and years (Table 1.1). However, egg-to-fry survival differed substantially among rivers and study sites (Table 1.1, Figures 1.3 and 1.5). Further, within sites, standard deviations ranged from 0 - 49.6% (mean: 26.8%), suggesting high variability in the quality of spawning habitats at our study locations, even though Chinook salmon have been repeatedly recorded spawning there. Observed variability was largely explained by the magnitude of scour and fine sediment infiltration over the period of incubation, environmental metrics that varied at multiple scales across our study

(Table 1.1). Our results both identified and quantified causal relationships between Chinook survival and both scour depth and fine sediment infiltration, and did so at a river-basin scale.

Scour depth had the largest per-unit effect size on egg-to-fry survival in general (Figure 1.6). The effects of scour depth on salmonid survival are perhaps most often associated with egg displacement (Montgomery et al. 1996; DeVries 1997), although few studies empirically quantified mortality from scour (Malcom et al. 2012). Interestingly, given the effect size, scour depth averaged only 4 cm, or 14% of egg pocket depth across our study design. This suggests that scour had a large effect on survival even at depths less than that of the egg pocket. Apart from the physically dislodging eggs from the nest, bed load movement (i.e., scour) can affect redd morphology (DeVries 2002), altering the flow dynamics of the incubation environment in ways that may reduce survival of incubating embryos, such as an increase in fines (Lisle 1989) or excessive interstitial flow (Brannon 1965; Deverall et al. 1993). We observed a moderate positive correlation between scour depth and fine sediment infiltration; thus, even moderate levels of scour may decrease the overall quality of the incubation habitat. These results are consistent with those of Holtby and Healey (1986) who reported altered gravel quality after floods, and decreased coho salmon embryo survival (see also Quinn 2018). Additionally, shallowing of egg pocket depth relative to the surface from moderate scour events may also increase the susceptibility of incubating eggs to other factors, such as invertebrate predation. Aquatic invertebrates have been documented in association with egg box studies (Johnson et al. 2012; Roni et al. 2016; Stark et al. 2018), and direct predation on salmonid eggs has been observed in laboratory settings (Claire and Phillips 1968; Brown and Diamond 1984). However, it is difficult to distinguish predation from scavenging, and predation may be infrequent in natural environments (Ellis 1970; Brown and Diamond 1984).

We observed comparatively high rates of scour depth (> 9.3 cm) in three of the four rivers where survival rates were also low (Table 1.1): Nason Creek, the Teanaway River, and the White River. Further, all but three of the rivers we studied: the Chiwawa, Cle Elum and Methow rivers, experienced some degree of egg box loss, and the proportion of egg boxes lost to scour events ranged between 3% and 70% of within-river replicates in a given year.

Of the 1,148 egg boxes, 94 (8.2%) were lost to substrate scour attributable to flow-related scour or redd superimposition. Although our study design and methodology were not explicitly intended to distinguish between losses from these two processes (see Johnson et al. 2012), observations while monitoring study sites provide some information on the specific mechanism leading to scour-related mortality. Egg boxes lost to scour (excluding those that may have been removed by fishermen etc.) were categorized as related to flow or superimposition, inferred from fish actively digging or spawning on the egg box’s location, obvious evidence of recent digging, or an area that had been excavated en masse (as with spawning sockeye salmon). From these data, we estimate that 6.8% of all replicates were lost to flow-related events, primarily in Nason Creek, and the Teanaway and Little Wenatchee rivers (Table 1.1). The remaining 1.4% of the replicates were likely lost to redd superimposition from later spawning summer Chinook or sockeye salmon. Evidence of superimposition was most prevalent in the White, Little Wenatchee, and main-stem Wenatchee rivers, where the maximum percentage of estimated annual losses were 17.4%, 16.7%, and 11.1% respectively.

In addition to high relative scour rates, many of the low survival sites also had more fine sediment infiltration (Table 1.1). Although accumulation of fines can adversely affect salmonid incubation survival (Chapman 1988; Reiser 1998; Greig et al. 2005), the degree to which embryos are affected varies by species (Jensen et al. 2009), and the influence of fine sediment on

Chinook salmon egg-to-fry survival in natural environments remains unclear, as field studies specifically relating fine sediment accumulation to Chinook salmon survival are scarce. Roni et al. (2016) found that accumulated fines < 2 mm (the same definition we used), explained little of the variation in estimated egg-to-fry survival. The authors noted that fine sediment rarely exceeded 20%, a level lower than the 25-30% most generally associated with high mortality in spring Chinook salmon embryos (Chapman 1988; Jensen et al. 2009). In contrast, using data from three additional watersheds, we found levels of fine sediment greater than 25% in approximately 13% of the egg boxes recovered. The higher frequency of fine sediment may be attributable to differences in annual flow conditions. In contrast to most of the Yakima River basin, river flows the Wenatchee, Entiat, and Methow basins are unregulated, and those areas likely have higher rates of sediment transport, corresponding with more variable flow conditions throughout the incubation period (Sear 1993). However, despite the greater frequency of replicates with comparatively higher percentages of fine sediment accumulation, our analysis suggested a notable, but more subtle influence of fines on Chinook salmon survival compared to that reported in other studies (see Jensen et al. 2009). We surmise that the combined effects of generally low levels of fines in most of our replicates (Table 1.1), the duration of incubation, and incubation temperatures conducive to oxygen supply tended to offset otherwise critical levels of fine sediment infiltration. Lastly, substrate size and composition, apart from fines, also influence alevin survival (Tappel and Bjornn 1983; Kondolf 2000). Our study provides measures of alevin survival over a wide range of existing spring Chinook salmon spawning habitats, with variable substrate composition (Table 1.1). Thus, the effect of fine sediment on survival might also be moderated by location-specific differences in larger gravel sizes.

Generally, we found that (together) variables describing fine sediment infiltration and scour best predict Chinook salmon survival, with knowledge of the specific river system improving any of the models we compared. Consistent with the previous findings of Roni et al. (2016), scour depth alone contributed little to the prediction of egg-to-fry survival in comparison to other variables and more complex models (Table 2). Despite the effect size of scour depth on survival when scour is present, most instances of scour throughout our study were to depths representing only a small proportion of the egg burial depth. We suspect that limited predictive ability of scour alone is reflective of our full dataset; although we note that substrate scour did sizably affect survival in some study areas and years.

Improved prediction of survival when the river system is a categorical predictive variable suggests the presence of moderately influential variables apart from those directly measured in this study. There are multiple factors known to potentially influence egg-to-fry survival, but that were outside the scope of our study. Examples of these include surface/ground water exchange (Peterson and Quinn 1996b; Malcolm et al. 2005, 2012), redd morphology (Hughes and Murdoch 2017), and temperature tolerance (Murray and McPhail 1988). The influence of these factors would be consistent with increases in predictive ability when including days of incubation, temperature accumulation, D_{50} (median substate size), or substrate embeddedness to the model structure (tables 2 and 3). Although we note that improvements to prediction with the addition of these variables were small.

Parentage appears to have the potential to sizably influence egg-to-fry survival in natural environments over the period of incubation, as indicated by our analysis, and consistent with our own and other previous studies (Johnson et al. 2012; Roni et al. 2016; Thorn and Morbey 2019). However, our model suggests that, given our data, the overall effect among matings is quite low, perhaps at a level one would expect in a normally distributed population (Figure 1.5). It is worth noting that our study design incorporated only a few distinct matings across the spawning range in each basin and year. Further, it was not possible to replicate matings across basins or years. Thus, it's possible that differences in reproductive success attributable to parental traits may be under-represented in our study design when compared to those among individuals within the population. However, our full sample consists of 104 individual matings, each observed over numerous spawning habitats of varying quality. Therefore, we suspect that, generally, parental effects expressed during incubation are small relative to the influence of environmental effects, perhaps with the exception of systems with low relative environmental variability (see Roni et al. 2016). The same might be true for egg size. Although egg size has been shown to influence survival in natural environments (Thorn and Morbey 2019), such effects were not apparent across our design. Fines sediment infiltration across the study was generally moderate in comparison to the observed range, averaging 13.7 percent (Figure 1.7), and thus may have limited exposure to conditions in which egg size may have been influential to survival (i.e. conditions in which oxygen delivery was limited.). Further, as with parental effects in general, egg size in our study may have been less variable than that of the population, thus minimizing our ability to detect existing effects. However, we note that Chinook salmon egg mass in our study ranged between 0.14 g and 0.34 g (mean: 0.21, sd: 0.03), values very similar to those reported by Thorn and Morbey (2019), who found relationships between Chinook egg mass and in situ survival in two of three river systems they studied.

Chinook salmon are often reported as having higher incubation survival than other Pacific salmonids (Healey 1991; Quinn 2018; Roni et al. 2016). Chinook are the largest of the Pacific salmonids (Quinn 2018) and can therefore select spawning habitats across a wide range of stream depths and flow conditions (Geist 1999). Their larger size allows them to construct redds in courser gravels, deeper water, and in higher velocity flows (Groves and Chandler 1999; Beechie 2008), perhaps resulting in greater relative interstitial flow (Sear et al. 2014) and a lower probability of scour related mortality (Montgomery 1996; see also DeVries 1997). Chinook also spawn under relatively low densities (especially true for listed populations), perhaps reducing the probability of density-dependent mortality (Bradford 1995). Lastly, Chinook salmon have larger eggs than other species of Pacific salmonids, which (notwithstanding the results of this study) can provide survival advantages during incubation (Einum and Fleming 2000; Thorn and Morbey 2019).

Our results confirm previous mean values of survival and extend these estimates to multiple upper Columbia River Chinook populations; but they also reveal a significant level of variation in egg-to-fry survival within and among spawning sites, and among river systems (Figures 1.3 and 1.4). The variation in survival among river systems alone, suggests that basin specific measurements of egg-to-fry survival are necessary for management purposes. Such variation also highlights the complexity and dynamic nature of habitat quality, perhaps even when spawning locations are clustered, as most of our replicates were within a few meters of one another. We calculated the maximum difference in both percent fine sediment accumulation and scour depth among replicates at each of our study sites (within a given study year) to better understand the possible range of values we would expect to encounter at the site scale. We observed an average within-site difference in fine sediment infiltration of 6% (SD: 12%), but ranging as high as 52%. Scour also varied substantially within-site, with a 5.1 cm difference on average among artificial redds (SD: 6.2 cm; 16% of the egg pocket depth), ranging has high as 30 cm. These values and the corresponding survival estimates underscore environmental variation that is apparently present at even small spatial scales within sites of known spawning activity and highlights the need to incorporate within-site variation when estimating incubation survival within a Chinook salmon spawning population. To our knowledge, our study is the first to document the variability in Chinook salmon egg-to-fry survival among (ESA listed) populations and at a spatial and temporal scale believed necessary to adequately inform salmon recovery efforts (see Roni et al. 2016).

Because all rivers were not sampled in all years, we cannot fully account for inter-annual effects among basins. However, variation in environmental conditions and especially ones linked to flows probably contributed to lower overall survival in brood years 2014 and 2015 (Figure 1.5). Interannual variation was well documented by Roni et al. (2016), where flow events were suggested as potential drivers of inter-annual variation in the magnitude of scour and fine sediment infiltration. Our results also appear to reflect these and similar influence in years 2014 and 2015 (Figure 1.5). Such year effects are likely driven by larger scale factors affecting the entire system, such as annual snowpack, rain-on-snow events, and ambient temperatures which govern snowmelt and subsequent river flows (Honea et al. 2016). Although the population specific outcomes related such changes are uncertain, research suggests that warming temperatures in snowmelt dominated streams, such as those in our study area, may reduce salmonid incubation survival from an increase in oxygen demand during incubation (Goode et al. 2013), or directly affect alevin development and emergence timing (Steel et al. 2012). Additionally, higher spring temperatures may increase the probability of flood events, increasing mortality attributable to scour and fine sediment transport (Leith and Whitfield 1998; Goode et al. 2013; Wobus et al. 2015; Crozier and Ziegel 2023). Our modeling suggests lower relative survival in approximately 9% of our study sites, translating to lower comparative survival in roughly 30% of the river systems we studied. Environmental factors negatively affecting survival included high fines, flow-related scour, dewatering, evidence of exceeded temperature thresholds, and redd superimposition. We would expect an increase in the influence of each of these environmental variables as the systems experience warming trends, likely resulting in a decrease in overall survival for these already ESA listed populations.

Our study provided estimates of survival across a range of habitats selected by returning Chinook salmon, within populations that are ESA listed, and for which productivity is a concern, and documented the extent to which factors influencing survival are present across spawning ranges at multiple spatial scales and among years. We provide new relationships linking Chinook salmon egg-to-fry survival to causal effects of substrate scour and fine sediment accumulation in the natural environment and assess the influence of parental effects and egg size across our study design. Lastly, we provided a ranking of environmental variables with respect to their predictive ability in estimating Chinook salmon egg-to-fry survival. Our findings suggest that incubation survival of upper Columbia River Chinook salmon depends largely on the presence of scour and fine sediment infiltration, and that these factors can vary substantially among spawning habitats. Our results highlight the need to examine and account for site-scale environmental variability when evaluating Chinook salmon egg-to-fry survival. Additionally, our results demonstrate that salmon egg-to-fry survival can vary widely among populations or basins and thus population or basin-specific egg-to-survival measurements are likely warranted for life cycle modeling, salmon recovery, and restoration planning.

