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Elevated stream temperature, origin, and individual size influence Chinook salmon prespawn mortality across the Columbia River Basin

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ABSTRACT

Conservation and restoration efforts for Pacific salmon *Oncorhynchus* spp. can be hampered by prespawn mortality, when adult fish reach reproductive sites but die before spawning. We examined annual estimates of female Chinook salmon *O. tshawytscha* prespawn mortality relative to individual fish traits (77,707 individual females) and reach-scale variables in 49 study reaches from 41 streams throughout the interior Columbia River Basin. Mean annual prespawn mortality estimates across 14 years ranged from 0 % to 65 %. For spring-run Chinook salmon, the probability of prespawn mortality decreased over the spawning period, was positively associated with mean August stream temperature and individual fish length, and was higher for hatchery-origin than natural-origin fish. Based on the basin-wide statistical model and future stream temperature predictions, average spring-run Chinook salmon prespawn mortality rates in 2040 were predicted to increase by 0–17 % for fish of natural origin and 1–17 % for fish of hatchery origin. Climate change is likely to exacerbate conditions that lead to prespawn mortality, particularly in low elevation stream reaches, for larger fish, and for those of hatchery origin.

1. Introduction

Each year, fisheries managers expend considerable effort to ensure that sufficient numbers of adult Pacific salmon *Oncorhynchus* spp. return to their natal habitats to reproduce. These efforts include limitations on the extent and duration of commercial and recreational fisheries (Mundy, 1997; Wang et al., 2018), trap and transport of adult salmon around impassable dams (Keefer et al., 2010; Lusardi and Moyle, 2017), and removal or non-lethal deterrence of marine mammals (Keefer et al., 2012; Schakner and Blumstein, 2013). However, the desired outcome of these actions—more reproducing fish—can be severely hampered by mortality along the migration route (termed *en route* mortality) and on the breeding grounds prior to completion of spawning (termed prespawn mortality; Gilhousen et al., 1990). Recent declines in several salmon populations have been attributed to high rates of adult mortality after their return to freshwater (Hinch et al., 2012). A combination of targeted studies and anecdotal evidence suggests that the phenomenon has increased in prevalence and scope in recent decades (Barnett et al., 2020; Hinch et al., 2012; Scholz et al., 2011), and reports of episodic salmon die-off events have become more common (Westley, 2020).

Anthropogenic and environmental factors can contribute to elevated premature mortality rates for adult salmon after they return to freshwater. *En route* mortality has been associated with exposure to pathogens (Hinch et al., 2012; Kocan et al., 2004) and environmental factors, such as elevated water temperatures (Farrell et al., 2008; Keefer et al., 2008; Martins et al., 2012) and high flow conditions (Martins et al., 2012; Minke-Martin et al., 2018). Environmental stressors and pathogens may in turn increase metabolic costs, leading to energetic depletion prior to reaching spawning grounds (Rand et al., 2006), since Pacific salmon cease feeding upon entering freshwater and energy stores steadily decrease until death (Brett, 1995).

In some cases, prespawn mortality may occur as a delayed result of the conditions encountered during migration (Minke-Martin et al., 2018). In other cases, salmon acquire diseases or encounter environmental conditions after arriving at the spawning grounds that may lead to physiological stress and reduced energy stores (Quinn et al., 2007). Depending on the salmon species and population, the period between arrival on spawning grounds and spawning can range from several days to many months (Quinn et al., 2016), so the effect of migration versus holding conditions varies. Understanding how environmental and anthropogenic factors contribute to premature death is important for fisheries forecasts and population recovery efforts. In many managed

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fisheries, escapement goals (the designated number of fish allowed to migrate up river to spawn) are established under the assumption that nearly all fish that escape the fishery go on to spawn (Cunningham et al., 2018). Mortality that occurs upstream of the fishery would therefore not be included in these estimates, potentially leading to lower recruitment than expected for escapement goals. Further, an understanding of factors that lead to prespawn mortality is an important component of salmon population models used to evaluate critical life stages for recovery planning (e.g., Honea et al., 2016; Jorgensen et al., 2009). Population projections indicate that even moderate prespawn mortality rates of 0.20 (i.e., 20 % of females that return to spawning grounds fail to lay eggs) can lead to a dramatic reduction in adult abundance in as few as 20 years and can thereby impede conservation, reintroduction, and restoration efforts (Spromberg and Scholz, 2011).

Prespawn mortality has been linked to a range of factors across Pacific salmon species, including elevated water temperatures (Barnett et al., 2020; Bowerman et al., 2018), infectious pathogens (Benda et al., 2015; Bradford et al., 2010), and pollutants in urban run-off (Scholz et al., 2011; Spromberg et al., 2015). In many cases, a combination of factors may interact to influence the likelihood of prespawn mortality. For example, high fish density coupled with warm temperatures can lead to anoxic conditions resulting in fish death near spawning grounds (Sergeant et al., 2017; Tillotson and Quinn, 2017). The effect of particular stressors can vary among species (Scholz et al., 2011) and even among individuals within a population. Certain individuals may be more susceptible to prespawn mortality due to the timing of migration or arrival on spawning grounds (Barnett et al., 2020; Hinch et al., 2012; Hruska et al., 2011), river conditions encountered during migration (Minke-Martin et al., 2018), or injuries related to infection, predation, or fisheries interactions (Baker and Schindler, 2009; Keefer et al., 2010). Miller et al. (2011) identified a genomic signature associated with premature mortality in sockeye salmon *O. nerka*, which the authors hypothesized occurred in response to a viral infection prior to freshwater entry.

Prespawn mortality has been observed in Chinook salmon *O. tshawytscha* populations throughout their range (Bowerman et al., 2016), but information is limited regarding factors that influence the phenomenon. Chinook salmon, the largest of the Pacific salmon species, have tremendous cultural, economic, and ecological importance throughout the west coast of North America. Chinook salmon express considerable variability in many life-history characteristics, including age at juvenile seaward migration and the timing of adult migration to natal streams (run timing) (Bourret et al., 2016). Populations are distinguished by this latter characteristic, identified as the season in which adults enter freshwater (e.g., spring-, summer-, or fall-run). The freshwater prespawn holding period in most Chinook salmon populations ranges from days (fall-run) to months (spring-, summer-run), as spawning occurs in the fall of the year in which they leave the ocean. Chinook salmon have experienced widespread population declines, and numerous population groups, known as Evolutionarily Significant Units (ESUs), are listed as threatened or endangered under the U.S. Endangered Species Act (National Marine Fisheries Service, 2005). Understanding factors that contribute to prespawn mortality within and among ESUs is therefore an important component in developing recovery plans for at-risk populations.

For many salmon populations, managers estimate annual prespawn mortality rates based on carcasses gathered during routine spawning ground surveys. The purpose of this study was to analyze existing data on individual Chinook salmon carcasses to examine large-scale patterns in potential factors affecting prespawn mortality throughout the diverse Columbia River Basin. First, we standardized data provided by numerous management agencies to calculate annual prespawn mortality rates for Chinook salmon in 49 study reaches in 41 streams over 14 years. Next, we examined the relationship between prespawn mortality and the following factors hypothesized to affect the likelihood of mortality: 1) Work, a measure of migration difficulty which we expected might be positively correlated with mortality; 2) annual stream temperature in the spawning area with the expectation that mortality would increase at higher water temperatures (Bowerman et al., 2018; Gilhousen et al., 1990); 3) origin, whether a fish reared in a hatchery or natural setting, since previous research has shown higher rates of prespawn mortality in populations with more hatchery fish (Bowerman et al., 2018; Young and Blenden, 2011); 4) individual fish length because the likelihood of premature mortality has been associated with fish size (Westley, 2020); and 5) relative date of carcass recovery because mortality risk changes with residence time on spawning grounds (Bowerman et al., 2016; Hruska et al., 2011). Finally, because model results for spring-run ESUs showed clear water temperature effects, we used the statistical model to forecast prespawn mortality rates under predicted future climatic conditions in spring Chinook salmon spawning streams throughout the Columbia River Basin.

2. Methods

2.1. Study area and populations

Chinook salmon carcasses were assessed annually during routine spawning ground surveys in 2000 through 2013 by state, federal, and tribal fisheries biologists in tributaries to the Columbia River in Oregon, Idaho, and Washington (Fig. 1). The Columbia River Basin encompasses a 670,000 km^2 area that supports numerous spatially and genetically distinct Chinook salmon populations with diverse life-history characteristics, including adult run timing (peak entry into freshwater), spawn timing (peak reproductive activity), and smolt age (age at which juveniles typically migrate to the ocean) (Hess et al., 2014; Waples et al., 2004). Populations have been grouped for management and conservation purposes into ESUs based on similarities in genetics and life-history characteristics (Waples, 1991). Sampled populations were from four distinct Chinook salmon ESUs (Fig. 1): the Snake River spring/summer-run (hereafter Snake River ESU), Middle Columbia River spring-run (Mid-Columbia ESU), Upper Columbia River spring-run (Upper Columbia spring ESU), and Upper Columbia summer/fall-run (Upper Columbia summer ESU). Under the U.S. Endangered Species Act, the Snake River ESU is listed as Threatened and the Upper Columbia spring ESU is listed as Endangered (National Marine Fisheries Service, 2005). The Snake River, Mid-Columbia, and Upper Columbia spring ESUs consist of populations in which adults begin their upstream migrations in March through June, peak spawning occurs from late August through early October, and juveniles migrate to the ocean at age 1–3 (Hess et al., 2014; Waples et al., 2004; Weitkamp et al., 2015). In contrast, adults from populations within the Upper Columbia summer ESU generally initiate freshwater migrations in June through September and spawn in October and November; juveniles outmigrate at age 0–1 (Mann and Snow, 2018; Waples et al., 2004; Weitkamp et al., 2015).

