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Authors

Dusek Jennings, Eva
Hendrix, A. Noble

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RESEARCH

Spawn Timing of Winter-Run Chinook in the Upper Sacramento River

Eva Dusek Jennings*¹, A. Noble Hendrix²

ABSTRACT

Spawn timing in anadromous Pacific salmon may be especially sensitive to environmental cues such as river temperature and flow regimes. In this study, we explored correlations between peak spawn timing and water temperature in endangered Sacramento River winter-run Chinook Salmon. In recent drought years, rising water temperatures during egg incubation have negatively affected the winter-run Chinook Salmon population. This paper seeks to understand how winter-run spawn timing may be affected by temperatures during the staging period prior to spawning, and how water releases from Shasta Dam might affect these dynamics. We fit a proportional-odds logistic regression model to evaluate annual spawn timing as a function of average temperatures in April and May below Keswick Dam. While the start date of spawning remains relatively constant from year to year, the timing of peak spawning varies

annually. Cool springtime temperatures trigger winter-run Chinook Salmon to spawn earlier, whereas warm springtime temperatures trigger fish to spawn later. Before dam construction, winter-run Chinook Salmon spawned in cool, spring-fed streams that are now inaccessible to migrating salmonids. In their natal spawning grounds, temperature-driven spawn timing would have primarily ensured sufficient time for egg maturation in cool years, while secondarily preventing egg and alevin mortality in warm years. In the current winter-run spawning grounds, the relationship between temperature and spawn timing may have important applications to management of Shasta Dam water releases, especially during conditions when thermal mortality can affect developing winter-run Chinook Salmon eggs.

KEY WORDS

spawning, temperature, winter-run Chinook Salmon, model, spawn timing

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* Corresponding author: itseva@gmail.com

1 Cheva Consulting
Seattle, WA, 98116, USA

2 QEDA Consulting
Seattle, WA 98103 USA

INTRODUCTION

The reproductive cycle in anadromous salmonids consists of two events that are not necessarily synchronous (e.g., LovellFord 2013): upstream migration from the ocean to river systems; and the spawning event, whereby a mate and nesting

site are selected, and eggs are deposited into redds (nests) in the gravel. Reproductive success requires both the presence of potential mates, as well as specific habitat conditions that may be temporally limited. As a result, spawn timing in anadromous Pacific salmon may be especially sensitive to environmental cues (Sandercock 1991).

Upriver migration timing is considered to be a heritable trait in Pacific salmon, determined mostly by selection over generations (Quinn 2018). River temperature and flow regimes can shift the timing from year to year, however (Sandercock 1991; McCullough 1999; Beechie et al. 2008; Quinn 2018). Once salmon are present at spawning grounds, spawning activity appears to be triggered by certain environmental cues, most notably flow and temperature. A link between increased stream discharge and spawning activity has long been observed, especially in areas where water levels limit access to spawning grounds (Neave 1943; Briggs 1953; Sandercock 1991). For example, in the Stillaguamish River, Washington, peak spawn timing of Chinook Salmon (*Oncorhynchus tshawytscha*) appears to be correlated with the first freshet during the spawning period (Beechie et al. 2008). Increased Stillaguamish River flow may simply expand the availability of suitable spawning sites, but it also generally decreases stream temperature. Stream temperature has been shown to at least partly affect spawn timing in some salmon populations (Brannon 1987; Heard 1991; Beer and Anderson 2001). For example, Sockeye Salmon stocks in the Fraser River, Canada, spawn over a 5-month period: the streams with lower mean temperatures have earlier-spawning stocks; the streams with higher mean temperatures have later-spawning stocks (Brannon 1987). Correlations between spawn timing and stream temperature are believed to synchronize spawning behavior to match ideal environmental conditions during the period of juvenile emergence (Miller and Brannon 1982; Brannon 1984; Angilletta et al. 2008). Additionally, salmon species may have preferred thermal limits for spawning activity or egg survival (Beacham and Murray 1990).

Along the Pacific coast of North America, Chinook Salmon display wide variation in upriver migration timing; however, spawn timing for most Chinook occurs in the fall (Healey 1991). An exception is Sacramento River winter-run Chinook Salmon (hereafter SRWC), which exist as a single population that spawns in the mainstem Sacramento River over a 4-month period from late April through mid- to late August. This unusual spawn timing differentiates winter-run from other populations of Chinook (Fisher 1994), and results in egg and alevin incubation during the summer months, when air and water temperatures are usually their warmest.

Historically, natal streams for SRWC included upper-elevation headwaters of the Little Sacramento, McCloud, Fall, and Pit rivers, and the North Fork of Battle Creek (Yoshiyama et al. 2001; [Figure 1](#)). To access this habitat, winter-run Chinook migrated in large numbers from the ocean through San Francisco Bay between November and May or June (USBR 2008), passing Sacramento's historic canneries during the winter months (hence the name "winter-run") (Killam and Krebs 2008). Winter-run Chinook then ascended the main stem of the Sacramento River and entered their natal spawning streams in late spring and early summer. The historic natal spawning streams probably provided the only available cool, stable temperatures over the summer (Slater 1963). Thus, summer spawning in the natal streams would have provided winter-run Chinook eggs and alevin with temperatures cool enough for survival, yet warm enough for successful development before emergence.