1.6 TABLES

Table 1.1 Mean values of predictive variables: scour depth, percent fines, days of incubation, substrate particle size (16th, 50th, and 84th percentiles) and the percent of embedded substrate (%EB), by river basin, river, and study year.

River	Year	n	%Surv	Scour cm	%Fines	Days	D_{16}	D_{50}	D_{84}	%EB
Entiat	2020	39	77.8	1.8	7.8	233.7	14.9	41.5	76.4	3.6
Entiat	2021	39	87.1	0.2	9.8	210.3	14.4	38.3	72.3	3.3
Chewuch	2017	30	46.0	2.1	17.3	257.4	16.1	41.4	84.4	8.7
Chewuch	2018	30	73.9	1.8	7.0	250.2	16.8	44.8	87.1	7.8
Chewuch	2019	30	55.8	2.1	12.5	260.5	18.6	43.6	79.1	5.2
Methow	2017	30	76.5	1.8	6.3	185.8	24.4	55.5	115.0	9.2
Methow	2018	30	49.2	0.3	8.9	180.5	20.9	47.8	90.7	5.3
Methow	2019	27	76.1	1.7	9.9	183.9	25.3	50.4	93.2	6.0
Twisp	2014	23	69.5	1.3	7.7	237.5	12.2	44.4	102.0	14.3
Twisp	2015	24	52.6	5.2	22.2	239.4	23.5	46.5	83.8	12.2
Twisp	2017	36	85.3	1.7	10.3	239.7	16.7	41.4	98.9	11.8
Chiwawa	2009	20	72.7	NA	17.3	212.1	NA	NA	NA	NA
Chiwawa	2010	55	50.5	NA	17.7	213.2	NA	NA	NA	NA
Chiwawa	2011	49	44.7	NA	13.9	231.3	NA	NA	NA	NA
Chiwawa	2012	56	62.8	NA	11.9	216.4	NA	NA	NA	NA
L. Wenatchee	2014	12	8	17.1	34.6	196.5	19.1	39.0	68.3	6.3
L. Wenatchee	2015	12	49.9	6.9	14.6	235.7	16.7	36.8	67.2	14.3
L. Wenatchee	2016	12	65.1	1.3	17.5	263.0	13.6	33.0	59.2	4.7
MS Wenatchee	2014	12	0	1.2	5.9	65.0	14.7	32.7	58.0	4.7
MS Wenatchee	2015	18	41.7	1.7	12.1	96.0	23.2	43.8	67.1	6.3
MS Wenatchee	2016	18	40.6	1.8	8.8	97.0	7.3	27.3	56.5	0.7
Nason Creek	2009	19	61.5	NA	21.5	193.1	38.7	82.6	179	19.6
Nason Creek	2014	40	35	7.5	24.6	179.8	14.1	33.7	63.6	6.3
Nason Creek	2015	40	8.4	20.5	36.8	212.2	22.3	41.0	78.7	11.0
Nason Creek	2016	40	54.2	4.0	15.7	252.4	12.4	29.4	59.4	3.4
White	2014	24	36.8	4.2	19.4	204.4	16.6	40.8	85.4	6.5
White	2015	23	15.1	14.0	25.9	230.0	16.8	36.5	71.0	15.0
White	2016	24	38.9	10.0	13.0	262.9	9.4	29.3	69.8	3.8
Cle Elum	2009	9	77.9	0	2.0	148.4	23.9	45.2	78.6	0.3
Cle Elum	2010	9	91	5.2	5.9	108.1	11.9	37.0	75.9	3.7
Cle Elum	2011	9	59.6	0	6.8	106.1	25.3	40.0	57.4	4.3
Cle Elum	2012	9	73.4	0.3	9.2	92.2	15.3	37.0	63.9	4.3

Cle Elum	2013	6	75.2	1.2	5.0	114.3	16.5	32.2	52.2	0.5
Teanaway	2009	17	61.9	7.2	18.5	239.1	31.2	59.6	127.0	5.8
Teanaway	2010	15	17	48.7	21.1	231.1	18.1	47.7	100.0	12.8
Teanaway	2011	18	48	6.4	15.6	246.3	28.1	49.7	90.2	20.7
Teanaway	2012	18	58.7	5.2	17.3	216.5	27.5	65.7	133.0	17.4
Teanaway	2013	6	29.3	1.8	32.4	240.5	17.0	39.8	82.7	11.5
Yakima	2009	54	69.7	1.6	7.5	171.1	27.0	53.3	90.3	0.6
Yakima	2010	49	43.3	7.4	15.9	163.9	19.3	43.4	77.9	8.0
Yakima	2011	51	48.8	0.9	13.1	167.1	27.6	47.0	74.5	11.8
Yakima	2012	54	64.0	0.2	9.4	140.2	21.9	47.9	79.5	6.3
Yakima	2013	12	47.3	1.0	7.7	168.5	14.4	31.9	66.4	7.8

Table 1.2 Differences in expected log pointwise predictive density (elpd_diff) between the model exhibiting the best out-of-sample prediction, and other candidate models. Columns se_diff and 95ci represent the standard error and 95% confidence interval around each estimate of elpd_diff. We considered a quotient of elpd_diff by se_diff > 2, and a confidence interval exclusive of zero, as evidence supporting a difference expected predictive ability between candidate models.

Predictive variables	elpd_diff	se_diff	95ci
River, scour depth, fines, atu, days	0	0	[0,0]
River, scour depth, fines	-439.7	595.8	[-1631, 752]
River scour depth, fines, atu	-515.1	420.2	[-1356, 325]
River and fines	-717.1	736.8	[-2191, 756]
Scour depth, fines, atu, days	-1690.1	723.2	[-3137, -244]
Scour depth, fines, atu	-1846.6	759.1	[-3365, -328]
Scour depth, fines, days	-1902.5	744.5	[-3391, -414]
Scour depth, fines	-2015.4	763.6	[-3543, -488]
Fines	-3063.5	856.6	[-4777, -1350]
River, scour depth	-5080.2	902.7	[-6886, -3275]
River	-6611.7	1020.5	[-8653, -4571]
Scour	-7674.1	972.3	[-9619, -5730]
Intercept only	-11482.9	1147.5	[-13778, -9188]

Table 1.3. Differences in expected log pointwise predictive density (elpd_diff) between the model exhibiting the best out-of-sample prediction, and other candidate models. Columns se_diff and 95ci represent the standard error and 95% confidence interval around each estimate of elpd_diff. Data over-which the models were compared necessarily excludes the Chiwawa River replicates. We considered a quotient of elpd_diff by se_diff > 2, and a confidence interval exclusive of zero, as evidence supporting a difference expected predictive ability between candidate models.

Predictive variables	elpd_diff	se_diff	95ci
River, scour depth, percent fines, D_{50}, percent embedded	0	0	[0,0]
River, scour depth, percent fines	-413.3	201.8	[-817, -10]
Scour depth, percent fines, D_{50}, percent embedded	-2027.8	479.0	[-2986, -1070]
Scour depth, percent fines	-2359.3	516.8	[-3393, -1326]

1.7 FIGURES

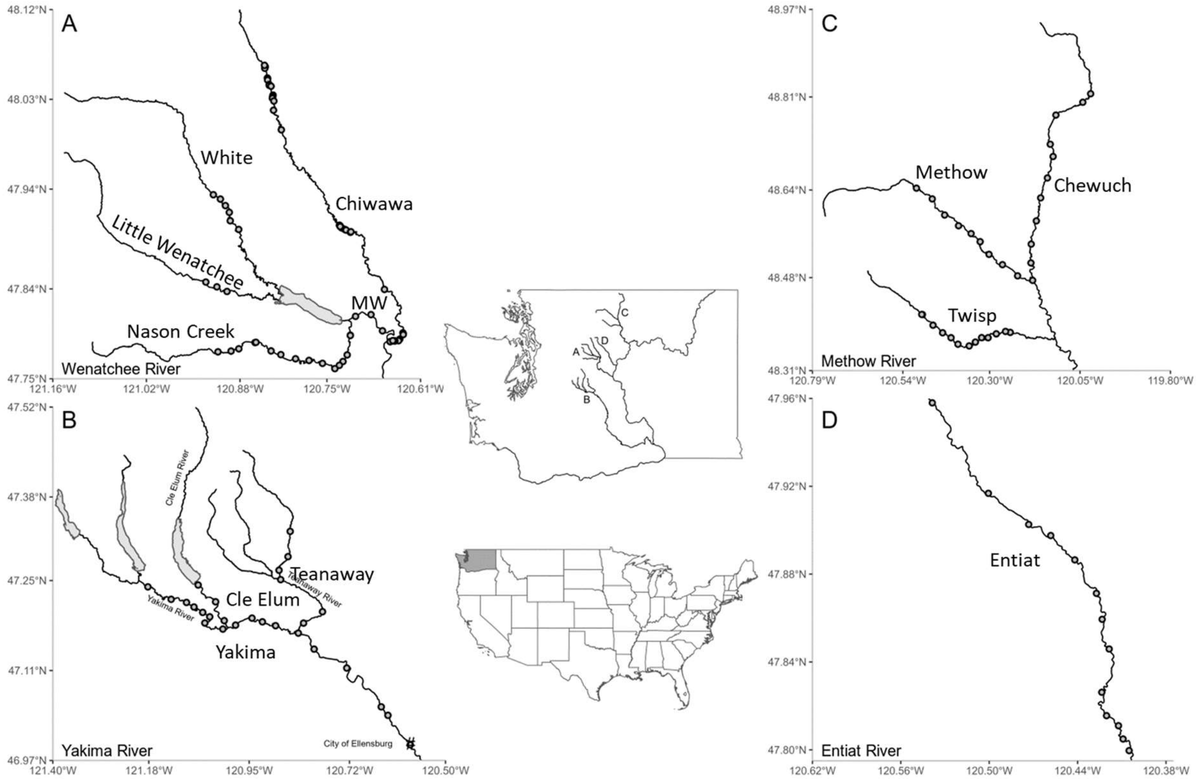

Figure 1.1 Study sites (n = 130) established in the Entiat, Methow, Wenatchee, and Yakima river basins.

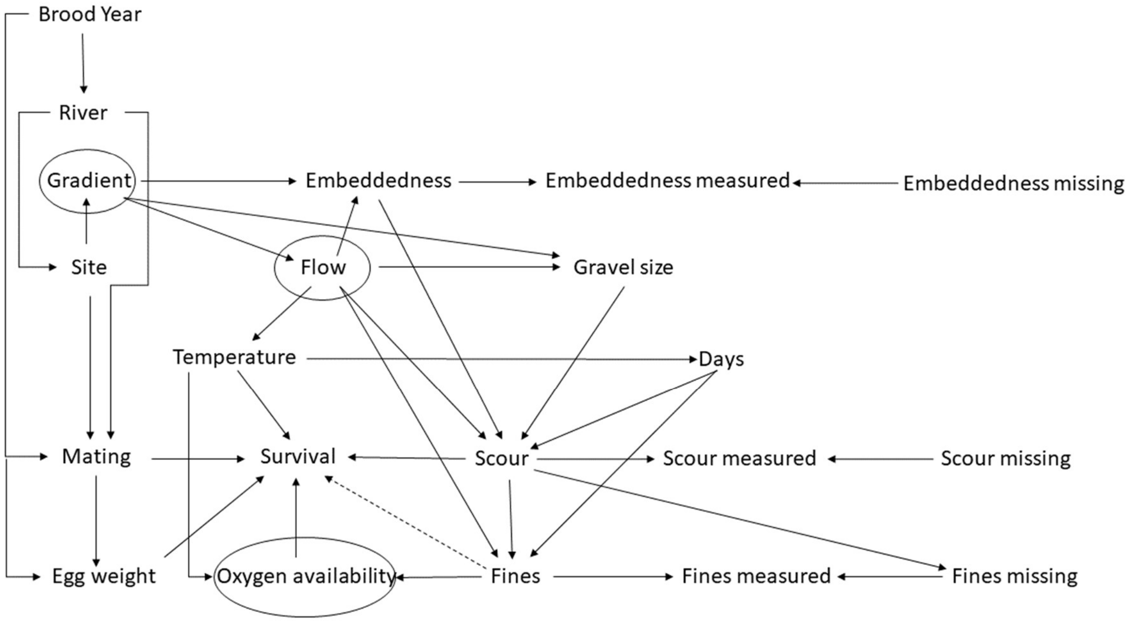

Figure 1.2. Causal diagram of measured and unmeasured (circled) variables hypothesized to affect Chinook salmon egg-to-fry survival directly or indirectly.