We initially received data from >60 distinct streams (some of which were tributaries to others in the dataset). We collated data at the scale of study reaches (5−35 km in length) based on locations of georeferenced individual carcasses recovered in spawning areas, which were available for at least a few years in most datasets. Where georeferenced data were unavailable, we relied on agency descriptions of carcass survey locations to identify and map specific study reaches. In most cases, the study reach encompassed a single stream (Fig. 1). In three locations where spawning habitat in a small tributary was adjacent to a primary stream, these data were combined. In locations where spawning occurred over a large spatial scale (e.g., 20−50 km) with high density spawning in multiple distinct geomorphic segments, streams were divided into two (South Fork Salmon River) or three (Umatilla River) study reaches that were demarcated by differences in habitat and spawn timing. In the Wenatchee and Methow rivers, the higher elevation study reaches were used by both the Upper Columbia spring and summer ESUs, which were differentiated by the date of carcass recovery; carcasses found prior to October 1 were considered part of the Upper Columbia spring ESU and

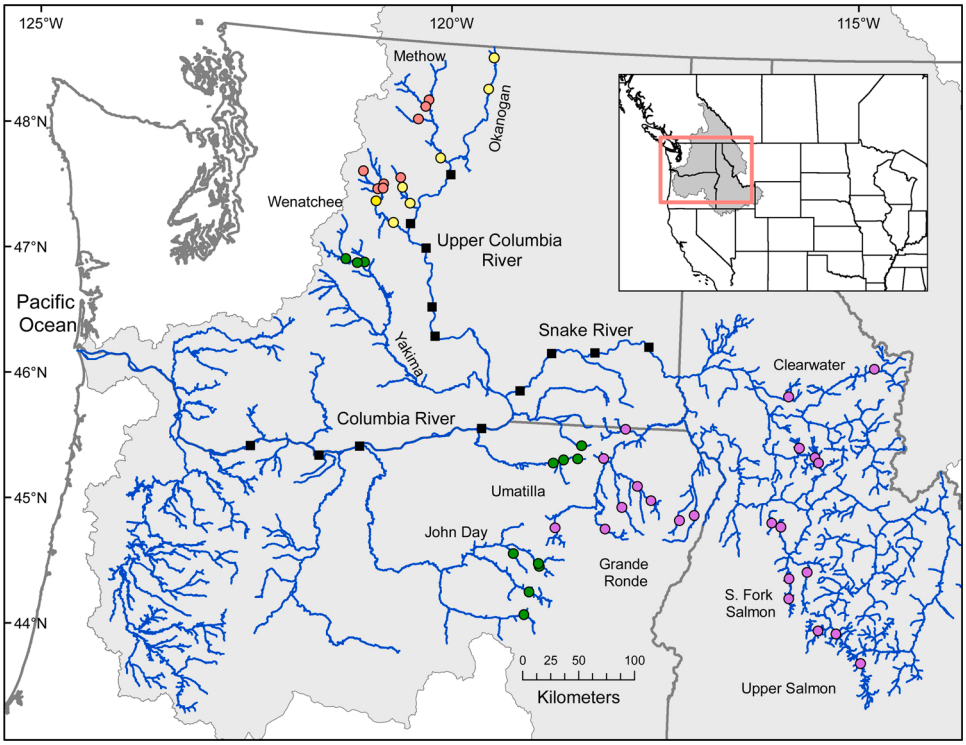

Fig. 1. Location of study reaches where female Chinook salmon carcasses were collected to estimate prespawn mortality within four Evolutionarily Significant Units: Snake River spring/summer Chinook (purple), Middle Columbia spring Chinook (green), Upper Columbia spring Chinook (red), and Upper Columbia summer/fall Chinook (yellow). Black squares indicate location of major dams with fish passage.

those found after belonged to the summer ESU (Murdoch et al., 2009).

2.2. Individual Chinook salmon data

Spawning ground survey methods differed among locations and source organizations. We made every effort to understand methods from each location and to standardize the data to minimize biases associated with variations in sampling methods and sample size. To this end, we only included data from study reaches where data were available for at least five years in which spawning status was known for 10 or more female carcasses, and where at least three surveys were conducted at regular intervals throughout an annual spawning season. The latter criterion was meant to ensure sampling throughout the spawning season, since early season carcasses were more likely to be prespawn mortalities and thus sampling only during this period could bias annual estimates high whereas sampling only later in the season would not detect early mortalities and could bias annual estimates low (Bowerman et al., 2016).

We estimated annual prespawn mortality rates over 5–14 years in 49 study reaches (within 41 streams) that met the inclusion criteria (Table 1). The mean number of carcasses collected annually per study reach ranged from 16 to 759. In some locations, carcass surveys began during the holding period, weeks to months before spawning commenced (e.g., 50 days before the first spawned out carcass was observed). Many of these "holding period" surveys were conducted in only a portion of the total spawning area, and in some locations holding period surveys were performed in only a few years of the study. Holding period carcasses were defined as an unspawned carcass recovered >7 d prior to the date of the first spawned carcass (void of eggs) observed in a study reach. To evaluate the sensitivity of results to inclusion of mortality observed during the holding period, we ran all analyses twice: once including all data (holding period dataset), and once with the holding period data removed (spawning period dataset). There were three study reaches in which a substantial percentage of total carcasses was collected during the holding period and therefore removal of these data affected annual prespawn mortality estimates: the upper South Fork Salmon River, Imnaha River, and Newsome Creek (Table 1). No such comparisons were made for Upper Columbia summer ESU; Because this group was defined as carcasses collected after 1 October, there were no early season carcasses included in this dataset (hence, it is possible that some holding period mortalities for summer-run populations could have been ascribed to spring-run spawning season mortalities in locations where the two ESUs overlap).

We analyzed data from female carcasses recovered on spawning grounds, where female prespawn mortality was assessed by opening the body cavity to examine the gonads (Bowerman et al., 2016; Hughes and Murdoch, 2017). In almost all datasets, 100 % of fresh carcasses were assessed for egg retention, so there was no need to account for differences in sampling rate. Carcasses for which spawning success could not be determined because of predation or decomposition were excluded from analyses. In some locations, prespawn mortality was recorded simply as a binary outcome, which we scored as 1 when the body cavity of a carcass was full of eggs, or an egg skein was still intact (prespawn mortality) and 0 for an empty body cavity (presumed successful spawner). When percent spawned had been recorded, whether based on visual estimates or egg mass or volume, the female was considered a prespawn mortality if observers estimated >50 % of eggs remained at time of death (note that most of these were recorded as >75 % egg retention, but methods differed slightly among study reaches). In a few locations, prespawn mortality was reported as a categorical response with three outcomes: spawned (<25 % of eggs retained), partially spawned (25–75 % of eggs retained), or unspawned (>75 % of eggs retained). In these datasets, partially spawned carcasses were included as prespawn mortalities; the percentage of partially spawned carcasses was typically less than 10 % of all carcasses evaluated. We excluded from analyses partially spawned carcasses from the Entiat River, as these data ambiguously included females that had retained anywhere from 2 %–99 % of eggs (111 partially spawned Upper Columbia summer

Table 1
Locations throughout the Columbia River Basin where female Chinook salmon carcasses were collected annually in years 2000 through 2013 to estimate prespawn mortality. Study reaches are organized within major population groups (in italics) and evolutionarily significant units (ESU in bold). Within the Upper Columbia River, spring- and summer/fall-run Chinook Salmon are denoted with SP and SU, respectively. Summary data show the number of years over which data were collected, mean number of carcasses collected annually, mean annual prespawn mortality (PSM) rate (and range), mean average August temperature (Stream Temp; i.e., annual *MeanTemp* averaged across years), and mean proportion of natural-origin spawners. Work was calculated as distance from ocean to spawning grounds (km)×elevation gain (m)/1000. Data include carcasses collected during the prespawn holding period; prespawn mortality estimates based on a subset of data with these early season carcasses excluded were within 0.02 of what is listed here, except where noted.