Over the last century, spawning and rearing habitats for California's four seasonal runs of Central Valley Chinook (fall, late-fall, winter, and spring runs) have been altered by the Central Valley's regulated water system (USBR 2008; Perry et al. 2010; Cavallo et al. 2013). In 1933, the Central Valley Project (CVP) began devising a series of canals, aqueducts, reservoirs, and pump plants in the northern half of the state to store and regulate water. In 1945, Shasta Dam was completed, followed by Keswick Dam in 1950, located 14km downstream of Shasta Dam

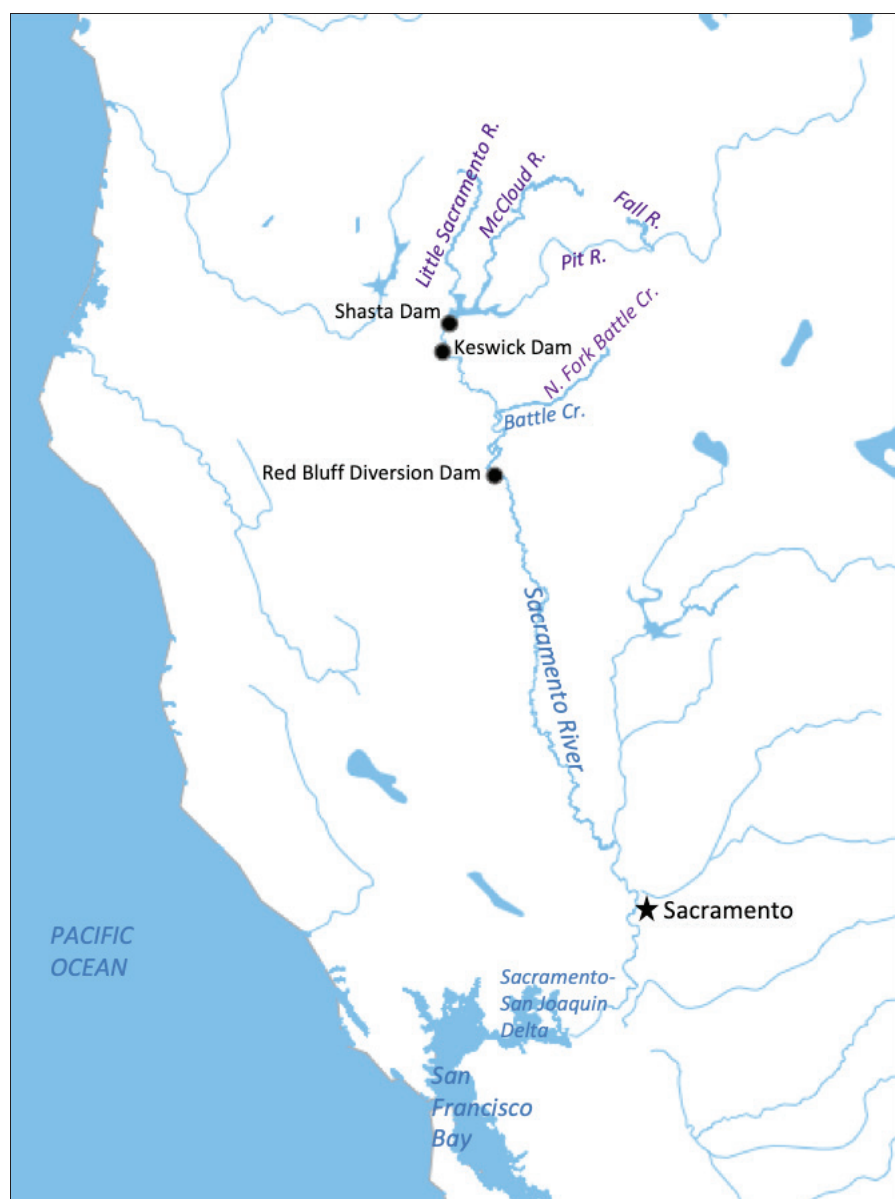


Figure 1 Historic and current freshwater spawning habitat of winter-run Chinook Salmon. Historic spawning habitat (*labeled in purple*) includes the McCloud, Pit, Fall, and Little Sacramento rivers located north of Lake Shasta, and the North Fork of Battle Creek. These natal spawning areas have been inaccessible to Chinook Salmon since dam construction in the 1940s. Current spawning habitat is the main stem of the Sacramento River below Keswick Dam, with occasional spawning in Battle Creek. Keswick Dam is impassable for winter-run Chinook, while Red Bluff Diversion Dam is passable for winter-run Chinook.

(Figure 1). These dams together block access to 58% of historic winter-run Chinook habitat (USBR 2008). Currently, SRWC spawn almost exclusively in the upper mainstem of the Sacramento River between Keswick Dam and Red Bluff Diversion Dam.

Between the late 1960s and late 1980s, the number of returning SRWC declined by more than 97% (Fed Regist 1987). In subsequent years, lack of recovery and continued decline (NMFS 1997) led to their classification as endangered under the federal Endangered Species Act in 1994 (Fed

Regist 1994; NMFS 2016). The decline of winter-run Chinook can be traced to displacement of spawning and rearing habitat by dams and water diversions, inadequate water temperature conditions in the upper Sacramento River, pollution, and the exacerbating effects of natural environmental variability (NMFS 1997). In drought years, water temperatures during egg and alevin incubation can exceed lethal temperatures, leading to high levels of mortality (Martin et al. 2017). During 2 recent drought years, egg-to-fry survival rate was approximately 5%, whereas the survival rate for this life history stage is

15% to 50% in non-drought years (NMFS 2016). Furthermore, escapement 3 years after drought events (the dominant age at return for SRWC) is typically reduced by an order of magnitude (NMFS 2014), contributing to overall decline of the population. Such temperature-related mortality was likely not experienced in historic winter-run habitat, where water temperatures were generally constant and cool (Yoshiyama et al. 2001). In contrast, the current spawning reach below Keswick Dam is subject to temperature management via a temperature control device that was installed on Shasta Dam in 1998 (USBR 2008).