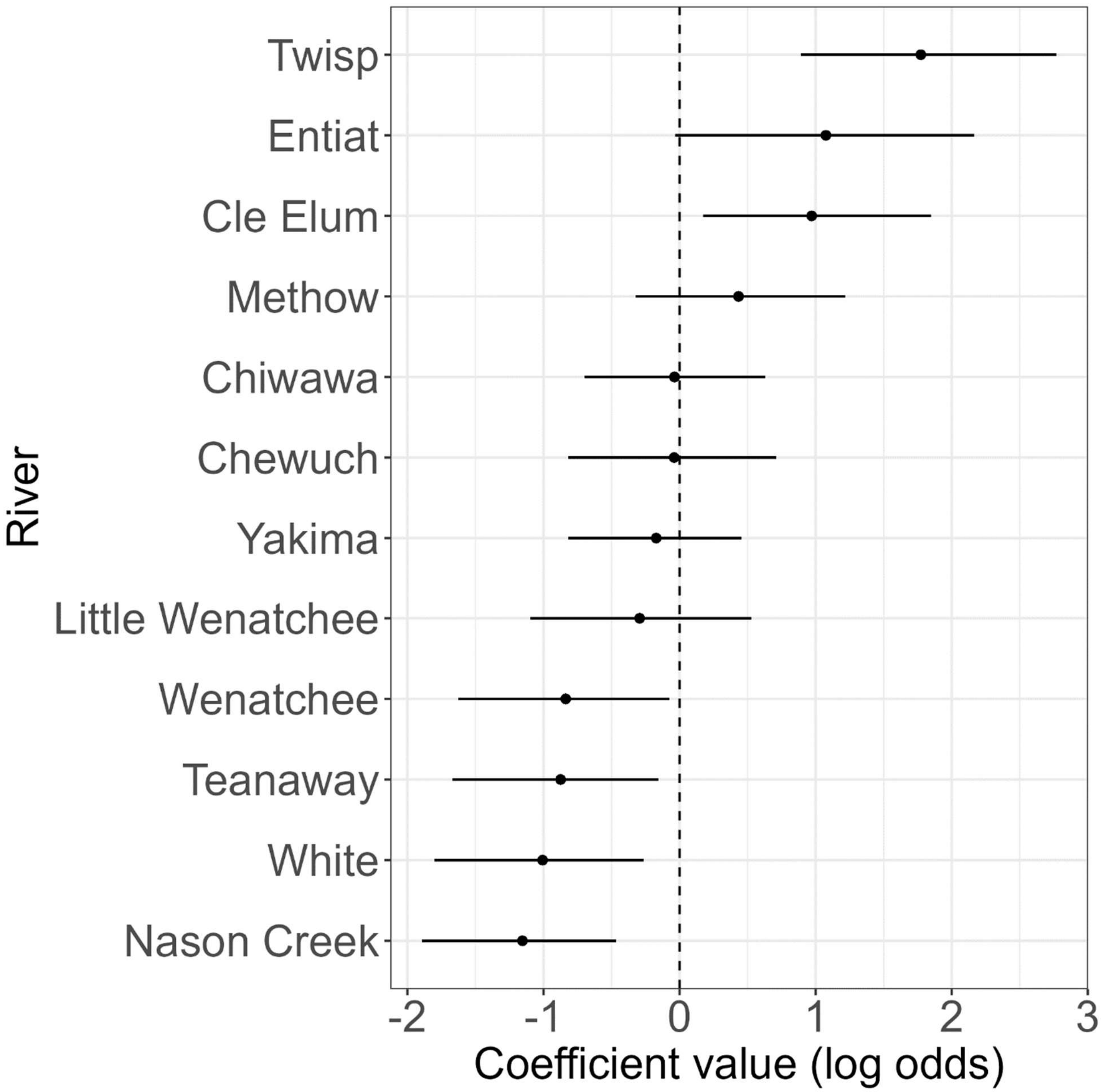

Figure 1.3. Ranked coefficient estimates of Chinook salmon embryo survival for the 12 study rivers. Points represent the mean estimate, and lines 90% compatibility intervals.

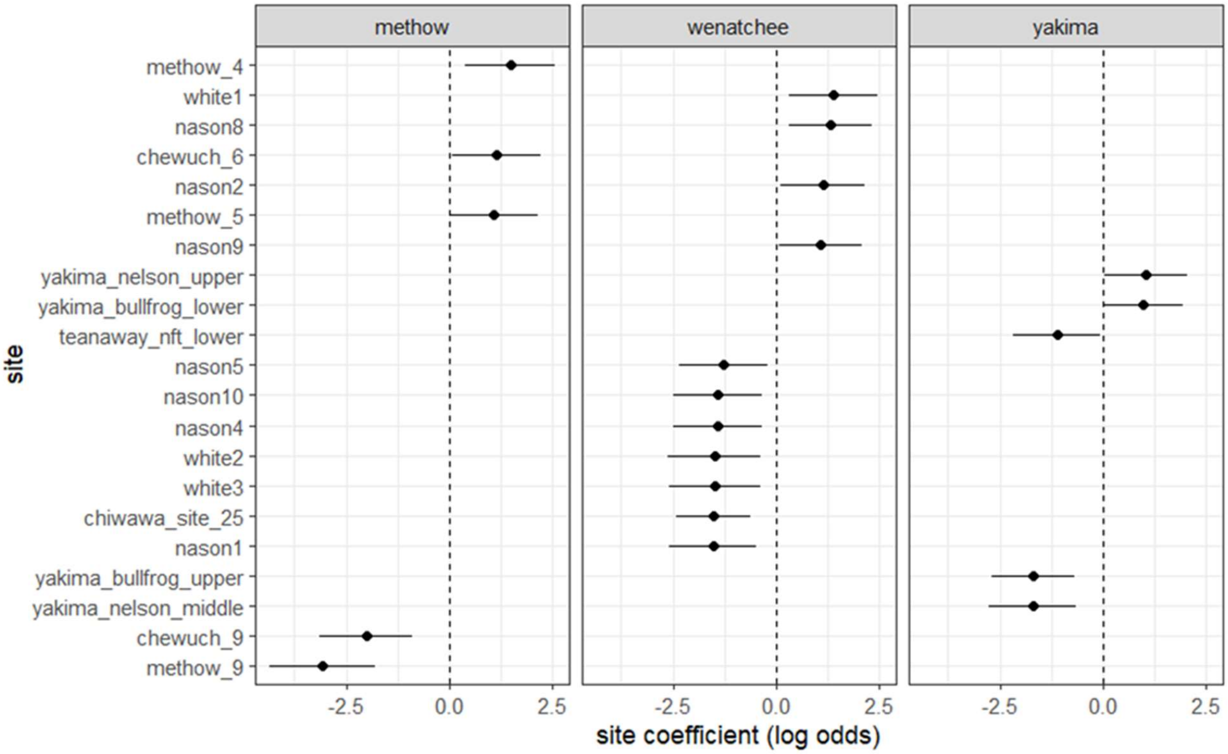

Figure 1.4. Coefficient values for study sites which indicate higher or lower relative egg-to-fry survival. Points represent the mean estimate, and lines 90% compatibility intervals.

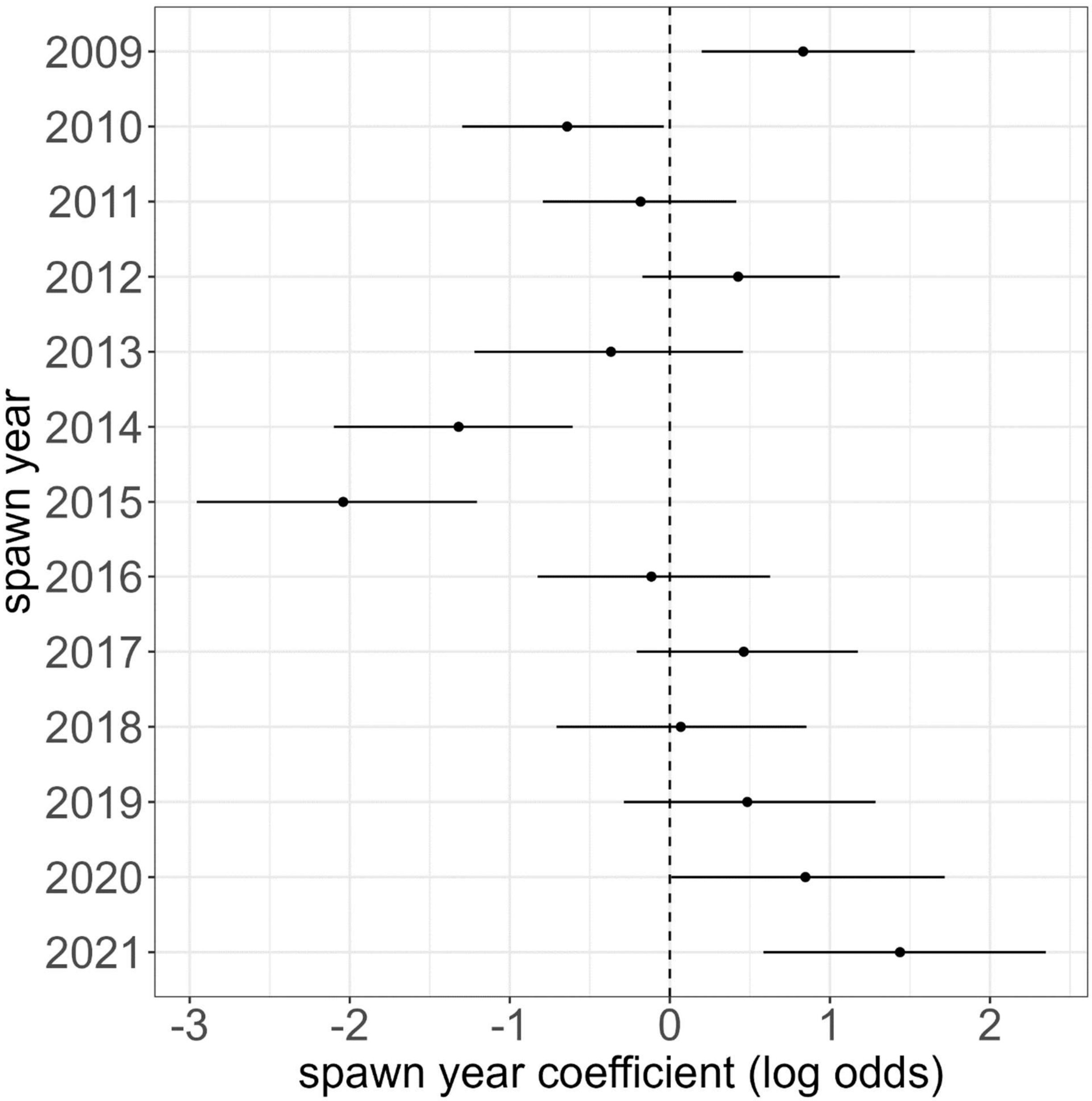

Figure 1.5. Ranked coefficient estimates of Chinook salmon embryo survival for the 13 study years. Points represent the mean estimate, and lines 90% compatibility intervals.

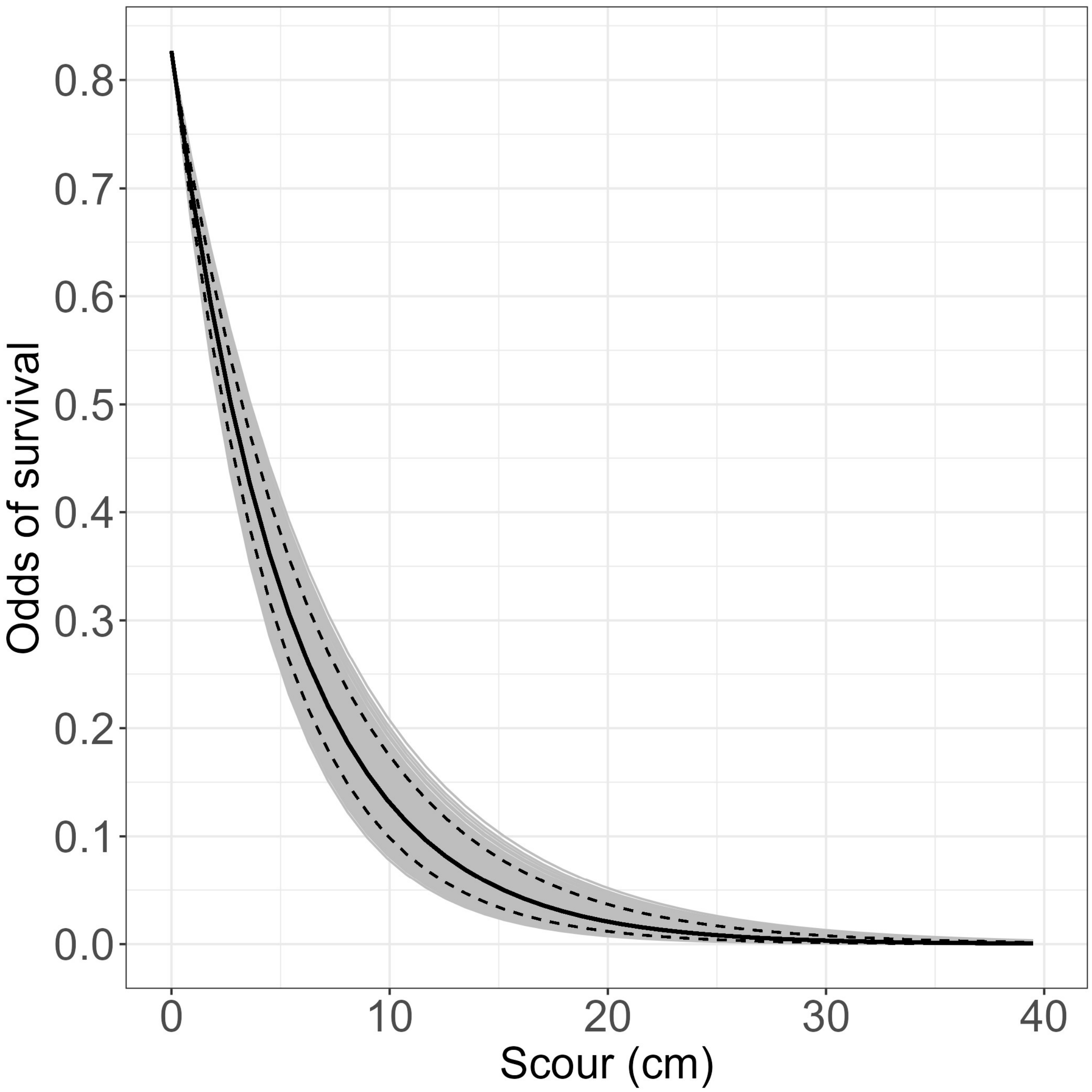

Figure 1.6. In gray, 1000 posterior draws (plausible modeled values) of the scour coefficient, expressed as odds of salmon embryo survival with increasing centimeters of scour. The y-intercept denotes the intercept value for survival. The x-axis is truncated for the purpose of illustration (maximum observed scour depth = 80 cm). The solid black line indicates the mean coefficient estimate, and dashed lines 90% compatibility intervals.