ESU/*population group*/ study reach	Years (*n*)	Carcass (*n*)	PSM rate (range)	Stream Temp (℃)	Natural origin	Work
Snake River spring/summer-run ESU						
Grande Ronde-Imnaha						
Catherine Ck.	13	83	0.05 (0.00–0.14)	16.47	0.43	950
Grande Ronde R.	10	87	0.26 (0.00–0.82)	16.45	0.31	1264
Lookingglass Ck.	11	89	0.08 (0.00–0.15)	11.21	0.17	750
Lostine R.	14	179	0.16 (0.05–0.35)	15.25	0.39	914
Minam R.	14	33	0.04 (0.00–0.14)	13.85	0.95	1019
Wallowa R.	9	19	0.02 (0.00–0.09)	15.49	0.79	1112
Wenaha R.	13	25	0.00 (0.00–0.04)	13.18	0.91	566
Big Sheep Ck.	7	24	0.25 (0.03–0.54)	13.56	0.08	1104
Imnaha R.[a]	14	219	0.16 (0.03–0.51)	15.79	0.40	833
Clearwater River						
American R.	9	44	0.05 (0.00–0.19)	14.78	0.35	1176
Legendary Bear Ck.	5	25	0.10 (0.00–0.16)	12.17	0.52	1032
Lolo Ck.	9	39	0.13 (0.04–0.29)	17.53	0.70	753
Newsome Ck.[b]	6	23	0.35 (0.15–0.50)	13.57	0.46	1152
Red R.	11	98	0.25 (0.00–0.76)	16.38	0.24	1255
S. Fork Salmon River						
Johnson Ck.	14	167	0.12 (0.03–0.39)	12.80	0.72	1734
Lake Ck.	14	75	0.03 (0.00–0.14)	11.63	0.98	2102
SF Salmon R. low	14	225	0.17 (0.05–0.48)	15.64	0.45	1336
SF Salmon R. up[c]	14	182	0.28 (0.00–0.57)	13.74	0.73	1866
Secesh R.	14	89	0.03 (0.00–0.19)	12.68	0.96	1971
Upper Salmon River						
Marsh Ck.	12	72	0.01 (0.00–0.07)	11.86	0.99	2628
Bear Valley Ck.	6	45	0.03 (0.00–0.11)	14.46	1.00	2580
Up. Salmon R.	14	80	0.10 (0.00–0.35)	14.10	0.65	2232
Middle Columbia River spring-run ESU						
Blue Mountains						
NF Umatilla R.	10	38	0.04 (0.00–0.20)	11.34	0.44	456
Umatilla R. low	13	75	0.65 (0.20–0.97)	19.05	0.21	284
Umatilla R. up	14	191	0.42 (0.13–1.00)	16.88	0.20	337
SF Walla Walla R.	6	50	0.08 (0.00–0.25)	10.11	0.69	424
John Day River						
Desolation Ck. (NF)	7	16	0.11 (0.00–0.29)	14.56	0.83	865
Granite Ck. (NF)	13	64	0.12 (0.00–0.55)	16.16	0.97	980
Upper John Day R.	12	53	0.03 (0.00–0.09)	16.22	0.98	825
MF John Day R.	13	90	0.05 (0.00–0.38)	17.52	0.98	907
NF John Day R.	13	98	0.09 (0.00–0.30)	14.84	0.94	964
Yakima River						
Cle Elum R.	9	97	0.02 (0.00–0.07)	16.33	0.60	522
Teanaway R.	7	46	0.03 (0.00–0.12)	17.49	0.22	480
Yakima R.	9	759	0.03 (0.00–0.11)	15.93	0.42	474
Upper Columbia River spring-run ESU (SP) and summer/fall-run ESU (SU)						
Entiat River						
Entiat R. low SU	13	34	0.43 (0.10–0.67)	16.59	0.40	240
Entiat R. up SU	11	39	0.02 (0.00–0.10)	15.13	0.92	387
Entiat R. up SP	12	38	0.02 (0.00–0.08)	14.03	0.58	415
Methow River						
Chewuch R. SP	13	102	0.03 (0.00–0.09)	14.67	0.26	537
Methow R. low SU	14	368	0.03 (0.00–0.08)	18.03	0.62	242
Methow R. up SP	13	212	0.03 (0.00–0.07)	13.32	0.17	501
Twisp R. SP	11	32	0.05 (0.00–0.20)	13.00	0.48	618
Okanogan-Similkameen						
Okanogan R. SU	13	329	0.04 (0.01–0.32)	21.35	0.63	254
Similkameen R. SU	13	569	0.09 (0.00–0.87)	19.94	0.46	272
Wenatchee River						
Chiwawa R. SP	14	156	0.08 (0.01–0.19)	12.52	0.32	523
Nason Ck. SP	14	104	0.08 (0.00–0.19)	15.69	0.43	487
Wenatchee R. low SU	14	649	0.02 (0.00–0.06)	18.18	0.67	191
Wenatchee R. up SU	14	288	0.01 (0.00–0.03)	17.97	0.96	425
Wenatchee R. up SP	8	36	0.27 (0.15–0.40)	17.92	0.14	474
White R. SP	9	35	0.03 (0.00–0.10)	12.49	0.49	511

[a] Without holding period mortalities, carcass $n = 208$; PSM rate = 0.13 (0.03−0.34).
[b] Without holding period mortalities, carcass $n = 19$; PSM rate = 0.04 (0.00−0.10).
[c] Without holding period mortalities, carcass $n = 135$; mean PSM rate = 0.14 (0.00−0.57).

Chinook and 10 Upper Columbia spring Chinook salmon were excluded).

We included three predictor variables that were measured on individual Chinook salmon carcasses: fork length (cm; hereafter *Length*), *Origin*, and *Day*. We included a length variable in analyses to examine the potential for differential mortality among fish of different sizes (Westley, 2020). Fork length was used because it was the most widely collected size metric. When a different length measurement was used (e.g., post-orbital to hypural length or mid-eye to hypural length), we estimated fork length based on a linear relationship with the alternative length metric developed with available data that included both measurements. We hypothesized that prespawn mortality would be higher in salmon of hatchery origin, as has been suggested by previous studies (Bowerman et al., 2018). *Origin* (hatchery [1], natural [0]) was determined by a variety of different methods depending on the location, including via fin clips (adipose fins were removed from hatchery-origin fish), coded wire tags found in hatchery-origin fish, and scale pattern analysis (e.g., Murdoch et al., 2010). Fish whose origin was marked as unknown were omitted from later analyses because sample sizes were small and inconsistent among study reaches, leading to data balance issues without adding to biological inference. We included a variable *Day* that represented relative date of carcass recovery in a given year and study reach to account for the effect of within-season sampling variation on the probability of prespawn mortality (Bowerman et al., 2016). This was calculated as: $Day_{ijk} = recoverydate_{ijk} - meanrecoverydate_{ij}$ for a carcass k in year j in reach i.

2.3. Reach-scale variables

Two predictor variables were assembled at the study reach scale. The variable *MeanTemp* referred to the modeled annual mean August stream temperature for each year of data collected (2000 through 2013), which was generated using the publicly available NorWeST stream temperature model (Isaak et al., 2017). Stream temperature has been linked to prespawn mortality in previous studies (Bowerman et al., 2018; Keefer et al., 2010; Quinn et al., 2007) and the NorWeST mean August temperature data were used because they provided consistent, spatially continuous annual temperature estimates for streams throughout the entire Columbia River Basin. Estimates of *MeanTemp* were taken at the farthest downstream location of observed high-density spawning within each study reach. In the upper Wenatchee River and upper Entiat River study reaches, spawning distributions overlapped spatially for spring- and summer-run Chinook salmon but reach-scale variables were different because the summer-run ESU high-density spawning areas were located farther downstream in the reach.

The variable *Work* was a combination of distance and elevation described by *Work* = distance*elevation/1000 where distance was the linear stream distance (km) from the ocean to the downstream end of the study reach and elevation (m) above sea level was measured at the same location (Quinn, 2018). Elevation measurements were taken from the NorWeST dataset, and were derived from digital elevation models associated with the NHDPlus dataset (Isaak et al., 2017). *Work* was included as a predictor variable because we hypothesized that Chinook salmon populations with more strenuous migrations might be more susceptible to prespawn mortality. There was a single *Work* value assigned to each study reach (i.e., the value did not change among years).

2.4. Statistical analyses

Before running any statistical analyses, we performed a range of preprocessing data checks to look for potential data errors, outliers, and collinearity among variables. Variables included in analyses showed no indication of collinearity (VIF < 2 in all datasets), and parameter estimates were minimally affected by influential observations. We used generalized linear mixed effect models (GLMMs) in the LME4 package in R (Bates et al., 2015) with a binomial error structure to evaluate the effects of individual salmon traits and reach-scale variables on the probability of a female Chinook salmon dying prior to discharging eggs. GLMMs were used to predict the probability of prespawn mortality (1) or successful spawning (0). We used the model structure

$$logit(PSM_{ijk}) \sim \beta_0 + \beta_1 Day_{ijk} + \beta_2 Length_{ijk} + \beta_3 Origin_{ijk} + \beta_4 MeanTemp_{ij} + \beta_4 Work_i + a_i + b_j$$

where PSM_{ijk} is the probability of an individual fish k dying prior to spawning in year j in reach i. Study reach a_i and year b_j were included as crossed random effects to account for random variation among sites (i.e., site effect across years) and among years (i.e., year effect among sites). Prior to analyses, all predictor variables aside from *Origin* were standardized by subtracting the mean value and dividing by the standard deviation to aid model convergence and comparison of effects sizes among variables (Harrison et al., 2018).

We developed a set of candidate models that included all additive combinations of explanatory variables and the following two-way interactions: *MeanTemp* x *Length*, *MeanTemp* x *Origin*, and *Origin* x *Length*. We compared models based on Akaike's information criterion for finite sample sizes (AICc). For top-ranked models from each dataset (<4 AICc), we evaluated goodness-of-fit based on examination of residuals from 500 simulations of the fitted model with the DHARMa package in R (Hartig, 2019). For these models, we also estimated the amount of variation explained by the predictor variables (marginal R^2) relative to the total variation explained by both the predictors and the intrinsic differences among years and study reaches (conditional R^2) using the package MuMin (Barton, 2018). Standardized coefficients were model averaged using the natural average method, which takes into account model weights (Burnham and Anderson, 2002).

To better understand prespawn mortality patterns within salmon management units, we initially modeled each of the four ESUs separately. We then analyzed data from the Snake River, Mid-Columbia, and Upper Columbia spring Chinook ESUs collectively to create a general model that would allow us to predict future prespawn mortality rates for spring Chinook salmon throughout the Columbia River Basin (combined spring Chinook model). We omitted the Upper Columbia summer ESU from the latter analysis because salmon in this ESU are genetically and phenotypically distinct from the other three ESUs, as described above. For all spring-run Chinook ESUs and the combined spring-run data, we ran the same analysis twice: once with the complete dataset that included holding period prespawn mortalities (holding period dataset), and once with those early season mortalities excluded from the data (spawning period dataset). All modelling steps described above were replicated for each dataset. To better understand the potential influence of individual study reaches on model results, we performed a leave-one-out cross validation by running the top-ranked models with a subset of the data in which each study reach was sequentially removed (with replacement), and additionally with the entire stream removed for streams with more than one study reach.