Although the CVP has created a major barrier for winter-run Chinook spawners, the timing of migration remains approximately the same. The majority of winter-run adults pass Red Bluff Diversion Dam (RBDD; Figure 1) between January and May, with the peak occurring in mid-March (Hallock and Fisher 1985; USBR 2008). Spawners migrate the remaining 97 km to the base of Keswick Dam, arriving between February and June, and “staging” for up to several months (Rutter 1904; Moyle et al. 1989; Reynolds et al. 1993) before spawning between late April and mid- to late August. Before 2000, several authors identified late May or early June as the peak of spawning (Hallock and Fisher 1985; Fisher 1994), although carcass data collected after 2000 indicate that the spawning peak now occurs later (see Appendix C-1 in Killam et al. 2017).

Given the displaced spatial distribution of spawning and the potential for temperature management to affect survival of eggs and alevin, the purpose of this study was to explore the temporal distribution of SRWC spawn timing and quantify how stream temperature affects patterns in annual variability of spawn timing. The timing of adult spawning determines the dates that eggs and alevin develop in the gravel and the temperatures they experience, including the possibility for thermal mortality. As a result, we also explore how spawn timing may affect egg-to-fry survival. To address these topics, we utilized winter-run Chinook female carcass data collected below Keswick Dam to describe spawning timing, and we examined April and May temperatures for

their role in affecting the temporal distribution of SRWC spawning. Furthermore, we aim to highlight how management of springtime water temperatures at Shasta Dam may affect egg-to-fry survival, particularly during drought years.

METHODS

Carcass Data

The California Department of Fish and Wildlife (CDFW) completed daily carcass surveys on the mainstem of the upper Sacramento River above RBDD between May and August from 2000 to 2016, recording carcass length, condition (fresh or not fresh), sex, hatchery origin, and location (Killam and Krebs 2008). The timing of winter-run Chinook spawning is inferred to be 1 week prior to appearance of fresh female carcasses near spawning grounds (2017 email from D. Killam, CDFW, to E. Dusek Jennings, unreferenced, see “Notes”). Although daily carcass surveys have been completed on the Sacramento River above RBDD since 1996, fresh female carcass data were only available from 2000 (Killam and Krebs 2008).

Winter-run fresh female carcass observations by date were shifted 7 days earlier to represent likely spawning date. From here on, the date-shifted fresh female carcass data are referred to as “observed female spawners.” We binned observed female spawners into ordinal 10-day periods p (Table 1), and spawners from early ($p \leq 14$) and late ($p \geq 23$) 10-day periods were summed to reduce the number of categories with few observations. We then calculated the annual proportion of observed female spawners for each period between $p14$ and $p23$. Before we selected the 10-day bin, we examined several bin sizes, including 7-, 10-, 14-, and 30-day periods. While all bin sizes displayed a similar correlation with springtime temperature, we selected the 10-day bin for its balance of temporal resolution.

Temperature Data

Hourly temperature data below Keswick Dam were obtained from the KWK gage operated by the US Geologic Survey (USGS) and US Bureau of Reclamation (USBR) (40.600983°N, -122.444458°W). Daily as well as monthly

Table 1 Ordinal 10-day period and corresponding date ranges for non-leap years and for leap years. Ordinal Period 1 (not shown) begins on January 1 each year. Only periods corresponding to winter-run Chinook Salmon spawning dates are shown.

Period	Date range: non-leap year	Date range: leap year
12	Apr 21–30	Apr 20–29
13	May 1–10	Apr 30–May 9
14	May 11–20	May 10–19
15	May 21–30	May 20–29
16	May 31–Jun 9	May 3–Jun 8
17	Jun 10–19	Jun 9–18
18	Jun 20–29	Jun 19–28
19	Jun 30–Jul 9	Jun 29–Jul 8
20	Jul 10–19	Jul 9–18
21	Jul 20–29	Jul 19–28
22	Jul 30–Aug 8	Jul 29–Aug 7
23	Aug 9–18	Aug 8–17
24	Aug 19–28	Aug 18–27
25	Aug 29–Sep 7	Aug 28–Sep 6

average temperatures were calculated by the National Marine Fisheries Service (NMFS), following QA/QC of hourly data (M. Daniels, unpublished data, see “Notes”). After standardization of April and May temperatures (mean equal to 0 and standard deviation equal to 1), we used monthly average temperatures for model fitting. Between 2000 and 2016, mean temperature below Keswick Dam (standard deviation in parenthesis) for April was 10.15 °C (sd=0.70), and for May was 10.53 °C (sd=0.74). We used daily average temperatures to calculate monthly means over all years, and to estimate embryonic and larval development timing under example cool and warm years.

Daily water temperature data for the McCloud River (41.0944°N, -122.1134°W, elevation 628 m) were obtained from The Nature Conservancy for years 2000 to 2016 (C. Babcock, unpublished data, see “Notes”). McCloud River temperature data were not available for all dates between April 1 and Nov 30. To compare McCloud River temperatures to those below Keswick Dam, we calculated monthly mean temperatures across all

years using available daily average temperature data. In most years, daily data collection on the McCloud River began in the second half of April, resulting in a potential upward bias in April temperatures.