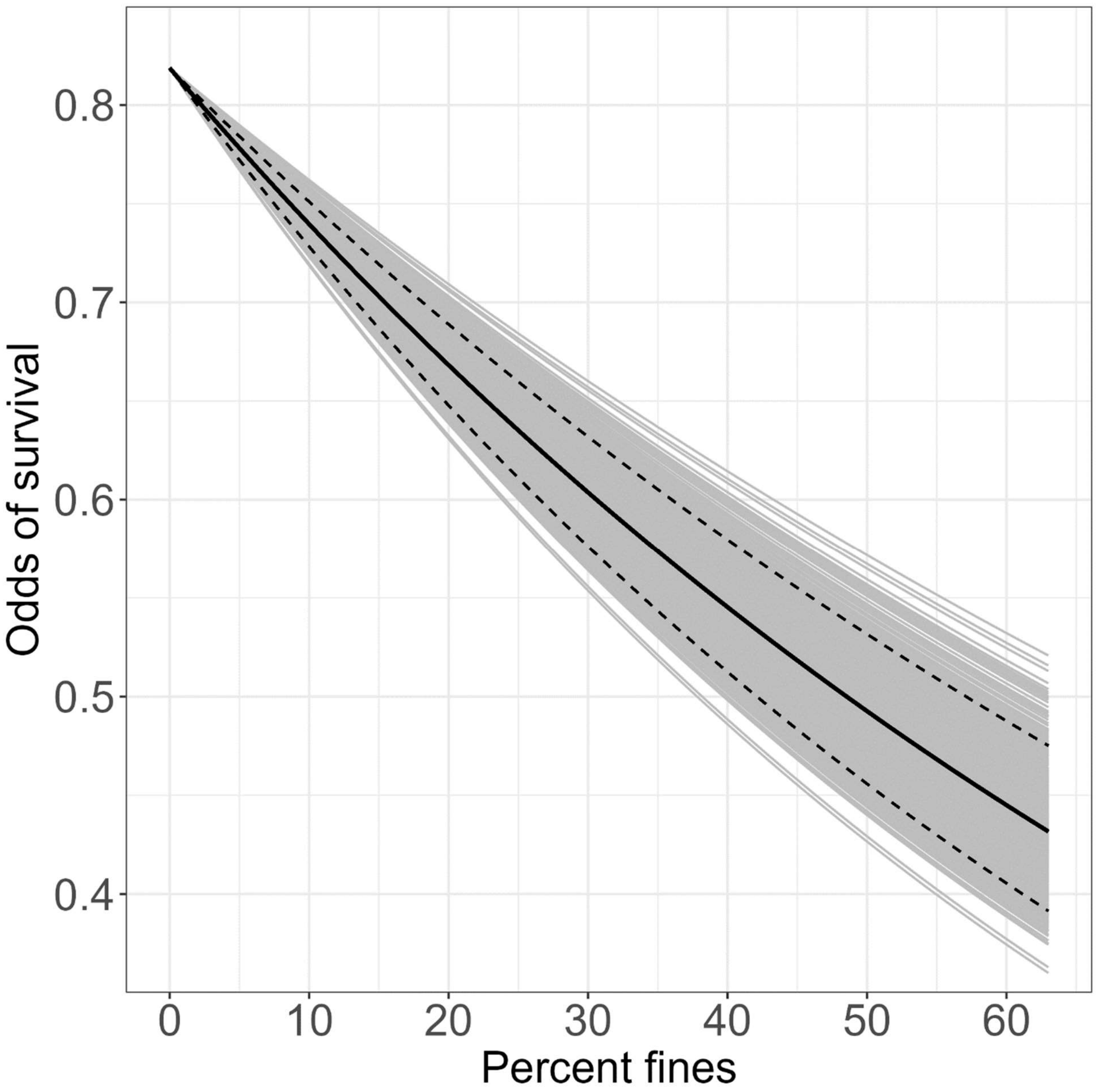

Figure 1.7. In gray, 1000 posterior draws (plausible modeled values) of the fines coefficient, expressed as odds of Chinook salmon embryo survival with increasing percentage of fine sediment ("fines") from 0% to the maximum observed value of 63%. The solid black line indicates the mean fines coefficient estimate, and dashed lines 90% compatibility intervals.

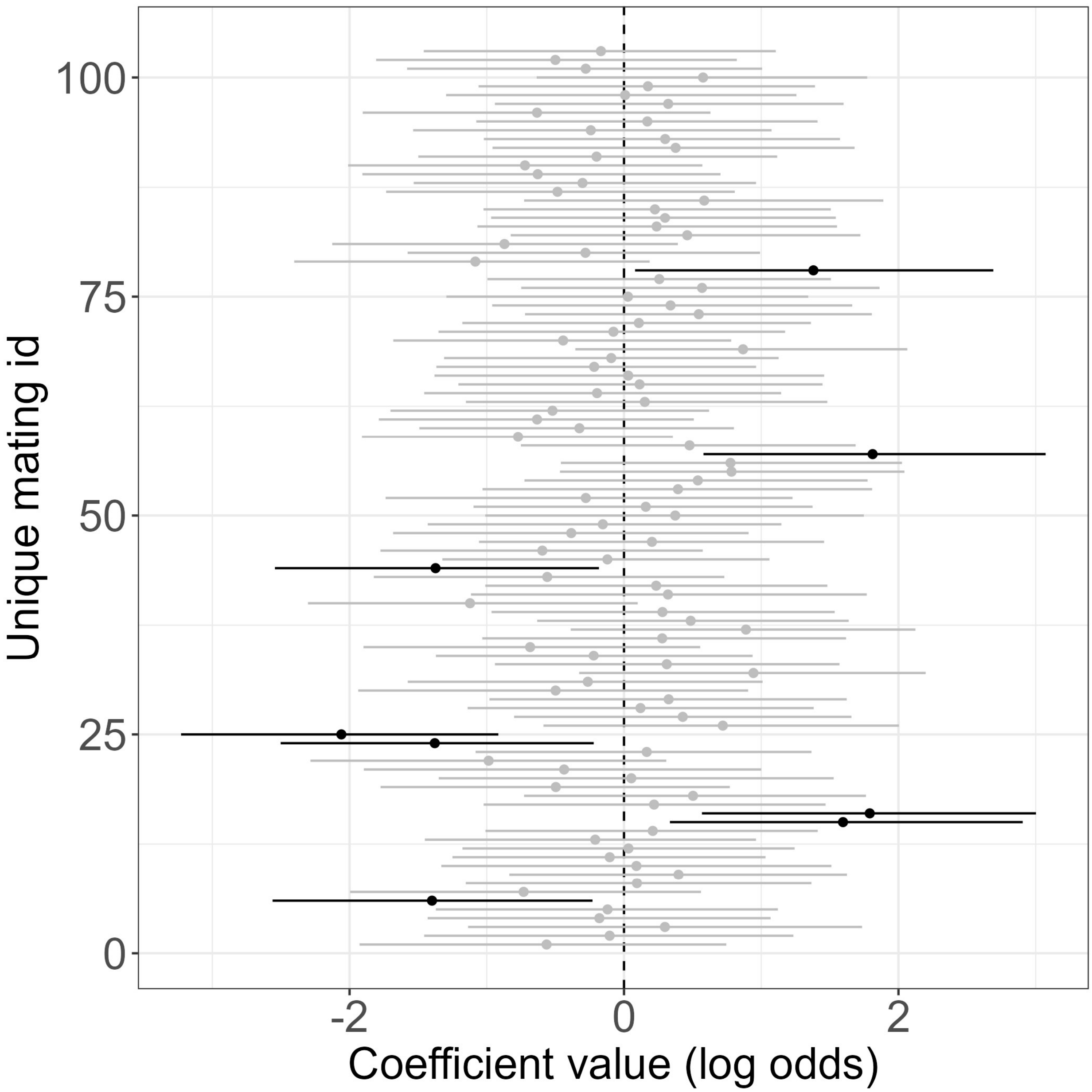

Figure 1.8. mating coefficient estimates of Chinook salmon embryo survival for each of the 103 unique matings. Points represent the mean estimate, and lines 90% compatibility intervals. Darker lines represent estimates found to range entirely above or entirely below zero.

1.8 ACKNOWLEDGEMENTS

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CHAPTER 2.

Divergent development rates of hatchery-origin Chinook salmon fry incubating in different natural thermal regimes: How well do models match reality?

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2.1 ABSTRACT

Salmonids, through natural selection and subsequent genetic adaptation, tend to spawn at a time that, given the habitat's long-term average thermal regime, enables their progeny to emerge at favorable dates months later. Development of embryos during incubation is strongly affected by the thermal regime, hence spawn timing commonly differs among even spatially proximate spawning populations. If hatcheries release fish from a common gene pool into a supplemented population, and those fish return as adults to these release locations, this may inhibit natural selection on timing, perhaps resulting in a mismatch between spawn timing and the thermal regime experienced by progeny of returning adults for the local population. Conditions such as these exist in the upper Yakima River Basin, Washington, where some adult Chinook salmon are collected downstream of the spawning grounds, spawned in a hatchery, and their offspring acclimated and released in various areas of the system. We hypothesized that emergence timing of hatchery origin offspring would differ among sites following their thermal regimes if placed in the gravel at the same time. To test this hypothesis, we installed and monitored 48 emergence traps in three such spawning areas with different thermal regimes between fall and spring. We monitored temperatures at each area, and evaluated three common models using temperature during incubation to estimate emergence timing to observed patterns. We used a Bayesian multilevel time-to-event model to estimate the median number of days required to emerge from the gravel. The observed number of days to reach median emergence varied greatly (range: 139 - 227 d), with differences in median estimates among reaches up to 25 d. However, given the variation observed and thus large compatibility intervals, median emergence timing did not detectably differ, but three models underestimated emergence timing by as much as 33 d.

2.2 INTRODUCTION

Seasonal timing of migration, reproduction, larval development, and first feeding by fishes and other aquatic animals vary with environmental conditions (Asch 2015) and affect recruitment through the match or mismatch between feeding demands by juveniles, the availability of food, and presence of predators and competitors (Cushing 1969, 1990). Breeding date is strongly affected by temperature in many marine (e.g., Danilowicz 1995; Carscadden et al. 1997; Jansen and Gislason 2011) and freshwater fishes (e.g., Leggett and Whitney 1972; Divino and Tonn 2007; Schneider et al. 2010). This environmental modulation of breeding may be combined with genetic differences among separate populations (e.g., Rogers et al. 2006) to control juvenile phenology. However, the prominence of genetic rather than environmental controls over timing seems especially strong in salmonid fishes (e.g., Quinn and Adams 1996), as indicated by controlled breeding studies (Neira et al. 2006), correlations between parental and offspring timing (Dickerson et al. 2005), evolution of populations transplanted to new environments (Quinn et al. 2000), and inadvertent selection in hatcheries (Quinn et al. 2002; Tillotson et al. 2019).

Once fertilized eggs have been deposited in the gravel, temperature has the largest influence on developmental rate of salmonids (Embody 1934; Jungwirth and Winkler 1984; Beacham and Murray 1990), though low dissolved oxygen levels slow development (Garside 1966; Shumway et al. 1974; Geist et al. 2006). The timing of emergence is important for survival, as those emerging early may be exposed to predators before they can feed and grow, and those emerging late may struggle to compete with earlier emerging conspecifics or miss the optimal growing conditions (Mason and Chapman 1965; Brännäs 1995; Einum and Fleming 2000). If they are small at the end of the summer, the juveniles may experience reduced survival rates in the winter (e.g., Quinn and Peterson 1996; Zabel and Achord 2004; Ebersole et al. 2006) and postpone seaward migration for another year (McCormick et al. 1998; Hall et al. 2016). Thus, stabilizing selection operates with opposing pressures against early and late spawning that vary from year to year within each population (e.g., Seamons et al. 2007). Because of thermal conditions, spawning timing is typically earlier in northern than southern populations, and earlier in cooler than warmer streams within regions (Sheridan 1962; Brannon 1987; Webb and McLay 1996; Brannon et al. 2004).