2.5. Model-predicted future prespawn mortality rates

The random effects structure of the combined spring Chinook GLMM enabled its use to predict prespawn mortality rates in locations where we lacked data (Harrison et al., 2018). To evaluate a general trend in future prespawn mortality rates under scenarios of climatic warming, we used projected mean August stream temperatures from the NorWeST stream temperature model (Isaak et al., 2017) as a fixed effect in the combined spring Chinook GLMM. Predicted stream temperatures were based on average projected August air temperature and stream discharge from a global climate model ensemble used to simulate the A1B emissions scenario for the 2040s (Intergovernmental Panel on Climate Change, 2000). Future stream temperature predictions accounted for differential sensitivity among streams to changes in air temperature such that the

coldest streams were less responsive to climatic variation than warmer streams (future scenario S30_2040_D; see Isaak et al., 2017 for details). Mean August stream temperatures projected by the NorWeST stream temperature model and used to forecast prespawn mortality in the 42 spring Chinook study reaches were between 1.2 °C and 1.9 °C higher in the 2040 scenario than the mean temperatures from 2000–2013.

Within the statistical model from the full dataset (including carcasses collected during the holding period), we used random intercept adjustments for individual study reaches from the Spring Chinook dataset ($n = 42$) with the average year intercept across sites to predict mean prespawn mortality rates for each of those reaches in 2040 for both natural- and hatchery-origin fish. We also used the combined spring Chinook GLMM to predict mean prespawn mortality rates for stream reaches that were not included in the initial statistical analysis due to insufficient carcass data ($n = 85$), but which were identified as spring Chinook spawning areas in the StreamNet database (StreamNet, 2019). For stream reaches where we lacked carcass data, we used the mean random effects values for both year and stream reach, and we estimated historic prespawn mortality rates based on mean August temperature estimates between 2002 and 2011 (scenario S2_02_11), and future rates in 2040 (S30_2040_D), both from the NorWeST model (Isaak et al., 2017).

3. Results

3.1. Prespawn mortality estimates

The mean annual reach-specific prespawn mortality rate for natural- and hatchery-origin fish combined ranged from 0.00 to 0.82 (*mean* = 0.17, $n = 247$ estimates) in the Snake River ESU, 0.00–1.00 in the Mid-Columbia ESU (*mean* = 0.12, $n = 126$), 0.04–0.40 in the Upper Columbia spring ESU (*mean* = 0.06, $n = 94$), and 0.00 to 0.87 in the Upper Columbia summer ESU (*mean* = 0.09, $n = 92$) (Table 1). When averaged across years and study reaches, mean estimates were 0.13 higher for hatchery-origin compared with natural-origin salmon in the Mid-Columbia ESU, 0.06 higher in the Snake River ESU, 0.05 higher in the Upper Columbia spring ESU, and 0.06 higher in the Upper Columbia summer ESU (Fig. 2). When observations were limited to study reaches with consistent returns of both hatchery- and natural-origin fish, average prespawn mortality rates were generally similar to or higher for hatchery-origin compared with natural-origin Chinook salmon in all four ESUs. However, many study reaches were predominated by either Chinook salmon of hatchery origin (e.g., Umatilla River and Upper Columbia spring ESU) or natural origin (e.g., Upper Salmon River and John Day River major population groups) and thus direct comparisons were not available for some study reaches.

3.2. River temperatures

Across all study reaches, *MeanTemp* estimates ranged from 9.52 to 21.93 °C, with *MeanTemp* estimates for most study reaches falling between 12.00 and 16.00 °C (Table 1). Only four study reaches regularly had mean August temperatures >18.00 °C, including three that were primarily used by Upper Columbia River summer-run Chinook salmon (Okanogan, Similkameen, and lower Wenatchee rivers), and one that was within the Mid-Columbia spring ESU (lower Umatilla River). Within study reaches, *MeanTemp* estimates showed minimal variability among years, such that among-year differences in *MeanTemp* values within individual study reaches ranged from 1.19 °C to 1.94 °C.

3.3. Prespawn mortality models

The best-supported GLMMs to predict the probability of prespawn mortality in all models included *Day*, the relative date of carcass collection. Models that included *Day* explained substantially more variation in the data compared to those without *Day* (e.g., marginal R^2 was 0.05–0.24 higher). By definition, all carcasses recovered prior to spawning season were prespawn mortalities, and the probability of prespawn mortality decreased from 1 to 0 over the course of the spawning period (Fig. 3). The effect of *Day* was smaller but still considerable when carcasses collected during the holding period were excluded from the dataset (Fig. 4).

After accounting for the effect of sampling date, *Length*, *MeanTemp*, and *Origin* and interaction terms had the greatest effect on the

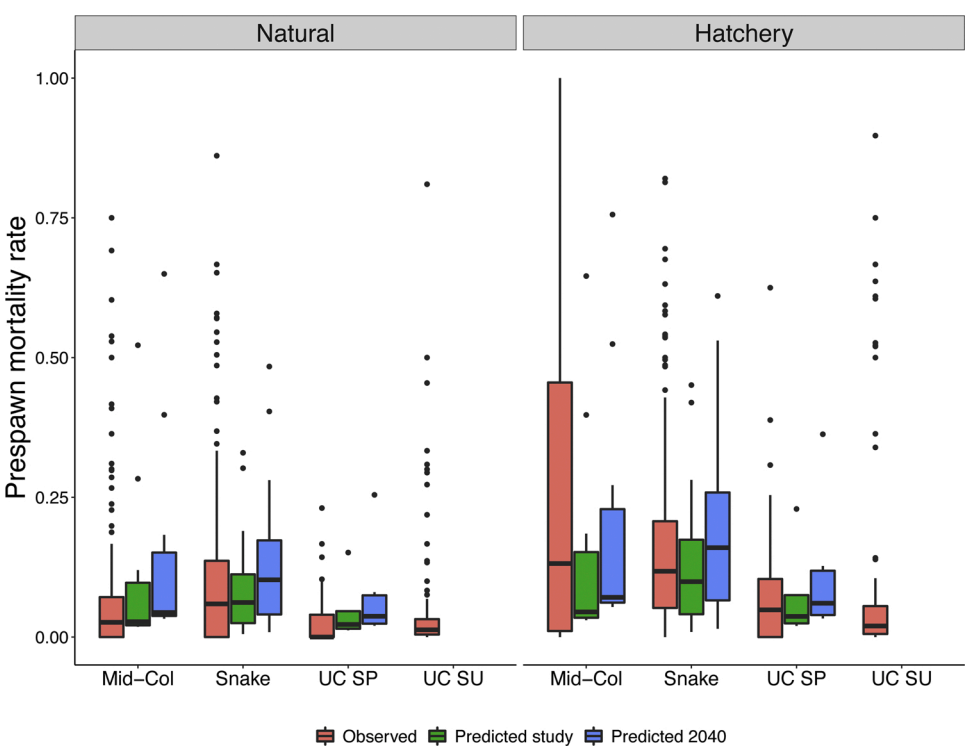

Fig. 2. Observed prespawn mortality rates (red) for Chinook salmon for the years 2000-2013, and predicted prespawn mortality probabilities based on mean August stream temperatures during the study period (2002-2011; green) and 2040 stream temperature scenarios (blue) in the same study reaches. Predictions for the Middle Columbia River spring-run (Mid-Col), Snake River spring/summer-run (Snake) and Upper Columbia spring-run (UC SP) Evolutionarily Significant Units were based on the combined spring Chinook GLMM for fish of median *Length* (76 cm) and mean collection date (*Day* = 0). Predictions were not made for Upper Columbia summer/fall Chinook salmon (UC SU) because stream temperature was not a significant predictor of prespawn mortality. Boxes and whiskers show median, interquartile range, and 10th and 90th percentiles; dots are outliers.

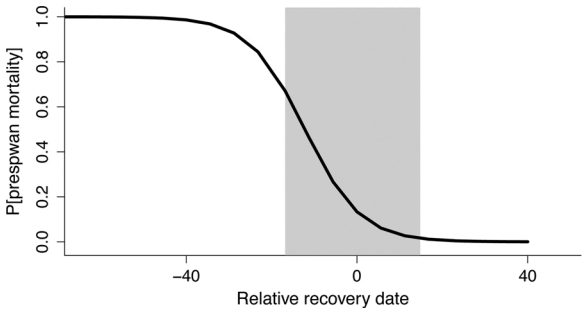

Fig. 3. Predicted probability of prespawn mortality in relation to the relative carcass recovery date ($Date_{ijk} = recoverydate_{ijk} - meanrecoverydate_{ij}$ for a carcass k in year j in reach i) from the combined spring Chinook GLMM. The gray shaded portion denotes a typical spawning period.

probability of prespawn mortality (Fig. 4). In the Mid-Columbia ESU, the probability of prespawn mortality increased with temperature, and there was in interaction between *Length* and *MeanTemp*, such that at higher temperatures (e.g., >16 °C) the probability of prespawn mortality increased more rapidly for larger individuals (Table 2; Fig. 5A). In the Snake ESU, the probability of prespawn mortality increased with *MeanTemp* and was higher for fish of hatchery *Origin*. There was also evidence of an interaction between the two variables (Fig. 4), suggesting that prespawn mortality probability was greater for hatchery origin fish at lower temperatures, but at higher temperatures the difference was less apparent (Fig. 5B). In the Upper Columbia spring ESU, model weight was shared among eight candidate models that were within 4 AICc units of the top ranked model (Table 2), but *MeanTemp* and *Origin* were the only variables besides *Day* for which 95 % confidence intervals did not overlap zero (Fig. 4). Model- averaged parameter estimates indicated that the probability of prespawn mortality increased with stream temperature and was higher for hatchery-origin fish (Fig. 5C).