Statistical Analysis

To model spawn timing, we used a proportional-odds logistic regression (POLR) model that accounts for individuals in mutually exclusive, ordered categories. Individual females $i = 1, \dots, N$ spawn in $j = 1, \dots, J - 1$ categories, where each j represents the boundary between J consecutive 10-day periods, such that $j = 1$ represents the $p14|p15$ boundary, $j = 2$ represents the $p15|p16$ boundary, and $j = 9$ represents the $p22|p23$ boundary.

The probability of a spawning event Y occurring at boundary j or earlier is $P(Y \leq j)$, while the probability of spawning after boundary j is $P(Y > j) = 1 - P(Y \leq j)$. Within the POLR model, the log cumulative logit function L_j defines the probability of an individual spawning at boundary j or earlier, relative to spawning after boundary j , as

$$L_j = \log \left(\frac{P(Y \leq j)}{1 - P(Y \leq j)} \right) = \text{logit}(P(Y \leq j)) \quad (1)$$

In the current context, we use the observations of individual female spawn timing $Y_{i,t}$ for individuals $i = 1, \dots, N_t$ over years $t = 1, \dots, T$ with period boundaries $j = 1, \dots, J - 1$. The model defines boundary-specific intercepts (α_j), and incorporates temperature covariates (Apr_t and May_t) that have the same coefficient values (β_{Apr} and β_{May}) for all boundaries. The model that includes both April and May temperatures is

$$\text{logit}(P(Y_{i,t} \leq j)) = \alpha_j - \beta_{Apr} Apr_t - \beta_{May} May_t \quad (2)$$

where the mean monthly temperatures were standardized over the $T = 17$ years.

Covariates and their coefficients $\beta_{Apr} Apr_t$ and $\beta_{May} May_t$ can shift the spawning distribution to have higher probabilities in later time-periods (positive covariate effect) or in earlier periods (negative covariate effect).

We used R Version 3.5.1 (R Core Team 2018) with package MASS (Venables and Ripley 2002) to implement the POLR model. We fit four models to the spawn timing data: (1) a model with April temperatures, (2) a model with May temperatures, (3) a model with April and May temperatures, and (4) a null model with no temperature covariates. Best fit was determined using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002).

Egg Incubation Timing: Warm vs. Cool Years

The timing of spawning and egg incubation in the gravel determines the exposure temperatures for developing eggs and alevin, and thereby affects survival during this sensitive life stage. We estimated egg and alevin incubation timing for 2008, an example year with cool April–May temperatures, and compared it to 2014, an example year with warm April–May temperatures. We used the proportion of observed female spawners each 10-day period to estimate the fertilization date of each “cohort” of eggs. We defined a cohort of eggs as those generated by spawning events during a single 10-day period. For simplicity, fish were modeled to spawn on the fifth day of each 10-day period, and cohorts of eggs were assumed to develop synchronously. Daily temperatures over developing eggs were assumed to match those below Keswick Dam.

Egg development and fry emergence timing speeds up with increasing temperature (Beacham and Murray 1989). We estimated winter-run Chinook egg and alevin incubation timing using Zeug et al's (2012) method: daily egg/alevin development as a function of temperature is calculated and then summed until egg/alevin development > 1, indicating fry emergence. The equation for daily maturation rate (dmr) is

$$dmr = 0.00058 * T_F - 0.018 \quad (3)$$

where temperature (T) is in degrees Fahrenheit ($^{\circ}F$). Eggs/alevin accumulate a percentage of total maturation each day based on the above equation, until 100% maturation is reached ($dmr \geq 1$) and fry emerge.

RESULTS

Spawn Timing

Spawning females were recorded as early as April 23 and as late as August 28, yet the vast majority of spawning occurred each year between May 11 and August 17 ($p14$ through $p23$; mean = 99.0%, $sd = 0.8\%$). Regardless of springtime water temperatures, the first observed spawning female was recorded each year within a short range of dates (April 23–May 1). During years with warm April–May temperatures, the last observed spawning female was often sighted later than in years with cool April–May temperatures (August 13–28 for warm years; August 2–17 for cool years).

Peak spawning in all years occurred between June 20–July 19 ($p18$ – $p20$; Figure 2, thickest color bands). During years with cooler April–May temperatures (2001, 2004, 2006, 2008, 2009), there tended to be a higher proportion of spawning in early periods ($p14$ – $p17$; Figure 2 and

Table 2 Proportion of females spawned by a given date each year. During leap years, given dates are shifted one day earlier: June 8, June 28, July 8, July 18. April through May temperatures are divided into cool (light blue shading), average (avg), and warm (darker blue shading).