The strong natural selection on breeding date and heritability for this trait in salmonids (Carlson and Seamons 2008) can conflict with artificial propagation, commonly practiced to restore or enhance populations (Naish et al. 2007), in two different ways. First, hatcheries may deliberately or inadvertently select for early or more compressed timing of breeding (Quinn et al. 2002; Tipping and Busack 2004; McLean et al. 2005; Tillotson et al. 2019). Second, hatcheries may release juveniles within the natal river basin to disperse the returning adults and more fully utilize the habitat for natural reproduction and rearing (e.g., Fast et al. 2015). In such cases, timing of breeding that evolved under hatchery selection regimes may not match the local thermal conditions at the outplanting site, hence the natural phenology where the adults will return and spawn. Consequently, there may be a mismatch between breeding timing and local optimum, based on temperatures during incubation, flow conditions (Jones et al. 2015) and other factors.

Emergence timing can be estimated from models, derived using laboratory data on temperature and incubation. However, three methodological problems arise when trying to do so, and our secondary goal was to assess how well these models performed. First, the water in the stream may differ from that in the gravel environment where embryos incubate (e.g., Shepherd et al. 1986), resulting in errors when using stream temperature data to estimate emergence, in addition the variation in developmental rate resulting from varying dissolved oxygen concentrations (e.g., Peterson and Quinn 1996). Second, most models of the relationship between temperature and developmental rate were established using constant temperature regimes in laboratory settings (e.g., Jungwirth and Winkler 1984; Rombough 1985; Brannon 1987; Murray and McPhail 1988; Beacham and Murray 1990) but natural incubation temperatures vary with seasonal and daily conditions, affecting development (Steel et al. 2012). Third, developmental rate varies among families (e.g., dams) (Kinnison et al. 1998; Steel et al. 2012; Sparks et al. 2017), and many studies neglect this important factor.

Our study was designed to account for family-specific variation when assessing developmental rates of embryos from a common hatchery population incubating in different parts of a basin and compare the observed results to those that would have been expected by typical thermal sums models (e.g., Beacham and Murray 1990). Specifically, we compared observed emergence timing of hatchery-origin Chinook salmon experiencing different natural thermal regimes during incubation in three areas within the Yakima River basin, Washington with the outputs from three established incubation rate models, driven with the local temperature data, while including family-levels effects.

2.3 METHODS

Study reaches and site locations

Our general approach was to install fry emergence traps mimicking the incubation environments of the surrounding habitat. First, we identified three study reaches to represent the areas of the upper Yakima River Basin where most spring Chinook salmon spawn (Sampson et al. 2017), but where temperature regimes differ during winter and spring: 1) the main-stem Yakima River above its confluence with the Cle Elum River. 2) the Cle Elum River below the Cle Elum Dam, and 3) the main-stem Yakima River below its confluence with the Cle Elum River (Figure 2.1). Within these three reaches, we established a total of 8 study sites: 2 in the upper reach at river kilometer (rkm) 325 and 302.5 (YAK1 and YAK2), 2 in the Cle Elum River at rkm 11.7 and 6.5 (CER1 and CER2), and 4 in the lower reach at rkms: 299, 303, 251, and 246 (YAK3:YAK6, Figure 2.1).

Gamete collection

Gametes were collected from the Cle Elum Hatchery (Cle Elum, WA), and each female was paired with a single male in all cases. Eggs were collected from three females in one week in 2011, from two females in each of three weeks in 2013, and from two females in each of two weeks in 2016. Thus, 13 unique male x female matings were used (i.e., 3 + 6 + 4). Each replicate emergence trap (see below for details) contained fertilized eggs from one of these 13 matings. Within each year, traps were distributed such that each mating was equally represented among the three study reaches described above (detailed in Table 2.1). See Johnson et al. (2013) for a complete description of stocking methodology.

Emergence traps

Traps were installed to bracket the estimated peak of spawning activity in the upper Yakima River in years 2011, 2013, and 2016 (n = 48 in total, Table 2.1). Traps consisted of 32 cm x 18 cm diameter cylinders constructed of 3.2 mm perforated metal. The perforation size was designed to be small enough to prevent fry from escaping the main body of the enclosure, yet sufficiently large to permit water movement and prevent sedimentation accumulation levels beyond that of the surrounding environment (see Wesche et al. 1989). Traps were installed 1-2 days prior to the addition of fertilized eggs, such that all traps, given travel time and site access, could be stocked with eggs on the same day. Eggs and milt were transported to each study site (100-200 eggs per emergence trap) and fertilized at a protected location along the bank. Fertilized eggs were then stocked in unscreened Whitlock-Vibert egg boxes (Garrett and Bennett 1996) using the methods outlined in Johnson et al. (2012), and placed within the trap. Developed fry could exit the egg box, move freely through the larger structure, and volitionally emerge from the gravels. A 5 x 15 cm slot just below the top of the trap on the downstream side allowed newly emerged fry to enter a tapered screen (also 3.2 mm mesh) and through a small (~5 cm) PVC funnel system designed to prevent movement back into the enclosure (Figure 2.2). An inline valve prevented exit while the trap was being sampled. Each trap was buried with 5-8 cm remaining above the substrate, ensuring flows similar to those in the surrounding environment. The traps were checked periodically until first emergence, and weekly thereafter until no additional fry were observed. Water temperature was recorded hourly using an Onset Hobo Water Temperature Pro v2 Data logger with an accuracy: ± 0.21°C, secured to the top of each emergence trap in 2016. Hourly water temperature in both 2011 and 2013 were obtained from a single on-site location using an Onset Hobo 64k Pendant Temperature Data Logger (waterproof), accuracy: ± 0.53°C. (www.onsetcomp.com)

Egg boxes

We also buried 12 egg boxes directly in the gravel (i.e. not within an emergence trap) at a subset of our study locations in years 2011 and 2013 as a part of an earlier study (Johnson et al. 2013, Roni et al. 2016). The egg boxes were modified slightly by removal of the top tray, enabling the addition of gravels, and allowing fertilized eggs to drift into the interstitial spaces, providing a better representation of condition in the surrounding environment. Whitlock-Vibert egg boxes are comprised of molded plastic sheets, having two sizes of mesh openings, ~ 3.2 mm square, from which fry cannot escape, but also wider "slots" from which they can easily migrate. Therefore, egg boxes which were buried outside the confines of an emergence trap had the additional modification of 3.2 mm screen placed across these larger slotted areas of the egg box, such that fry would be contained until retrieved. Independently buried egg boxes were retrieved at or near 1000 accumulated thermal units (ATU - a common thermal sums target for Chinook salmon emergence). See Johnson et al. (2012) for a detailed description of the methodology. Placing both emergence traps and egg boxes at the same locations allowed comparison of developmental stage (k_D) of fry (Bams 1970) recovered at 1000 ATU and developmental stage at median emergence estimated from traps with shared locations, matings, and spawn timing (see below).

Collection of Yakima River Chinook salmon fry were permitted under research and monitoring activities described in Section 1.2.4 of the National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS) biological opinion under Endangered Species Act (ESA) Section 7(a)(2). Permissions for in-river excavation were obtained through WDFW's Hydraulic Project Approval Process (RCW 77.55.021). All work described here meets the requirements of the University of Washington (UW) Animal Use Laws and Regulations, as well as those of the UW Institutional Animal Care and Use Committee (IACUC).

All recovered fry (weekly collections from emergence traps, and at ~1000 ATU from the egg boxes) were transported live to a lab where they were euthanized, counted, measured for length to the nearest 0.5 mm, and weighed (wet) to the nearest mg. Condition factor (k) as an index for the development ($_D$), (Bams 1970) was calculated for each fry using the equation:

$$k_D = \frac{10 * \sqrt[3]{Weight\ in\ mg}}{Length\ in\ mm}$$

These values provide a standardized index of developmental stage; index values decrease with progressive alevin development.

Analysis

Estimates of median emergence time

We used a hierarchical time-to-event model to estimate median emergence timing for each trap. The model allowed for grouping of traps by site location and considered the interval-censored data due to the time duration between sampling events (~7 d).

Data were organized as follows:

N = the number of emergent fry

J = the number of traps at the given study site

$trap[i], i = 1, \dots, N$ = numerical id for each trap

$interval\_lower[i], i = 1, \dots, N$ = lower bound of the time interval (days)

$interval\_upper[i], i = 1, \dots, N$ = upper bound of the time interval (days) parameters and priors:

$\mu[J]$ = trap level mean, $\mu[J] \sim Normal(5,1)$

$\sigma[J]$ = trap level standard deviation, $\sigma[J] \sim Cauchy(0,2)$

Likelihood:

$$log\_likelihood[i] = log\left(\Phi\left(\frac{ln(interval\_upper[i]) - \mu\big[trap[i]\big]}{\sigma\big[trap[i]\big]}\right) - \Phi\left(\frac{ln(interval\_lower[i]) - \mu\big[trap[i]\big]}{\sigma\big[trap[i]\big]}\right)\right)$$

where:

$$Median\_time[j] = exp(\mu[j])$$

Incubation temperature can alter the relationship between temperature accumulation and development. Specifically, at lower temperatures development is slower on an absolute basis, but fewer temperature units may be required to reach a given developmental stage compared to the value required in warmer water (e.g., Brannon 1987). Consequently, we regressed our estimates of median emergence by the rate of temperature accumulation at each of our study location. Here the rate of temperature accumulation was calculated as the number of days required for each emergence trap to reach 1000 ATU. We also investigated the possibility of a relationship between the timing of emergence and the developmental stage of fry at emergence among our study reaches. We hypothesized that hatchery origin fry incubating under warmer temperatures, and perhaps requiring a greater number of accumulated thermal units to do so, may also differ in the mean quantity of residual egg mass at emergence.

Additionally, variation in temperature might also influence the number of ATU required for emergence and also the amount of residual yolk sac at emergence (Steel et al. 2012). We used standard deviation of daily temperature at each study site location, from the day of spawning to the median date of emergence, as an indicator of temperature variation over the period of incubation. We then regressed this against our estimates of ATU at median emergence at all 36 of our emergence traps to test the hypothesis that developing fry experiencing greater daily variation over the incubation period would require a greater number of ATU to emerge in a natural environment. We also regressed our measure of variation against median developmental stage at emergence to test the hypothesis that developing fry experiencing greater daily temperature variation might emerge more fully developed than those in less variable incubation environments.

General linear models were used to assess relationships between median days to emergence or developmental stage at emergence with 7 predictive variables: study reach, week of spawning, ATU at emergence, the rate of temperature accumulation, parentage, egg size, and mean temperature variation (SD) throughout the incubation period. Models assessing differences in emergence timing among reaches also included study year as a predictive variable.

Where:

$y_i \sim \mathrm{Normal}(\mu_i , \sigma)$,

$\mu_i = \alpha + \beta_1 \times x1_\mathrm{i} + \beta 2 \times x2_i + \beta 3 \times x3_i$

priors:

$\alpha, \beta_{1:n} \sim \mathrm{Normal}(0, 10)$

$\sigma \sim exp(1)$

Models were generated with Markov chain Monte Carlo techniques using the probabilistic programming language Stan (Stan Development Team 2021). Model scripts were written using CmdStanR or Rstan packages in R (Gabry and Cešnovar 2022; Stan Development Team 2023). All models were fit with 2000 warm-up and 5000 sampling iterations for each of four chains. Chain convergence was checked through inspection of $\hat{R}$ and effective sample size metrics for each model parameter (< 1.05, and greater than 100/chain respectively). Overall diagnostics included checks for divergent transitions, saturated max treedepth, and low BFMI values.

Comparison with other developmental rate models

We used three widely used models based on temperature accumulation only (i.e., data that would be available for most systems) for our comparison of predictive models. Our goals were not to identify discrepancies with any given predictive model but to assess their general performance in predictions necessary to inform other in situ studies. To accomplish this, we calculated estimated emergence at each of our study sites in each year using each of the models defined below. We then calculated our metric of "model performance" as the difference between our estimates of median emergence and the median days predicted by each of the three candidate models.

Model 1: (Beacham and Murray 1990)

emergence days ~ $\exp\left(10.404 - 2.043 * \log(mean\ temperature\ deg.C + 7.575)\right)$

Model 2 is a modification of the Belehrádek model as presented by Jensen et al. (2009) using constraints for Chinook salmon as provided by Gerson et al. (2016):

$y=(mean\_temp-p3)p2p1$

where $p1 = 5.24090774 \times 10^6$

$p2 = 3.9184502$

$p3 = -19.0720758$

Model 3 simply used 1000 ATU as the target value, slightly above the pooled estimates from various studies of > 900 in the relevant range of 5° – 11° C (Quinn 2018) where:

$\Sigma\ (\overline{x}\ \text{daily temperature}) = 1000$

2.4 RESULTS

We installed 54 traps over the three study years but 18 of them, particularly in 2013, were dislodged or otherwise compromised during high-flow events, or experienced high mortality preventing any reasonable calculation of emergence timing, leaving 36 to provide data (Table 2.1).