For the combined spring Chinook dataset, prespawn mortality probabilities increased with *MeanTemp* and individual fish *Length* and were higher for hatchery- than for natural- *Origin* fish. An interaction term between *MeanTemp* and *Origin* indicated that at lower temperatures (e.g., <18 °C), prespawn mortality probabilities were slightly higher for hatchery-origin fish but estimates were similar as temperatures approached 20 °C (Fig. 6). In the combined spring Chinook model, 95 % confidence intervals on parameter estimates for the variable *Length* did not overlap zero, although the effect size of *Length* was smaller than that of *Temp*, *Origin*, and the *MeanTemp* × *Origin* interaction term (Fig. 4). Models that included the variable *Work* also ranked among the highest, but it was not considered an informative parameter, since parameter estimates for *Work* overlapped zero in all models where it was included (Fig. 4).

In the Upper Columbia summer/fall Chinook salmon ESU, *MeanTemp* and *Length* were included in the top-ranked models, but only *Origin* had a

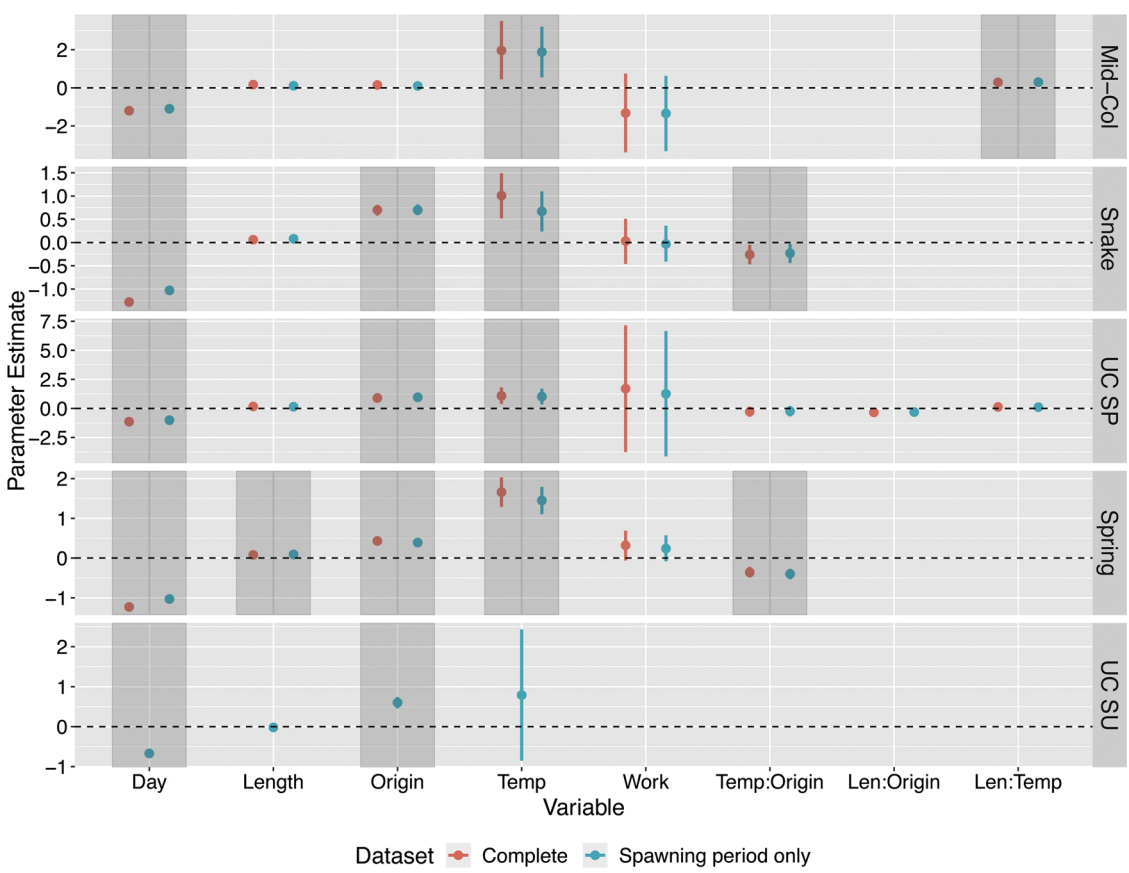

Fig. 4. Model-averaged parameter estimates for fixed effects predicting the probability of female Chinook salmon prespawn mortality in the Middle Columbia River spring-run (Mid-Col), Snake River spring/summer-run (Snake), Upper Columbia River spring-run (UC SP), combined spring-run (Spring), and Upper Columbia summer/fall-run (UC SU) Evolutionarily Significant Units. Continuous predictor variables were standardized prior to analysis. Parameters correspond with models shown in Table 2 and are defined as: relative date of carcass recovery (*Day* mean = 0.00, SD = 8.77), individual fork length (*Length* mean cm = 81.35, SD = 9.67), *Origin* (whether an individual had signs that it originated in a hatchery [1]; otherwise it was presumed of natural origin [0]), and mean August stream temperature (*MeanTemp* °C mean = 16.42, SD = 2.56), and a measure of migration difficulty (*Work* mean = 682.10, SD = 562.27). Models were run with a complete dataset that included prespawn mortalities collected during the holding period (red), and a subset of data collected only during the observed spawning period (blue). Error bars show 95 % confidence intervals; gray shading denotes those which do not overlap zero (dashed line). Note that some error bars are small relative to the size of the points; note the difference in y-axis scales.

Table 2
Comparison of the best-supported generalized linear mixed models (GLMM) predicting variation in female Chinook salmon prespawn mortality probability. AICc value, ΔAICc (the difference in AICc value between model and the candidate model with the lowest AICc value), and AICc weight (w_i ; the relatively likelihood of model *i* compared with the other candidate models) are given for models ranked within 4 AICc points of the best-supported model. All models included crossed random effects of study reach and year. Conditional R^2 (R^2 Cond) is the proportion of variance explained by the entire model (fixed and random factors) and marginal R^2 (R^2 Mar) is the proportion of variance explained by the fixed components of the model.

Dataset and Model	AICc	ΔAICc	w_i	R^2 Mar	R^2 Cond
A. Middle Columbia River spring-run ESU					
Day + Length + Origin + Temp + Length*Temp	6276.42	0.00	0.38	0.23	0.66
Day + Length + Origin + Temp + Work + Length*Temp	6277.07	0.65	0.27	0.27	0.63
Day + Length + Temp + Length*Temp	6277.09	0.67	0.27	0.23	0.66
B. Snake River spring/summer-run ESU					
Day + Length + Origin + Temp + Temp*Origin	11747.95	0.00	0.36	0.38	0.59
Day + Origin + Temp + Tempx*Origin	11748.59	0.64	0.26	0.38	0.59
Day + Length + Origin + Temp + Work + Temp*Origin	11749.93	1.98	0.14	0.38	0.59
Day + Length + Temp + Origin	11750.96	3.01	0.08	0.38	0.59
C. Upper Columbia River spring-run ESU					
Day + Origin + Temp	2988.85	0.00	0.22	0.30	0.40
Day + Origin + Temp + Temp*Origin	2989.29	0.44	0.18	0.30	0.41
Day + Length + Origin + Temp + Length*Origin	2989.63	0.78	0.15	0.30	0.40
Day + Length + Origin + Temp	2990.52	1.67	0.10	0.30	0.40
Day + Length + Origin + Temp + Temp*Origin	2990.98	2.13	0.08	0.30	0.40
Day + Length + Origin + Temp + Length*Temp	2991.27	2.42	0.07	0.30	0.40
Day + Length + Origin + Temp + Work + Length*Origin	2991.37	2.52	0.06	0.30	0.40
Day + Length + Origin + Temp + Work + Temp*Origin	2992.16	3.30	0.04	0.30	0.40
D. Combined Spring Run					
Day + Length + Origin + Temp + Work + Temp*Origin	21285.9	0.00	0.57	0.34	0.58
Day + Length + Origin + Temp + Temp*Origin	21286.59	0.70	0.40	0.35	0.59
E. Upper Columbia River summer-run ESU					
Day + Origin	7376.17	0.00	0.40	0.06	0.54
Day + Origin + Temp	7376.99	0.81	0.27	0.09	0.56
Day + Length + Origin	7378.03	1.86	0.16	0.09	0.56
Day + Length + Temp + Origin	7378.85	2.68	0.10	0.09	0.56

clear effect size with 95 % confidence intervals that did not overlap zero. The prespawn mortality probability was 0.01 higher for hatchery *Origin* individuals compared with those of natural origin.