Year	June 19 <i>p17</i>	June 29 <i>p18</i>	July 9 <i>p19</i>	July 19 <i>p20</i>	April–May temperatures
2000	0.33	0.57	0.81	0.93	avg
2001	0.24	0.41	0.67	0.83	cool
2002	0.32	0.5	0.69	0.86	avg
2003	0.17	0.33	0.55	0.81	avg
2004	0.1	0.24	0.5	0.77	cool
2005	0.17	0.33	0.57	0.81	avg
2006	0.25	0.4	0.64	0.9	cool
2007	0.16	0.28	0.49	0.82	avg
2008	0.25	0.55	0.81	0.92	cool
2009	0.21	0.52	0.81	0.96	cool
2010	0.21	0.37	0.68	0.84	avg
2011	0.07	0.21	0.43	0.7	avg
2012	0.07	0.14	0.31	0.63	avg
2013	0.04	0.1	0.35	0.61	warm
2014	0.09	0.2	0.43	0.67	warm
2015	0.13	0.26	0.47	0.77	warm
2016	0.16	0.27	0.51	0.61	warm

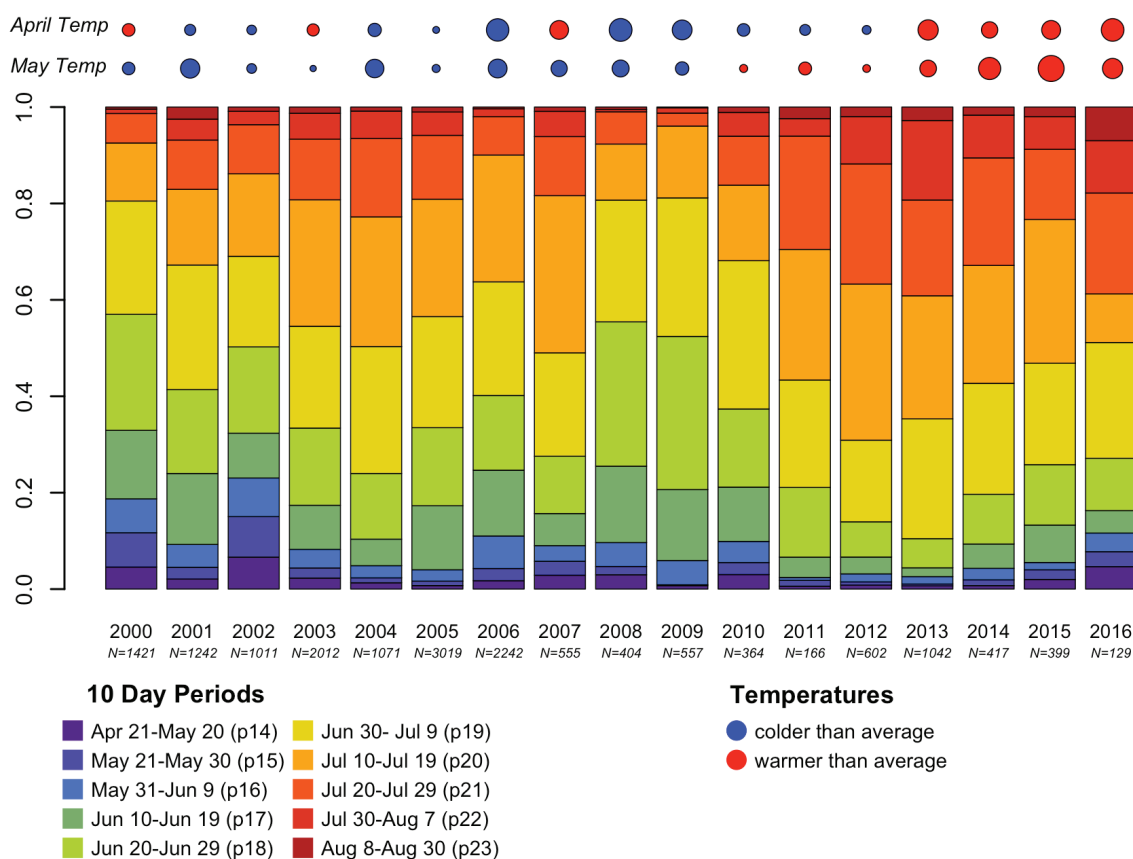


Figure 2 Cumulative proportion of winter-run Chinook spawning each year, grouped by 10-day periods from May 11 to August 17 (colored bands). Note that the first and last periods include spawning prior to May 11 or after August 17. Spawning proportions are derived from fresh female carcass data shifted one week earlier. Red and blue circles indicate whether April and May temperatures were cooler or warmer than average, with circle area corresponding to the magnitude of the April or May temperature anomalies. Years with a greater proportion of early spawning (e.g., 2008) have thicker yellow and green color bands, while years with a greater proportion of late spawning (e.g., 2013) have thicker orange and red color bands.

Table 2); whereas in warmer years (2013–2016), a higher proportion of spawning occurred in later periods (p21 – p22). Years with average April–May temperatures (2000, 2002, 2003, 2005, 2010–2012) varied in temporal distribution of spawn timing, with some years conforming more to patterns associated with cool spring temperatures (e.g., 2000, 2002, 2010), and others conforming to warm spring temperature patterns (e.g., 2011, 2012). The year 2007 had both a warm and a cool spring temperature anomaly, and observed spawn timing was intermediate to patterns associated with warm and cool spring temperatures.

By June 29 (p18), ≥40% of spawning had occurred in cooler years—with the notable exception of 2004—compared to warmer years, in which ≤27% of spawning had occurred by the same date (Figure 2, light-green color bands). Years with average April–May temperatures, or opposing temperature anomalies for April–May, displayed a variety of spawn timing patterns.

Spawning Location

While winter-run Chinook redds have occasionally been found 95km or more south of Keswick Dam, the vast majority of winter-run Chinook redds between years 2000 and 2016 were observed close to Keswick Dam (D. Killam,

Table 3 Model selection criteria for the four evaluated models: null model (no temperature covariates), April temperature covariate model, May temperature covariate model, and April & May temperature covariate model. Delta AIC values compare each of the four models to the April & May model, which best fit the data.