Emergence timing

We estimated between 139 and 227 d to median emergence, with considerable variation among replicate traps (Mean: 204 d, SD: 18 d; Figure 2.3). We also observed differences in timing among the three study reaches; Chinook salmon fry incubating in the Cle Elum River required, on average, 22 and 25 fewer incubation days compared to those in Yakima River sites above and below the Cle Elum River, respectively (Figure 2.3). However, the differences in median emergence among reaches were not significant, as 95% credible intervals around each of the reach coefficients spanned zero. The median emergence across all 36 replicates occurred at 1135 ATU (SD: 86), with a negative relationship between the number of days required to reach 1000 ATU and the number of accumulated thermal units on the date of emergence. That is, traps at sites with warmer water (largely within the Cle Elum River), required more ATUs before the fry emerged from the gravel (Figure 2.4; $\beta = -1.4$, BCI_{95}: -2.2, -0.6). All mating coefficient values were near zero: $\beta_{m[i]} \in (-0.02, 0.05)$, and 95% compatibility intervals for each of the estimates included zero. Additionally, the median number of days to emergence was not influenced by initial egg size given our data ($\beta = 0.03$, $BCI_{95} = -0.96, 1.01$). Finally, despite the wide range of fine sediment values (0.4% to 23.4%, mean: 5.8, SD: 5.6), we detected no relationships between the fine sediment in our traps at recovery and either the median number of days to emergence ($\beta = 0.94$, $BCI_{95} = -0.05, 1.92$). Lastly, we found no indication that variation (SD) in daily temperature was related to the number of days to median emergence among our emergence traps ($\beta = 0.9$, $BCI_{95} = -6.6, 8.6$), or that daily variation in temperature was related to the total number ATU at median emergence ($\beta = 16.6$, $BCI_{95} = -58.4, 92.7$).

Developmental stage

The developmental stage (k_D) of emergent Chinook salmon fry averaged 1.89 (SD: 0.04) across the 36 traps. Fry in the Cle Elum River tended to be less developed (slightly higher mean k_D values) in comparison to those in the Yakima River reaches. However, differences were minimal and overall, we found no significant relationship between days to emergence and developmental stage, indicating that fry emerged at similar developmental stages across the study design. This was further supported by the absence of any relationship between developmental stage and ATU at emergence; either the number of days required to reach 1000 ATU ($\beta = 2.0 \times 10^{-04}$, $BCI_{95} = -1.7 \times 10^{-04}, 5.7 \times 10^{-04}$), or the total ATU at emergence ($\beta = -1.5 \times 10^{-4}$, $BCI_{95} = -2.8 \times 10^{-4}, 2.0 \times 10^{-5}$).

It appears that given the variation we observed, neither the mating used (Table 2.1), or the initial egg weight influenced developmental stage at emergence. All mating coefficient values were near zero: $\beta_{m[i]} \in (-0.8 \times 10^{-3}, 0.5 \times 10^{-2})$, and 95% compatibility intervals for each of the estimates included zero. Likewise, the estimated coefficient for initial egg size (weight in mg), with k_D as the response variable also spanned zero, indicating no effect given our data ($\beta = 0.42$, $BCI_{95} = -0.12, 0.94$). Fine sediment values (described above) were not associated with median developmental stage at emergence ($\beta = -5.0 \times 10^{-4}$, $BCI_{95} = -2.6 \times 10^{-3}, 1.6 \times 10^{-3}$).

Lastly, we found no relationship between mean variation (SD) in daily temperature and or developmental stage (k_D) at emergence ($\beta = 0.01$, $BCI_{95} = -0.02, 0.04$).

Model comparisons

Estimates of the number of days required to median emergence were similar among the three temperature-based models, but generally underestimated the observed number of days to emergence (i.e., 27 - 41 d earlier than was observed; Figure 2.5). Model #2 (the modified Belehrádek model, Jensen et al. 2009) best matched the observed patterns, underestimating the median by 29 days on average. Predictions varied compared to our estimates of median emergence, with SD between 28 and 33 d (Figure 2.5). Predictive performance differed by reach, with the greatest difference between temperature model predicted emergence and median trap emergence occurring in the Cle Elum River ($\beta = -21.9$, $BCI_{95} = -33.9, -9.92$). Generally, model performance was best when incubation conditions were cooler on average.

2.5 DISCUSSION

Our overall study objectives were to 1) identify potential differences in Chinook salmon emergence timing among three reaches of the upper Yakima River basin that differ in temperature accumulation throughout the incubation period, all of which contain spawning habitat utilized by returning hatchery origin spring Chinook salmon; and 2) evaluate our ability to predict emergence timing in a natural environment, using temperature data alone. We hypothesized that differences in thermal regime among the study reaches would cause differences in emergence timing among hatchery origin Chinook salmon if adults returned to spawn at these reaches at the same time but the differences in emergence timing between the Cle Elum River and adjacent reaches of the main-stem Yakima River were small and varied among study sites within reaches and among years (Figure 2.3), though point estimates of median days to emergence indicated slightly earlier emergence in the Cle Elum River on average. Consequently, the parsimonious interpretation is that there is enough variation in timing among redds within the three reaches that if hatchery-origin fry from a common hatchery were outplanted and then returned to spawn there, their progeny would differ but only slightly in emergence, given the other sources of variation.

Our study was limited by the loss of several replicates and we had data for the entire basin in only two years. Our model suggests high variability both within and among our replicates, and thus low power to detect small differences in emergence timing. Additional data would be required to more definitively determine if there are differences in emergence timing among reaches of the upper Yakima River. For example, Chinook salmon fry in the Cle Elum River emerged from the gravel an average of 22 and 25 d earlier than the upper and lower sections of the main-stem Yakima River, respectively (Figure 2.3). If genuine, this earlier emergence could provide enhanced growth opportunity (Mason and Chapman 1965; Einum and Fleming 2000), if food resources were adequate. Post-emergence growth data appears to support this hypothesis. Chinook salmon fry were collected bi-weekly throughout the upper Yakima and Cle Elum rivers between mid-March and early June in 2021, 2022, and 2023 (Johnson and Mankus, report to Bonneville Power Administration, in preparation, 2024). The fry collected from the Cle Elum River were approximately 2 mm larger than those collected in the mainstem of the Yakima River both above and below its confluence with the Cle Elum River, as would be predicted from earlier emergence. A prior study indicated that despite some size advantage, Chinook salmon fry grow slower in the Cle Elum River, likely due to cooler temperatures following emergence relative to the mainstem Yakima River (Johnson et al 2019). Together, these studies suggest that the larger size of Cle Elum River fish observed probably result from earlier emergence. Smaller differences in median emergence timing were also present between the upper and lower study reaches of the main-stem Yakima River; those in the warmer areas downstream of, and influenced by, the Cle Elum River emerged ~ 6 d earlier than those at higher elevation above the confluence of the Cle Elum River. Although small, these differences may be biologically relevant in the context of high intra-specific competition among Chinook salmon in the Yakima River Watershed (Pearsons et al. 2008), and the diverse life history patterns displayed by interior Chinook salmon (e.g., Copeland et al. 2014). Ultimately however, despite the associated evidence, the environmental effects of temperature differentials within upper Yakima River remain unclear. Given the variation observed, progeny of hatchery adults returning to our study locations may not incur either cost or benefit associated with the timing of emergence.

Our design allowed us to investigate the potential influence of factors other than temperature regime which may also influence the timing of emergence. However, we found no evidence supporting either genetic or environmental influence on the timing of emergence beyond that of temperature accumulation in this study, nor any relationship between egg size or parentage and emergence timing, despite the fact that both egg size (maternal traits) and parentage (combined maternal and paternal traits) can influence timing of emergence. There are known advantages to larger egg sized with respect to size at emergence and corresponding post-hatch competitive advantages, and both parentage and specifically maternal effects of egg size have been shown to affect timing, alevin development, and survival (Einum and Fleming 2000, Roni et al. 2016, Thorn and Morbey 2019). Further, we found no influence of fine sediment accumulation on the timing of emergence, perhaps because the levels were too low to affect development. Percent fines measured with our emergence traps averaged less than 6% percent and were within the range of those previously reported in the Yakima and Cle Elum Rivers by Roni et al. (2016). Further, supporting data (WDFW unpublished) suggests that, generally, intra-gravel flow and oxygen saturation in the upper Yakima River is at or above thresholds of concern for incubating (> 2.6 mg/L; Silver et al. 1963), and such conditions may be favorable even when the percentage of accumulated fines is relatively high.

The three temperature-only models that we investigated all underestimated emergence timing compared to our empirical measures. The underestimate of emergence may be in-part due to the fact that newly emerged fry stay in the gravel post-hatch for some period of time (Groot et al. 1995). Thus stage of development and emergence behavior are not the same, and maximum alevins wet weight may be a good measure of readiness to emerge (Rombough 1985) but is difficult to determine in field situations. Although we cannot distinguish between the point of emergence and the point when fry would enter the water column (and would presumably enter the trap), we can in some instances directly compare developmental stages at 1000 ATU to that of volitionally emergent fry because, as indicated in this study, fry enter the water column at a comparable state of development, i.e. when they are “buttoned up”. Data from egg boxes buried in the substrate at a subset of our study locations in 2011 and 2013 (Roni et al. 2016) provide opportunity to measure the developmental stage of fry at a set ATU (here 1000 ATU), in a natural environment, and compare these directly to others allowed to volitionally emerge. Our data suggest median development at predicted emergence using mean temperature as the only predictor was considerably lower (greater k_D) than those emerging from the gravel volitionally, with similar degrees of variation between the two groups (Figure 2.6). Thus, at least in the Cle Elum River, estimated emergence timing as calculated using a thermal sums model would infer emergence of fry with greater amounts of residual egg mass in comparison to other areas of the Yakima basin (see Roni et al. 2016 for a comparison of k_D across the basin at ~1000 ATU). Given the similarity in developmental stage at emergence observed in our study, we propose that this discrepancy is likely attributable in-part to poor model performance when incubation temperatures are warmer. Further, although there may be differences between the predicted and observed emergence timing attributable to time fry spend in the upper portions of the gravel (Groot et al. 1995), and this difference may bias estimates of egg to fry survival, in that the transition from incubation to free swimming fry is pivotal in assumptions made regarding potential sources of mortality. Thermal variation throughout the incubation period can influence emergence timing (Steel et al. 2012) but we found that the rate of temperature accumulation was more important in determining emergence timing. Finally, predictive models may have been developed in temperature regimes that differ from those of eastern Washington, where surface water temperatures are at or below freezing for a portion of the incubation period. Temperature regimes across Washington state, due largely to weather patterns associated with the Cascade Mountains and the corresponding rain shadow effect (Siler et al. 2013) result in temperatures that differ not only with latitude (e.g. mean temperature increase from British Columbia through Washington to Oregon), but also longitudinally. Western Washington ranges in annual temperatures on the scale of 0° to 24°C, where eastern Washington temperatures may range annually between -34° to 41°, WRCC 2024). Therefore, both fine scale and regional scale differences in temperature norms are present across the state, which may influence our ability to accurately predict the timing of Chinook emergence when using temperature alone as the predictive variable.

To clarify this portion of the discussion, we compared temperatures between eastern and western Washington locations through the typical period of Chinook salmon incubation (here September 1st to June 1st), using trends in air temperature as an approximation for expected trends in water temperature. We calculated mid-range temperatures from reported minimum and maximum data report by monitoring stations daily. Figures 2.7 and 2.8 illustrate both the sizable difference in temperature regimes in Eastern and Western Washington generally, as well as the variation that exists over a relatively short period of time environmentally (75 years). In comparison to the west side of Washington State, which rarely encounters temperatures below freezing, average temperatures at or below freezing occur over the better part of three months on the east side of the state. As such, growth in east side streams may be slower than in more typical, coastal areas, leading to underestimates of the time required to emerge from the gravel. Model performance was negatively related to the rate of temperature accumulation and was therefore worse with respect to its relative difference from median emergence timing in the Cle

Elum River reach. Therefore, in addition to underestimation in natural environments, current predictive models may also spatially bias subsequent estimates (e.g. survival) for which the methodology is based in-part on predicting emergence over large spatial areas. As an example, it may be possible that environmental conditions in the spring, e.g., increased scour relative to winter months, contributes largely to population survival, but that this factor might be overlooked in warmer systems where boxes would have been recovered prior to these events, leading to overestimates of survival.

This study provides relevant information on timing of emergence, and associated estimates, that in practical use may affect inferences made in studies of Chinook salmon survival. Our results highlight the need to account for within-system variation in estimating and evaluating critical life-stage transitions of Chinook salmon, and it is our hope that the information provided here sets the stage for additional research testing assumptions in areas that are often considered reliable due to their consistency in controlled environments.

2.6 TABLES

Table 2.1. Emergence trap locations and within-year week of placement in study years 2011, 2013 and 2016 by study site (see Figure 2.1). n = the number of emergence traps installed at each site; n retained is the number of traps that withstood scour/flow throughout the duration of the study and had sufficient number of surviving fry. Matings A:M indicate individual families (i.e. each letter representing a mating made between a unique male and female).