3.4. Model sensitivity

Evaluation of model fit indicated that the combined spring Chinook GLMM captured the general pattern in prespawn mortality rates in the observed data, and model-predicted prespawn mortality rates based on average 2002–2011 *MeanTemp* estimates from the NorWeST model were within 0.05 of average observed prespawn mortality rates during the 2000–2013 period in 34 of 42 study reaches. However, the total amount

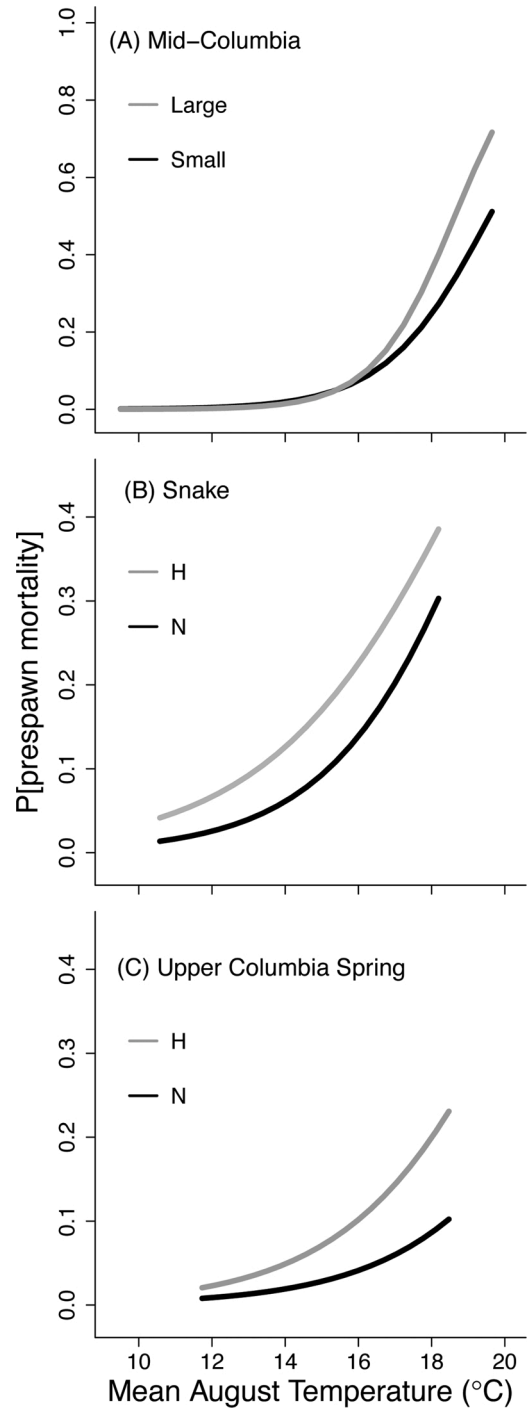

Fig. 5. Predicted probability of prespawn mortality for individual female spring Chinook salmon relative to mean August stream temperature for large fish in the (95th size percentile = 95 cm FL; gray line) and small fish (5th size percentile = 65 cm FL; black line) in the Middle Columbia spring-run ESU (A), and fish of and hatchery- (gray line) and natural-origin (black line) in the Snake River spring/summer-run ESU (B) and the Upper Columbia spring-run ESU (C). Note the difference in y-axis scales.

of variation in the data explained by the models ranged from 0.40 to 0.66 (Table 2), indicating that there were additional factors contributing to prespawn mortality that were not included in the modeling process. The random component of the models (year and study reach) explained a substantial portion of the variation in prespawn mortality, particularly in the Mid-Columbia and Upper Columbia summer ESUs, suggesting that there were inherent differences in populations, environmental

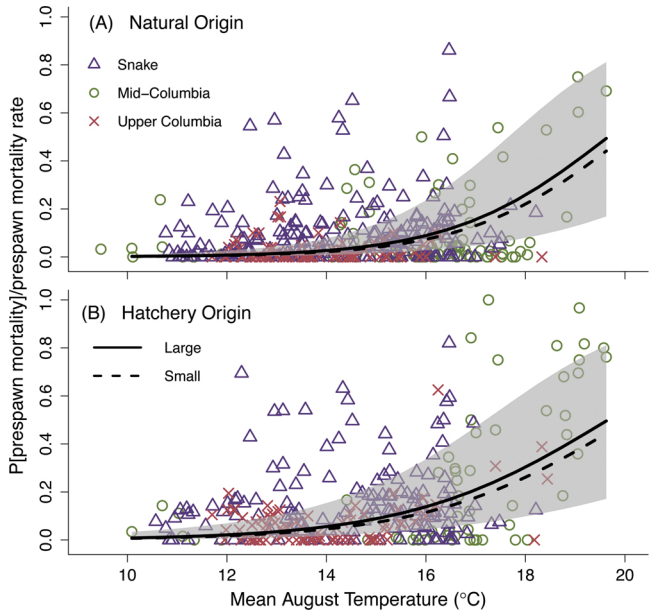

Fig. 6. Predicted prespawn mortality probability for individual female Chinook salmon based on the combined spring Chinook model (shaded area: 95 % confidence interval) relative to temperature for fish in the 5th size percentile of length (65 cm FL; dashed line) and the 95th length percentile (95 cm FL; solid line) of natural- (A) and hatchery- (B) origin. Observed reach-specific annual prespawn mortality rates are shown for each of three ESUs: mid-Columbia spring-run (green circle), Snake River spring/summer run (purple triangle), and upper Columbia spring-run (red X).

conditions, management strategies, and/or sampling methods that contributed to variation in prespawn mortality estimates among years and sites.

The cross-validation analysis indicated that within the Mid-Columbia ESU, model results were sensitive to the omission of data from a single stream. When data from the Umatilla River (three study reaches) were excluded from the analysis, *Day* was the only variable with an effect size that did not overlap zero. Overall model results of the other ESUs and the combined spring Chinook analysis did not change with the removal of individual study reaches or entire streams from the dataset.

Inclusion or exclusion of carcasses recovered during the holding period had minimal effect on model selection. All candidate models that ranked within 4 AICc of the top-ranked model were the same for both the holding period and spawning period datasets in all ESUs, although some of the rank orders differed. Parameter effect sizes were also similar when compared between the holding period and spawning period datasets (i.e., parameter estimates differed by <0.4 and confidence intervals overlapped; Fig. 4).

3.5. Predicted future prespawn mortality rates

Based on the combined spring Chinook model that accounted for study reach-specific differences in prespawn mortality rates with year held constant and forecasted 2040 stream temperatures (fixed effect assuming a constant mean fish *Length* and *Day*), predicted mean annual prespawn mortality rates ranged from 0.01 to 0.67 (an increase of 0.00−0.17 compared with model estimates for 2002–2011) for natural-origin fish, and 0.01 to 0.77 (an increase of 0.01−0.17) for hatchery-origin fish. When summarized by ESU, predicted 2040 prespawn mortality rates for natural-origin spring Chinook salmon were on median 0.04 higher than rates predicted by the model during the study period in the Snake River ESU, and 0.02 higher in the Mid-Columbia ESU and Upper Columbia spring ESUs (Fig. 2). For hatchery-origin Chinook salmon, predicted 2040 prespawn mortality rates were on median 0.06, 0.03, and 0.03 higher than average rates during the study period for the Snake River, Mid-Columbia, and Upper Columbia spring Chinook ESUs, respectively.

Forecasted 2040 prespawn mortality rates for natural-origin spawners exceeded 0.20 in eight study reaches (Fig. 7) compared with six study reaches in 2000–2013. Predicted prespawn mortality rates for natural-origin spawners exceeded 0.50 in the lower Umatilla River (predicted mean = 0.67) in the Mid-Columbia ESU and in Newsome Creek (predicted mean = 0.50) in the Snake River ESU. For hatchery-origin spawners, predicted 2040 mean prespawn mortality rates were >0.20 in 14 study reaches, compared with nine in the 2000–2013 data. Predicted 2040 prespawn mortality rates were >0.50 in four of those study reaches: the lower and upper Umatilla River reaches (predicted mean = 0.77 and 0.53, respectively), and two Snake River ESU locations, the upper South Fork Salmon River (predicted mean = 0.53) and Newsome Creek (predicted mean = 0.61). Notably, random intercept adjustments included holding period carcass data, which influenced annual prespawn mortality estimates in these two study reaches.

Prespawn mortality estimates for 85 streams with known spring Chinook salmon spawning that were not included in the GLMM data ranged from 0.00 to 0.46 for natural-origin fish and from 0.01 to 0.57 for hatchery-origin fish based on modeled August stream temperatures in 2002–2011. In 2040, predicted prespawn mortality rates in 2040 increased by an average of 0.05 for natural-origin fish and 0.06 for hatchery-origin fish. Based on modeled mean temperatures from 2002-2011, prespawn mortality estimates were >0.20 in three streams for natural-origin fish and in 12 streams for hatchery-origin fish. Projected stream temperatures in 2040 resulted in 11 streams in this dataset where prespawn mortality rates were predicted to exceed 0.20 for natural-origin fish (Fig. 7), and 21 streams for hatchery-origin fish.

4. Discussion

4.1. Patterns of prespawn mortality across the Columbia River Basin

Although there was considerable variability in prespawn mortality rates within and among study reaches in the large dataset collected by many different groups across a wide geographic range, associations between prespawn mortality and individual- and reach- scale factors were fairly consistent for all three spring-run Chinook ESUs. After accounting for variability in carcass sampling date, the probability of prespawn mortality increased with mean August stream temperature within each of the spring-run ESUs and for the combined spring Chinook salmon dataset. In the Snake and Upper Columbia spring ESUs, prespawn mortality probability was greater for fish of hatchery origin compared with those of natural origin, although this difference was less apparent at higher temperatures, and there was evidence of a length × temperature interaction in the Mid-Columbia ESU.