Model	AIC	Δ AIC	# of Parameters
Null Model	65750	505	9
April	65427	182	10
May	65259	14	10
April & May	65245	0	11

Table 4 Coefficients of the proportional-odds logistic regression (POLR) model that includes the effects of April and May temperatures on spawn timing (April & May model). Coefficients are in logit space.

Parameter	mean	SE	t value
β_{Apr}	0.08	0.02	3.92
β_{May}	0.34	0.02	13.50
$\alpha_{14 15}$	-4.00	0.05	-73.30
$\alpha_{15 16}$	-3.19	0.04	-84.18
$\alpha_{16 17}$	-2.50	0.03	-87.40
$\alpha_{17 18}$	-1.58	0.02	-74.70
$\alpha_{18 19}$	-0.73	0.02	-41.25
$\alpha_{19 20}$	0.24	0.02	14.13
$\alpha_{20 21}$	1.40	0.02	67.52
$\alpha_{21 22}$	2.65	0.03	81.29
$\alpha_{22 23}$	4.34	0.07	61.01

unpublished data, see “Notes”). Over these years, 80% of winter-run redds were identified within 10km of Keswick Dam, and an additional 14% were located between 10 and 20km of Keswick Dam, indicating that water temperature below Keswick Dam may affect a large percentage of winter-run Chinook spawners.

Model Parameters, Performance, and Predictions

The POLR model using both April and May temperatures as cofactors had the best fit to observed female spawner data based on AIC score (Table 3). Table 4 provides the POLR model

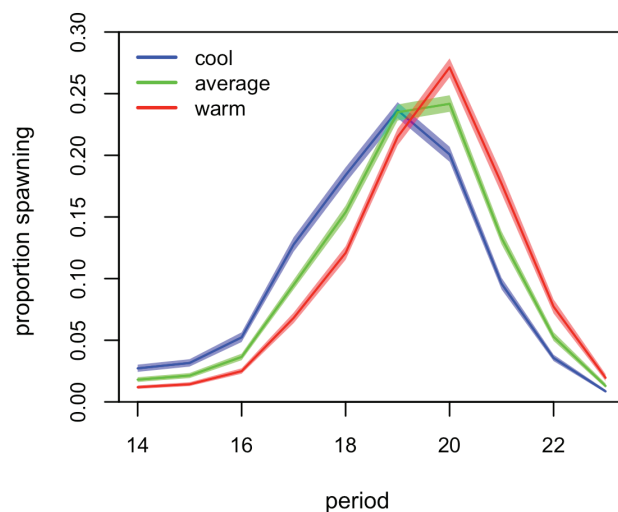


Figure 3 Model predictions of proportion spawning for warm, average, and cool conditions, showing mean prediction (solid line) and 95% confidence intervals (shading) based on standard errors around model parameters. Cool, average and warm conditions are defined as springtime temperatures of: April=9.5 °C, May=9.8 °C (cool); April=10.2 °C, May=10.5 °C (average); and April=10.9 °C, May=11.3 °C (warm).

parameters for the April & May model: β_{Apr} (April temperature coefficient), β_{May} (May temperature coefficient), and nine boundary-specific intercept parameters, α_j . Simulations of predicted spawn timing under cool (April: 9.5 °C; May: 9.8 °C), average (April: 10.2 °C; May: 10.5 °C) and warm (April: 10.9 °C; May: 11.3 °C) temperatures (standardized temperature values of -1, 0 and 1, respectively) highlight differences in model predictions under alternative thermal conditions (Figure 3). These simulations show a shift in the peak of spawn timing to earlier dates under cool temperatures and later dates under warm temperatures.

Figure 4 shows the annual observed female spawner proportions by period along with model predictions. In general, the model captured the peak spawning period in most years. When the model mis-predicted the period of peak spawning, it was within one period of the observed peak spawning (Figure 4). Furthermore, the POLR model captured the general patterns in spawning distribution, with the exception of 2012, where the model was shifted approximately one period