Year	River	Reach	Site	n traps placed	n traps retained	Week(s)	Matings
2011	Cle Elum	Cle Elum	CER2	6	6	2	A, B, C
2013	Yakima	Upper	YAK1	3	0	1-3	D, F, H
2013	Yakima	Upper	YAK2	3	0	1-3	E, G, I
2013	Cle Elum	Cle Elum	CER1	3	2	1-3	D, F, H
2013	Cle Elum	Cle Elum	CER2	3	3	1-3	E, G, I
2013	Yakima	Lower	YAK5	3	1	1-3	D, F, H
2013	Yakima	Lower	YAK6	3	3	1-3	E, G, I
2016	Yakima	Upper	YAK1	4	4	1-2	J, K, L, M
2016	Yakima	Upper	YAK2	4	2	1-2	J, K, L, M
2016	Yakima	Lower	YAK3	4	4	1-2	J, K, L, M
2016	Cle Elum	Cle Elum	CER1	4	4	1-2	J, K, L, M
2016	Cle Elum	Cle Elum	CER2	4	4	1-2	J, K, L, M
2016	Yakima	Lower	YAK4	4	3	1-2	J, K, L, M
Totals				48	36		

2.7 FIGURES

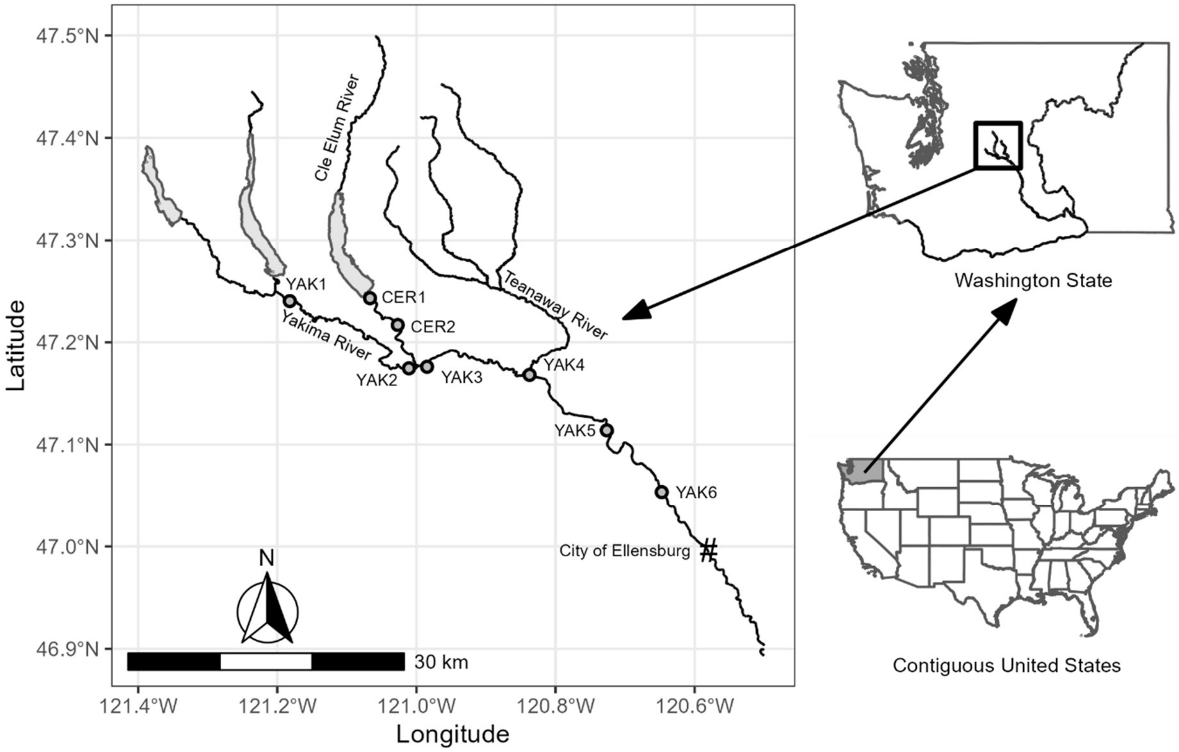

Figure 2.1 Study site locations in the Upper Yakima River basin. Two sites (YAK1 and YAK2) were positioned above the Cle Elum River confluence, and four sites below (YAK3 - YAK6). Two sites were situated within the Cle Elum River (CER1 and CER2).

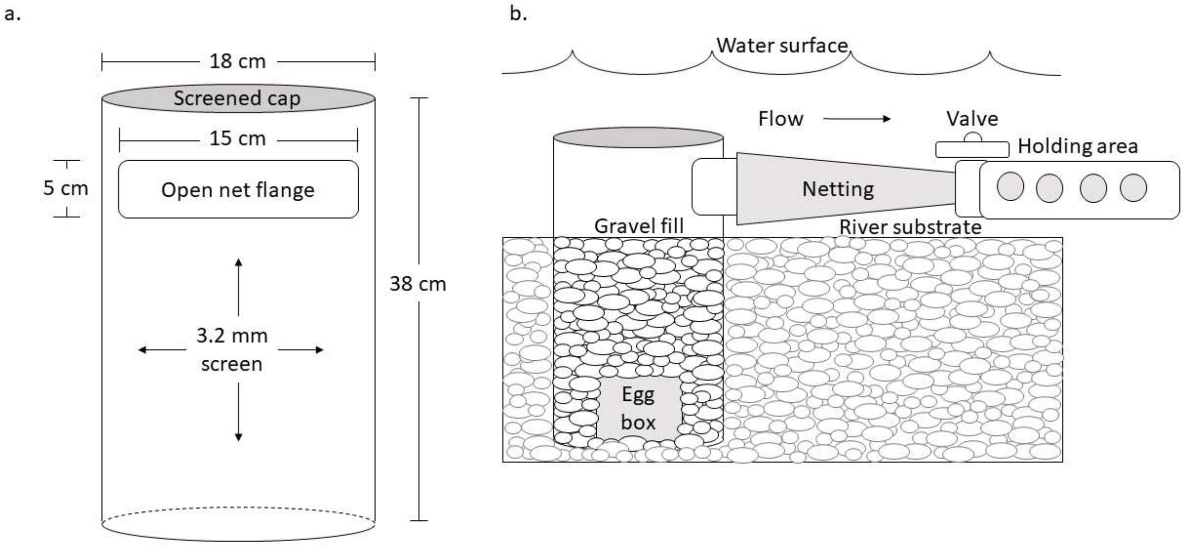

Figure 2.2. Emergence trap dimensions (a) and configuration when in the gravel (b).

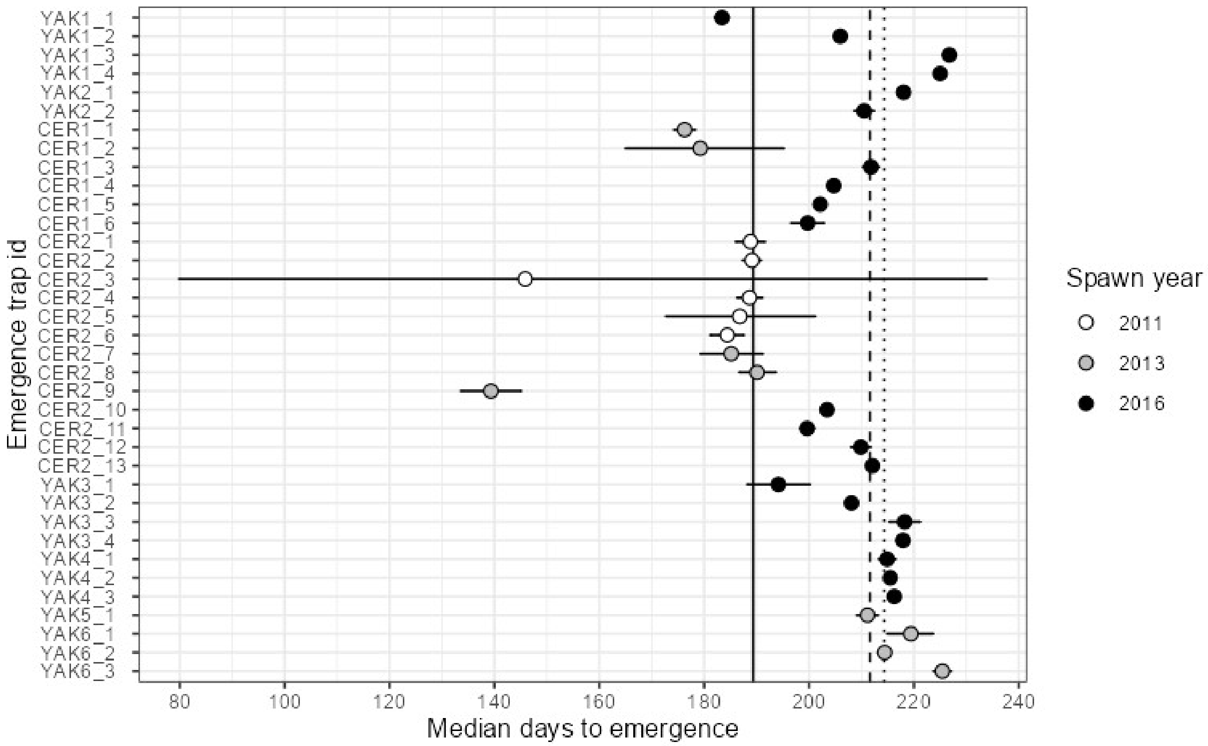

Figure 2.3. Estimated median days to emergence for hatchery origin Yakima River Chinook salmon by study site, trap id, and spawn year. Study sites along the y-axis are presented in order of upstream to downstream order (YAK1 being the most upstream location). Horizontal lines represent 90% compatibility intervals. Vertical lines represent the average days to emergence for all replicates within the Cle Elum River (solid line), Yakima River above the Cle Elum River confluence (dashed line), and the Yakima River below the Cle Elum River confluence (dotted line). Emergence traps deployed in 2011 (white points) were located in the Cle Elum River only. These estimates are provided for visual comparison and were not included in the calculation of average days to emergence (solid line).

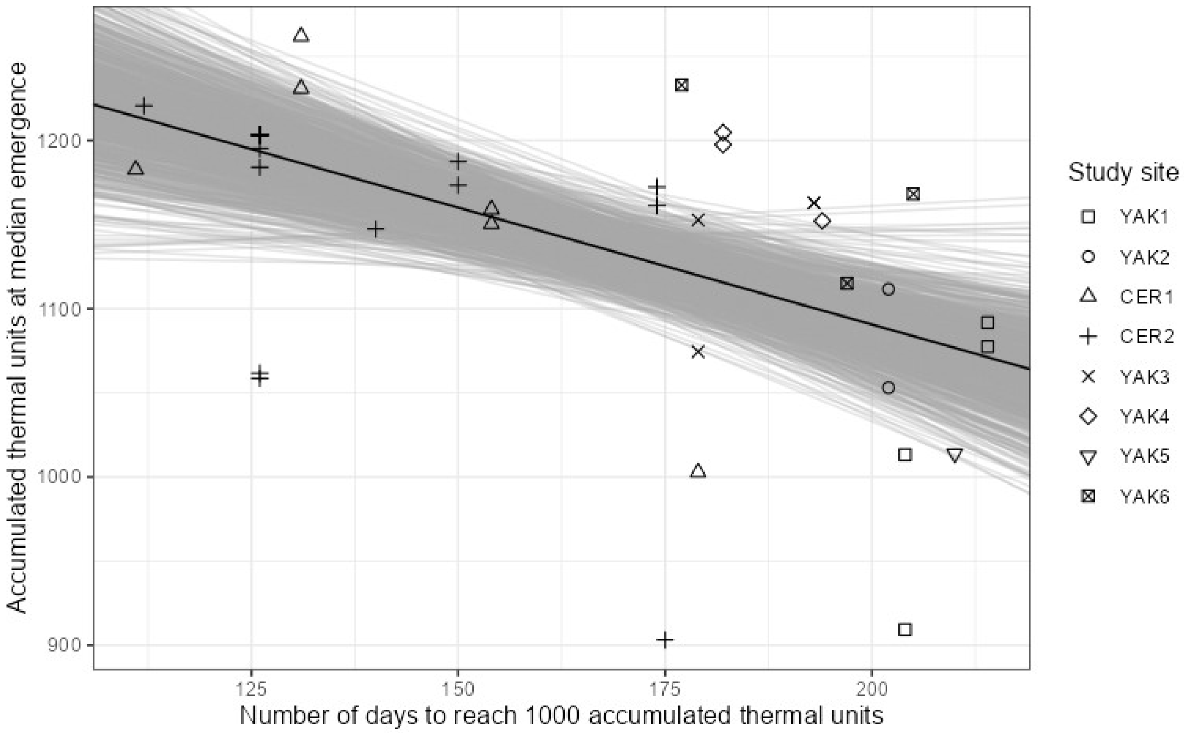

Figure 2.4. Modeled relationship between the rate of temperature accumulation and the total number of temperature units at median emergence for emergence traps placed in brood years 2011, 2013 and 2016. Point shapes denote the study site location of each replicate (n = 36). The dark solid line represents the average relationship between the predictive and response variables given the data. Gray lines (n = 1000) are plausible relationships using paired values of slope and intercept, randomly sampled from the posterior distribution of the regression model.