Prespawn mortality estimates never exceeded 0.10 in eight of the 42 spring Chinook salmon study reaches, many of which were located in higher elevation headwater areas, such as the Wenaha River in Northeastern Oregon, and Marsh Creek in Idaho. These low rates were similar to reports (<0.05 carcasses were unspawned) from several spring Chinook salmon populations in remote locations in British Columbia (McNicol, 1999; Potyrala and Nutton, 2011). In contrast, observed prespawn mortality rates were routinely >0.10 and averaged >0.25 in other study streams: Newsome Creek in the Clearwater River Basin, Idaho, two reaches of the Umatilla River in the Blue Mountains, Oregon, and the upper Wenatchee River. Elevated rates of prespawn mortality have been recognized as a potential threat to population persistence in other locations, such as for some threatened spring Chinook salmon populations in the Willamette River Basin (Bowerman et al., 2018; Keefer et al., 2010), several sockeye salmon populations in the Fraser River, British Columbia, that have been migrating upstream earlier than usual (Cooke et al., 2004; Hinch et al., 2012), and populations of Coho salmon *O. kisutch* in the Puget Sound region of Washington (Scholz et al.,

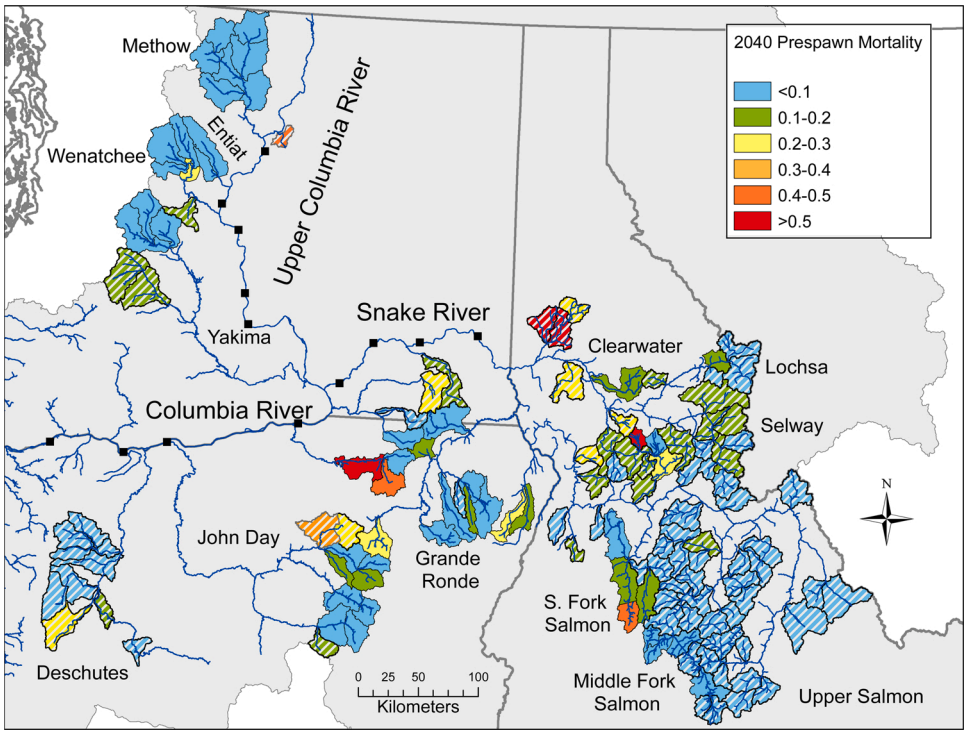

Fig. 7. Mean predicted prespawn mortality rates based on 2040 stream temperatures for natural-origin fish in watersheds throughout documented spring Chinook salmon spawning habitat in stream reaches where prespawn mortality data were used in the predictive model (solid shading) and watersheds where data were not used to inform the model (shaded lines). Chinook salmon in the Clearwater and Entiat rivers were considered functionally extirpated in the early 1900s and have since been re-introduced. Black squares indicate location of major dams.

2011; Spromberg and Scholz, 2011).

4.2. Prespawn mortality and stream temperature

Annual prespawn mortality rates showed a pattern of increasing relative to mean August stream temperatures in all three spring Chinook ESUs evaluated. Increased prespawn mortality has been linked to stream temperature in spring-run Chinook salmon populations in the Willamette River Basin, Oregon (Bowerman et al., 2018; Keefer et al., 2010), and in sockeye salmon in the Fraser River (Gilhousen et al., 1990; Hinch et al., 2012). Notably, we observed considerable variability in annual prespawn mortality rates at the highest temperatures, in part due to the relatively fewer observations at these temperatures, but also suggesting temperature itself is not the sole factor influencing mortality in warmer streams.

The correlation between prespawn mortality and temperature may reflect a suite of causal agents that are compounded by increased water temperatures, including stress, disease, and energy depletion, and factors associated with senescence (Benda et al., 2015; Karvonen et al., 2010). Thus, increased mechanistic understanding of the interactions between prespawn mortality and stream temperature could help identify management and conservation tactics that could ameliorate thermal effects via reduced pathogen exposure, improved water quality, or mitigation of other stressors during migration and holding. In particular, a mechanistic understanding of the effects of 'pulse' temperature metrics (e.g., daily maximum temperature) versus 'press' metrics (e.g., 7-day average maximum, monthly average) may help account for the wider range of observed prespawn mortality rates at the highest temperatures.

While the use of a broad temperature metric (*MeanTemp*) likely did not capture biologically important temperature variability that salmon encounter (Keefer et al., 2018; Steel et al., 2012), the metric allowed us to build a general model to predict the likelihood of prespawn mortality based on general stream characteristics across the entire Columbia River Basin. The mean predicted probability of prespawn mortality for natural-origin salmon rose above 0.10 in the combined spring Chinook model when mean August temperatures exceeded 16 °C on spawning grounds. Use of the variable *MeanTemp* was insufficient to examine direct effects of temperature, such as acute lethality as temperatures approach 23–25 °C or mortality related to prolonged exposure to elevated water temperatures (e.g., days at 21–22 °C) (Richter and Kolmes, 2005). In the lower Umatilla River reach, for example, maximum hourly water temperature often exceeded 24 °C (Contor, 2012), although *MeanTemp* observations clustered around 18 °C. Most of the spring-run Chinook salmon populations in this study spawned in late August through September, so mean August temperatures reflected temperatures at the end of the holding period and the onset of spawning. Notably, predicted *MeanTemps* in several Upper Columbia River summer/fall Chinook ESU study reaches frequently exceeded 18 °C, but fish in these reaches may be less affected by average August spawning habitat temperatures due to differences in life-history characteristics, as discussed below (Section 4.5).

Uncertainty around estimates at the highest range of observed temperatures in part reflect the relative scarcity of streams where mean August stream temperatures currently exceed 18 °C. Therefore, prespawn mortality predictions based on forecasted temperatures that extend beyond the range of observed data are speculative, but are likely to be conservative as these temperatures approach the thermal maxima for salmon species (Crossin et al., 2008; Keefer et al., 2008).

4.3. Prespawn mortality and fish origin

Prespawn mortality probabilities were higher for hatchery-origin Chinook salmon compared with those of natural origin in two spring Chinook ESUs, and *Origin* was the only significant predictor of prespawn mortality for the Upper Columbia summer/fall Chinook ESU. Higher prespawn mortality rates for hatchery- versus natural-origin individuals have been observed previously (some data were included in the current study; Young and Blenden, 2011), as has a general positive relationship between prespawn mortality with percent hatchery origin spawners (Bowerman et al., 2018). However, research has yet to identify a mechanism for this discrepancy, which could result from variations in behavioral or physiological traits.

Hatchery-reared Chinook salmon often display different spawning distributions, migration timing, and spawn timing compared with

naturally-reared fish (Hoffnagle et al., 2008; Hughes and Murdoch, 2017; Knudsen et al., 2006). Because reproductive timing is a heritable trait, hatchery management practices may inadvertently select migration and spawn timing mismatched to optimal environmental conditions during upstream migration, pre-spawn holding or spawning periods (Tillotson et al., 2019). Natal homing may also play a role, as the distribution of hatchery fish can be influenced by the location of juvenile acclimation and release sites (Dittman et al., 2010; Hoffnagle et al., 2008), potentially resulting in elevated density and/or use of stream reaches with lower habitat quality in hatchery-origin spawners. Lower reproductive success of hatchery-origin fish has been associated with differences in spawning location (Hughes and Murdoch, 2017; Williamson et al., 2010). To what degree increased potential for pathogen transmission and/or oxygen stress are associated with higher spawning density is unknown, but it should be examined in areas where hatchery fish congregate at higher densities under scenarios of low flow and high water temperature (Sergeant et al., 2017; Tillotson and Quinn, 2017). Hatchery and natural-origin fish may also differ in their exposure to acute or cumulative stressors during ocean rearing or migration (Crozier et al., 2016).

Although our modeling approach accounted for within-site correlations, several study reaches with the lowest prespawn mortality rates were dominated by natural-origin fish and were also those with the coldest, most pristine habitat. Conversely, several study reaches with the highest prespawn mortality rates were comprised mostly of hatchery-origin fish and located in areas heavily impacted by anthropogenic factors. These patterns illustrate the potential for large-scale correlations among habitat, management, and population attributes that can make it difficult to untangle causative mechanisms.

4.4. Prespawn mortality and fish length

Across datasets, there was some support for the inclusion of *Length* as a predictor of female prespawn mortality, but the effect size was much smaller than that of *MeanTemp* and *Origin*. Despite the small effect size, the relationship between fish size and prespawn mortality warrants further investigation, as higher prespawn mortality rates for larger salmon were evident in all subsets of the spring Chinook data, including when data were evaluated separately by origin, and within study reaches where there were sufficient sample numbers to generate separate prespawn mortality rates by multiple length bins. In a few locations, there were years in which the mean length of natural-origin carcasses was greater than hatchery-origin carcasses and others where there appeared to be a negative relationship between *Length* and *Day* (i.e., prespawn mortalities found earlier in the season were on average larger than those encountered later in the spawning period). These patterns were inconsistent among years and locations, and there was no evidence of statistical collinearity between any of the predictor variables within our datasets. However, within populations, complex interactions may exist among hatchery practices, fish size, and migration and spawn timing (and hence the length of time spent holding), which might influence the likelihood of prespawn mortality.

We hypothesize that a relationship between size of females and prespawn mortality could be attributed to either sampling or biological factors, or to a combination thereof. A sampling effect could arise if larger, unspawned carcasses are more likely to be recovered in surveys, either because they are easier for surveyors to see or because smaller, unspawned carcasses are more likely to be removed by predators, while a size bias does not occur in spawned-out carcasses. A biological basis for increased prespawn mortality with size could be related to higher energetic costs for large fish compared with small individuals, either because larger fish spend more energy competing for holding and spawning locations, or as a result of higher metabolic requirements (Gillooly et al., 2001). Additionally, large fish may arrive at spawning grounds earlier than smaller or younger individuals (Knudsen et al., 2006; Quinn et al., 2016), which could increase the duration of holding and therefore the total energetic cost.