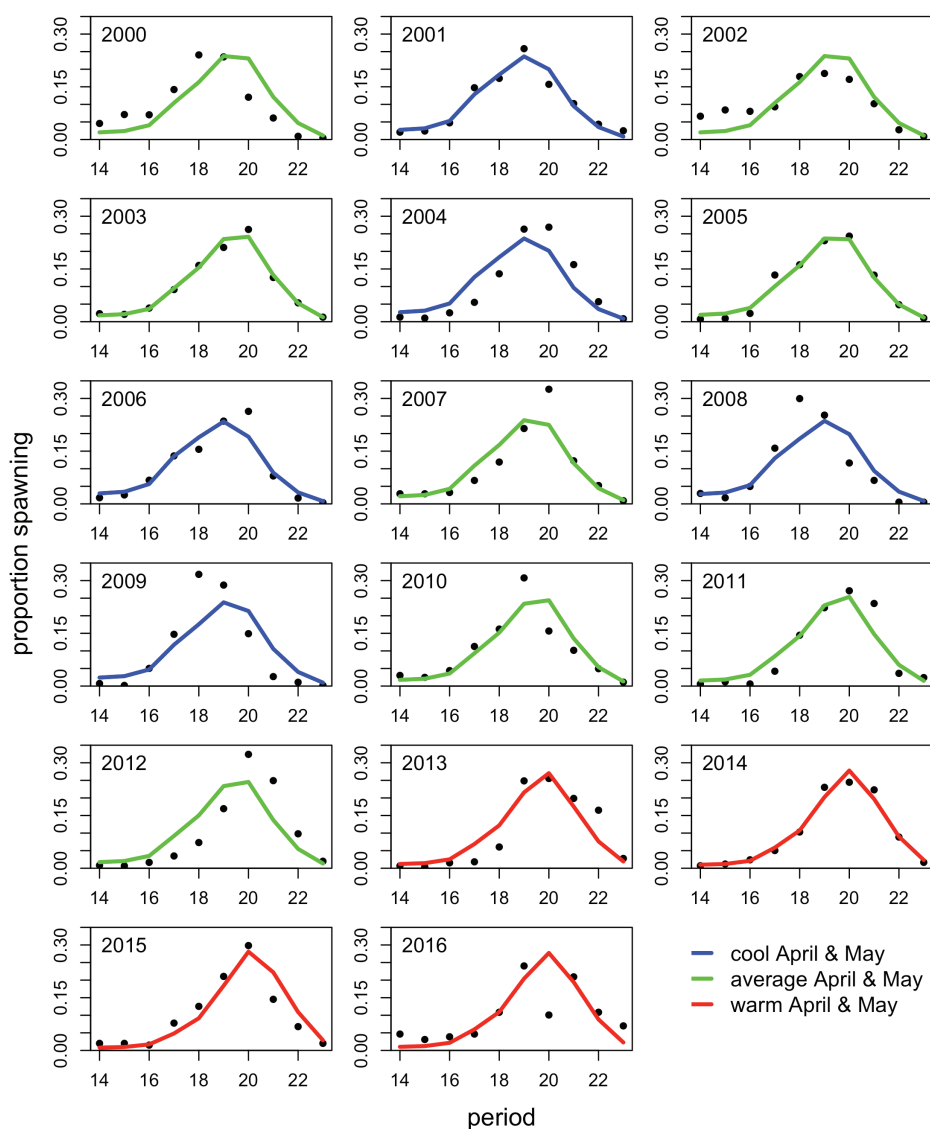


Figure 4 Observed (*black points*) and estimated (*colored lines*) proportion of winter-run Chinook spawning each 10-day period. The color used in each graph indicates whether April and May temperatures were cooler than average (*blue*; sum of standardized April-May temperatures < -1.5), average or mixed (*green*; sum of standardized April-May temperatures is between -0.6 and 0.6), or warmer than average (*red*; sum of standardized April-May temperatures > 2). Plots with a *green* colored line fall into two categories: average years in which both April and May standardized temperatures were close to 0; and mixed years in which one month had cool temperatures while the other had warm temperatures.

earlier than the observed distribution throughout the entire SRWC spawning season.

Egg and Alevin Incubation Timing in Warm and Cool Years

Timing of the egg through alevin stages varied in important ways between years with cool spring temperatures (e.g., 2008) and years with warm spring temperatures (e.g., 2014). While 70% of all spawning activity in 2008 (a leap year) occurred between June 9 and July 8 (*p17–p19*), the spawning peak was shifted 20 days later in 2014, with 70% of all spawning occurring between June 30 and July 29 (*p19–p21*; *Figure 5*). This difference in spawn timing also affected the timing of egg and alevin incubation in the gravel. In the

modeled cool year (2008), the majority of fry were predicted to emerge from the gravel by September 16, whereas in the modeled warm year, the majority of fry were predicted to emerge by October 1 (*Figure 5*). Note that the temperature of water below Keswick Dam begins to climb in early September in both cool and warm years (*Figure 5*), reflecting annual patterns in Shasta Reservoir operations. In the case of 2014, the end-of-September temperatures surpassed the 12.5 °C threshold while a majority of the eggs/alevin were still in the gravel due to delayed spawning that year.

Historic vs. Current Spawning Grounds

The spawn timing model can be used in conjunction with Zeug et al’s (2012) equation for