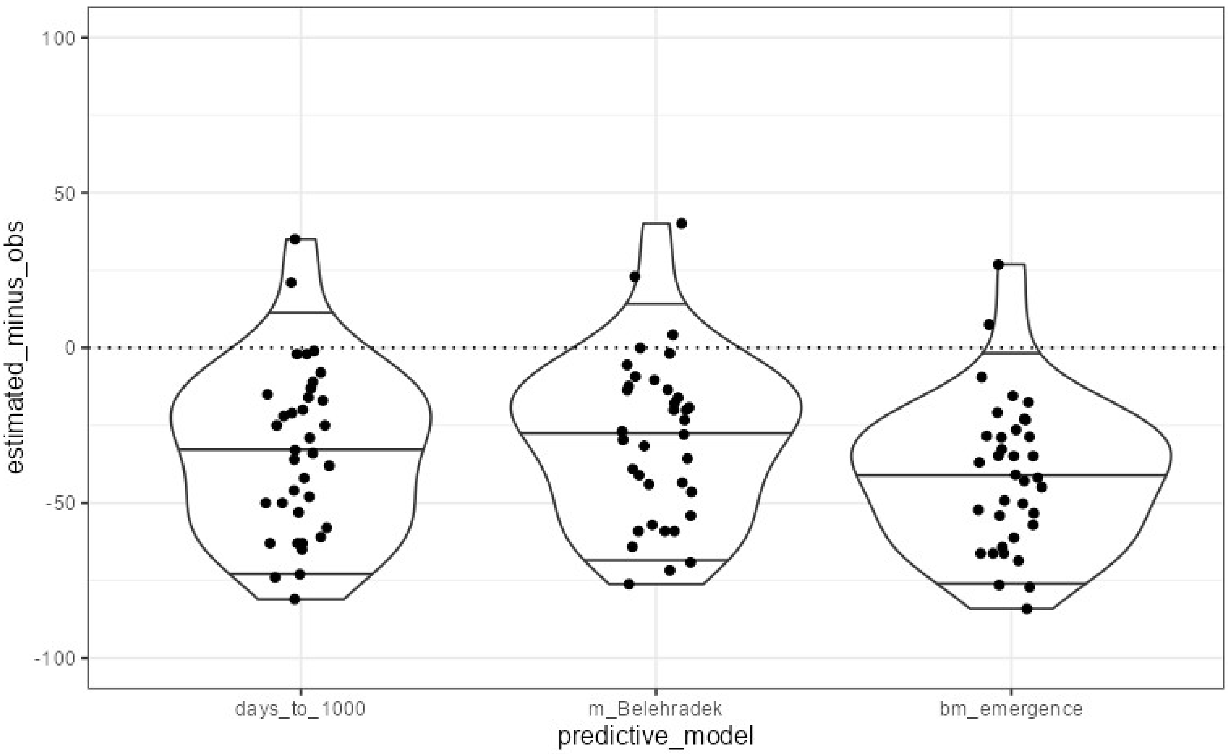

Figure 2.5. Violin plot illustrating the differences between predicted and observed days to emergence for three temperature-only models. Solid horizontal lines represent 5, 50, and 95th quantile ranges, and the dashed line the value at which an estimate would be equal to the observed median days of emergence for each trap.

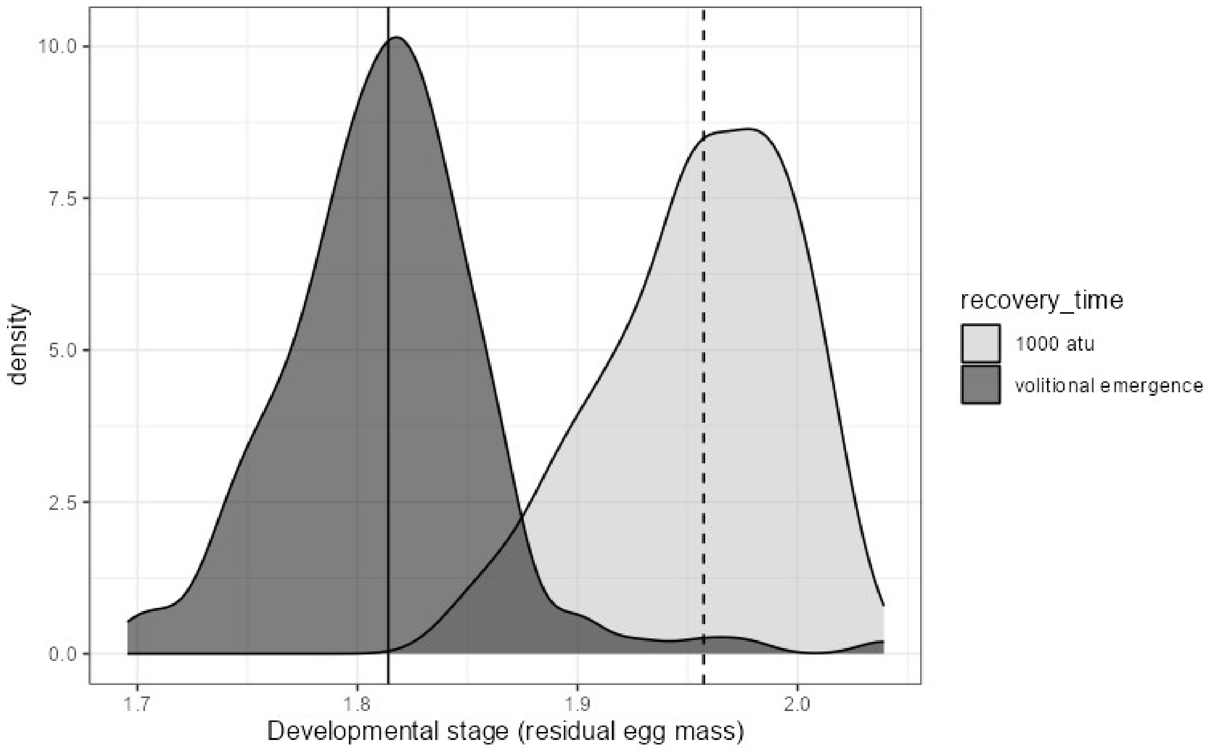

Figure 2.6. Distribution of developmental stage of Chinook salmon fry at emergence, and at predicted emergence based on a common temperature accumulation model.

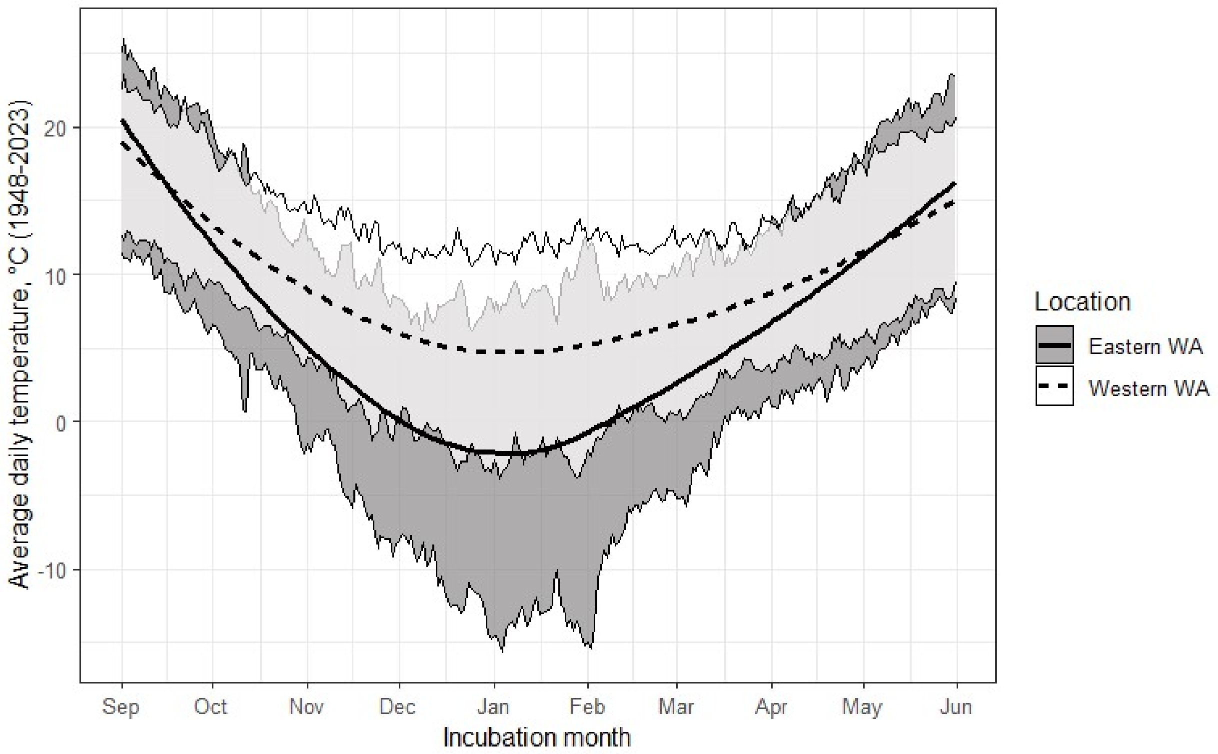

Figure 2.7. Average air temperature by the day of year over the period of incubation for Chinook salmon (1948-2023). Solid and dashed lines represent loess regression fits through daily temperatures in the city of Ellensburg Washington (Eastern WA; GHCND: USW00024220) and those in the city of Seattle Washington (Western WA; GHCND: USW00024234) respectively. Dark gray and white regions represent 2SD above and below the daily average temperature in Eastern and Western Washington locations respectively, and the light gray area overlap between the two.

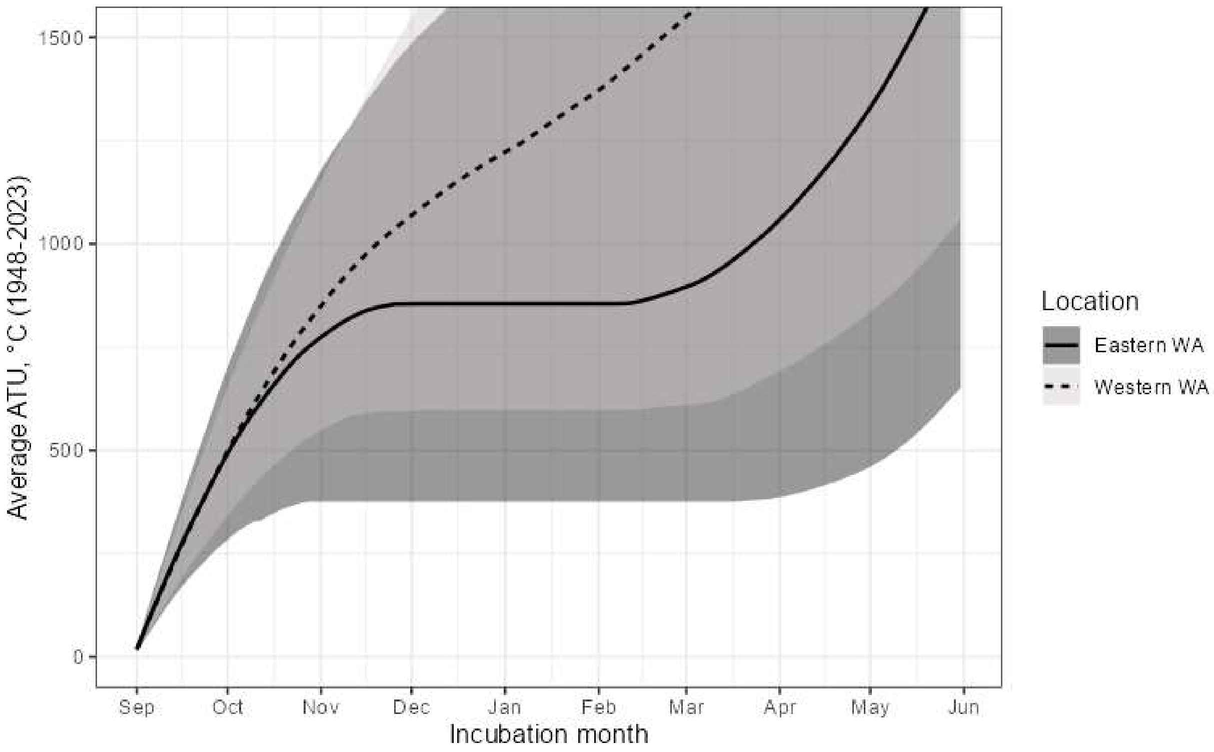

Figure 2.8. Average accumulated thermal units (ATU) by day-of-year, calculated from average air temperature over the period of incubation for Chinook salmon (1948-2023). Solid and dashed lines represent ATU from temperatures in the city of Ellensburg Washington (Eastern WA; GHCND: USW00024220) and those in the city of Seattle Washington (Western WA; GHCND: USW00024234) respectively. Dark gray and white regions represent 2SD above and below the mean in Eastern and Western Washington locations respectively, and the light gray area overlap between the two.

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