Our results imply a potential tradeoff between size-related survival and reproductive success in female Chinook salmon, consistent with Cunningham et al. (2013): large spring-run Chinook salmon may have a higher probability of dying prior to spawning, but those that do spawn typically have a greater fecundity benefit related to size, since they produce larger and more eggs, yielding larger offspring (Einum and Fleming, 2000; Kinnison et al., 2001) and dig deeper redds that are less vulnerable to scour (Steen and Quinn, 1999). In turn, these attributes may yield higher numbers of returning offspring for large fish (Janowitz-Koch et al., 2019). Whether size is related to prespawn mortality in males was not examined here but is potentially important given the importance of body size on reproductive success in male salmon.

4.5. Prespawn mortality and life-history characteristics

Summer/fall-run Chinook salmon of the Columbia River basin express life-history characteristics that may make them less susceptible to prespawn mortality compared with spring-run populations, including later migration and generally shorter freshwater prespawn holding periods. Although spawning reaches used by the Upper Columbia summer ESU experienced the warmest average August stream temperatures in our dataset, mean August stream temperature was not a significant predictor of prespawn mortality for these populations. Upper Columbia River summer/fall-run Chinook salmon migrate later than spring-run Chinook salmon, primarily in July and August; thus, the metric *MeanTemp* may not accurately represent conditions these fish experience while holding on spawning grounds. First, mortality during upstream migration may be more likely and thus may not be apparent in spawning ground carcass data. Second, although some fish move directly to spawning grounds, many remain downstream in larger river systems, where temperatures may be cooler than small tributaries, until shortly before spawning (Keefer et al., 2019; Mann and Snow, 2018). High water temperatures in spawning tributaries like the Okanogan River can act as a thermal barrier that delays summer Chinook entering spawning tributaries and forces migrants to remain in relatively cooler mainstem habitat until tributary temperatures decrease in the fall (Hyatt et al., 2003; Mann and Snow, 2018). Other fall-run salmon temporarily stray into non-natal tributaries to escape high water temperatures (Goniea et al., 2006), and many summer/fall-run Chinook salmon populations have relatively shorter prespawn holding periods than spring Chinook salmon, strategies that may mitigate thermal stress related to extended exposure to high temperatures. Similar to the three spring-run ESUs evaluated, the probability of prespawn mortality was higher for hatchery- compared with natural-origin Upper Columbia summer/fall-run Chinook salmon, but after accounting for reach and year effects, the predicted probability was only 0.01 higher, which may be biologically trivial but warrants further examination.

4.6. Research and management considerations

Results of this study illustrate some of the ways that prespawn mortality estimates can be affected by survey methods and locations. In all datasets, *Day* was an important predictor, demonstrating a clear pattern of decreasing prespawn mortality probability over the duration of the survey period. This pattern emphasizes the importance of conducting carcass surveys over the entire spawning period as recommended by Bowerman et al. (2016). If carcass surveys concluded before fish had finished spawning, annual prespawn mortality estimates would likely be biased high, and if surveys were only conducted during the middle to end of the spawning period, they would likely be biased low. Surveys conducted only once or twice annually may run the risk of a bias in either direction, depending on which portion of the spawning period they captured. Although there was little quantitative difference in results between the datasets with and without mortality that occurred during the pre-spawn holding period, there was a substantial difference

in annual prespawn mortality estimates in some locations and years where relatively large numbers of early season mortalities were observed. In particular, carcasses collected during the holding period dramatically influenced mean annual prespawn mortality estimates and 2040 predicted rates in the upper South Fork Salmon River and Newsome Creek study reaches. Targeted research during this time might lead to further insights into the magnitude of mortality prior to the onset of spawning.

Prespawn mortality probabilities based solely on carcass sampling may be conservative, since they do not account for mortality that occurs *en route*, including just before fish reach spawning grounds (e.g., Barnett et al., 2020; Murdoch et al., 2010). Research in locations where accurate enumeration of adult salmon returning to spawning grounds can be compared with successfully spawned fish, such as via redd counts (e.g., Murdoch et al., 2010) or those that track the fate of individually-marked returning adults (e.g., Mann and Snow, 2018), may provide more accurate estimates of prespawn mortality. Such studies could yield insights into additional factors that might affect mortality, such as migration timing, arrival timing at spawning grounds, and the duration of holding. However, researchers must also consider that additional handling to gather these data could increase fish exposure to other mortality-related stressors (e.g., Corbett et al., 2012; Murauskas et al., 2014). Managers should be aware that bias may be introduced into carcass-based prespawn mortality estimates in a number of ways including small sample sizes, high rates of scavenging, and low recovery or detection probabilities (Bowerman et al., 2016; DeWeber et al., 2017). Some of these potential biases may be obviated through improved sampling efficacy (e.g., Bowerman et al., 2016) and estimation approaches (e.g., DeWeber et al., 2017; Murdoch et al., 2010).

In addition to improved sampling efforts, quantifying physical variables and management actions along the migration route and on spawning grounds could help pinpoint factors that contribute to prespawn mortality. Models explained approximately 40−66 % of the observed variability in the prespawn mortality data, much of which was accounted for by the random effects of year and study reach. Explanatory variables only accounted for 6–38 % of the variability in the data (11–75 % of total variance explained by the models), indicating that additional factors not included in the current study likely influenced annual prespawn mortality. Other factors contributing to mortality could include individual physiological differences (Cooke et al., 2006; Miller et al., 2011), annual ocean conditions (Crossin et al., 2004) or cumulative exposure to non-lethal stressors encountered during the migration experience (Baker and Schindler, 2009; Farrell et al., 2008; Minke-Martin et al., 2018). Additional factors that could influence mortality in spawning tributaries and holding areas include management actions (e.g., fish handling, anthropogenic disturbance), exposure to pathogens (Benda et al., 2015), water quality (Scholz et al., 2011), and habitat conditions, including low streamflow and high conspecific density (Quinn et al., 2007; Tillotson and Quinn, 2017). Research to evaluate mechanisms driving prespawn mortality will help address some of these knowledge gaps. Elucidation of the key components of the thermal factors causing prespawn mortality (e.g., pulse versus press metrics) and the interactions of temperature with factors such as pathogenesis, density, and oxygen stress may be especially useful.

4.7. Prespawn mortality and climate change

Predictions of prespawn mortality in 2040 based on our statistical models indicated that numerous Spring Chinook salmon populations throughout the Columbia River basin are expected to have average annual prespawn mortality rates in excess of 0.20 under projected climate warming scenarios. A few study reaches are expected to exceed average annual prespawn mortality rates of 0.50, a level of adult mortality that impedes recovery efforts and increases the probability of extinction when holding other vital rates constant (Reed et al., 2011; Spromberg and Scholz 2011). With a few exceptions, mortality predictions in high-elevation spawning habitat in wilderness or relatively pristine locations remained below 0.10. Given the relationship between temperature and prespawn mortality, suitable spawning habitat could be greatly reduced or impaired for many spring-run Chinook salmon populations throughout the interior Columbia River Basin, particularly those that spawn at lower elevations. Hence, much of the habitat that is expected to remain thermally suitable will be available for those populations with the longest, most arduous migrations. These predictions illustrate the potential value of trap-and-transport protocols and benefit of access to high elevation habitats currently blocked by dams as long-term conservation tactics to provide access to 'climate refuges.' Such practices that include handling fish need to be carefully planned and used sparingly, since they may also stress fish and increase prespawn mortality (Colvin et al., 2018; Kock et al., 2020).

Predicted 2040 prespawn mortality rates were based solely on forecasted changes to average August stream temperature, with study reach-specific variance included for locations that were used to parameterize the model. We did not forecast prespawn mortality relative to variability in climate projections, which may include increased frequency and magnitude of extreme events, nor did we evaluate potential adaptive changes in migration or spawn timing. These details would be useful to include in future life cycle modeling, which should be aided by the baseline predictions of prespawn mortality described herein. Additional direct and indirect effects related to climate change, such as climate-driven changes in water management (Mote et al., 2003), changes to the timing and magnitude of precipitation events (Honea et al., 2016; Mantua et al., 2010), altered fire regimes and related geomorphic events such as landslides (Mote et al., 2003), all have the potential to alter prespawn mortality rates in ways that were not included in these predictions. Changes in disease prevalence or the interaction between pathogens and stream temperature could further impact future prespawn mortality rates (Benda et al., 2015; Crossin et al., 2008; Teffer et al., 2018). There was greater uncertainty in the warmest study reaches as a result of higher variance in predictions at high temperatures, and in one study reach (Lower Umatilla River), projected stream temperatures were higher than the range of values used in the predictive model for spring Chinook.

Already, spring Chinook salmon populations are in peril throughout much of the Columbia River Basin. Climate sensitivity analyses based on life-history characteristics indicate that interior spring Chinook salmon populations, particularly in the Snake River spring/summer ESU, are at risk of climate-related declines in survival and abundance (Crozier et al., 2019). Our findings emphasize the susceptibility of adult spring-run Chinook salmon to increased stream temperatures, as well as potential differences in individual fish characteristics that affect the probability of dying prior to reproduction. This research highlights the importance of considering the spawner life stage in life cycle models and restoration actions aimed at mitigating stream warming (Crozier et al., 2008; Honea et al., 2016; Reed et al., 2011).

CRediT authorship contribution statement

Tracy E. Bowerman: Data curation, Formal analysis, Methodology, Visualization, Writing - original draft, Writing - review & editing. **Matthew L. Keefer:** Conceptualization, Writing - review & editing. **Christopher C. Caudill:** Funding acquisition, Resources, Supervision, Conceptualization, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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