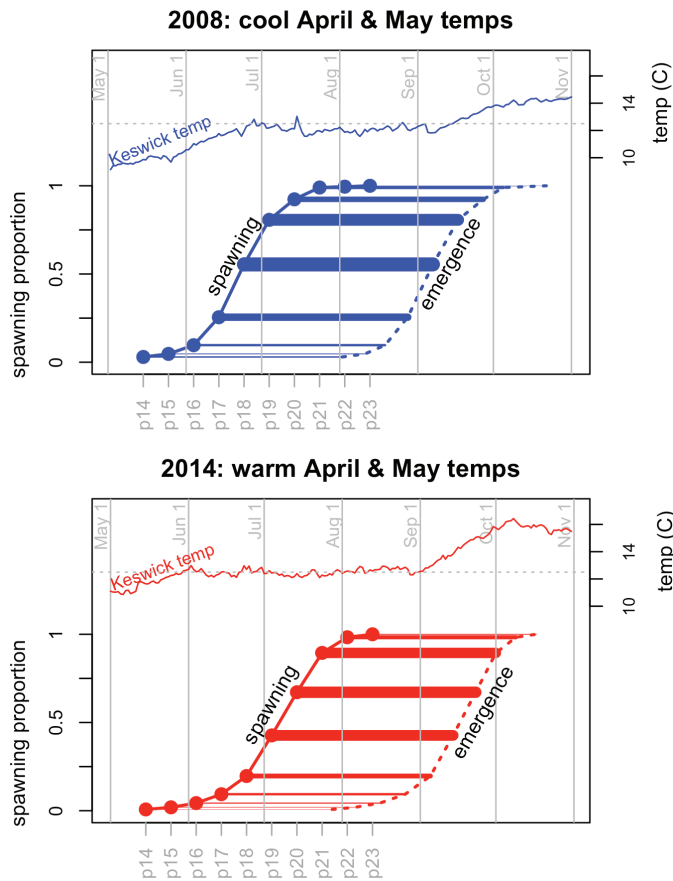


Figure 5 Cumulative spawn timing (*solid line*) and calculated egg incubation to emergence (*dotted line*) for example years with cool (2008) vs. warm (2014) April-May water temperatures below Keswick Dam. Individual points correspond to cumulative proportion of fish spawning during each 10-day period from *p14*–*p23* (labeled on the *x-axis* at day 5 of each 10-day period), and *thickness of the solid horizontal lines* shows the relative amount of spawning activity/egg deposition during each period. Daily water temperature below Keswick Dam is displayed in the *top half* of each plot, with the *secondary y-axis* providing the temperature scale. The *dashed horizontal gray line* indicates a temperature of 12.5°C.

egg and alevin incubation timing (Equation 3) to calculate winter-run spawn timing and egg incubation under average temperatures in the McCloud River, a historic winter-run spawning location, and at the current spawning location below Keswick Dam. Monthly mean water temperature in the spring-fed McCloud River is low in April, peaks in July, and then decreases again through November (Figure 6). In contrast,

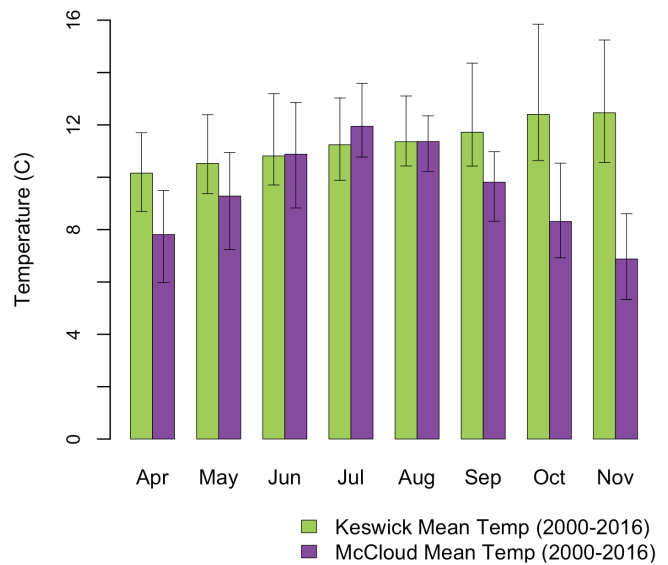


Figure 6 Monthly mean temperature on the McCloud River (41.0944°N, –122.1134°W, elevation 628 m) and on the Sacramento River below Keswick Dam from 2000–2016. *Error bars* show 95% confidence intervals around the monthly means. In most years, McCloud River daily data collection began in the second half of April, resulting in a potential upward bias in McCloud mean temperature for April.

the monthly mean temperature below Keswick Dam rises steadily from April through November. Under constant average monthly temperatures in both locations, model predictions show a higher proportion of early spawning in the McCloud River, with peak spawning occurring about 10 days earlier than below Keswick Dam (*p17*–*p20* for McCloud average conditions, compared to *p18*–*p21* for Keswick average conditions; Figure 7). Average temperatures in the two locations are similar from June through August, resulting in near-identical predicted emergence dates for eggs deposited between May 11 and July 9 (*p14*–*p19*), which is 56% of Keswick and 73% of the McCloud spawning distribution. As temperatures in the McCloud River begin to drop in September, the predicted embryonic and larval development times are longer for *p20*–*p23*, shifting emergence into November for eggs fertilized during *p22* and *p23*.

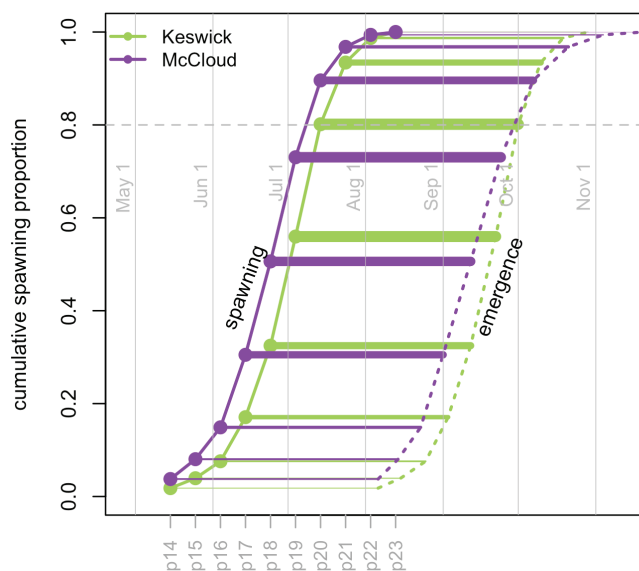


Figure 7 Modeled cumulative spawn timing (*solid line*) and egg incubation to emergence (*dotted line*) under Keswick and McCloud mean monthly temperatures. Individual points correspond to cumulative proportion of fish spawning during each 10-day period from *p14* to *p23* (labeled on the *x-axis* at day 5 of each 10-day period), and *thickness of the solid horizontal lines* shows the relative amount of spawning activity/egg deposition during each period. Note that 80% of spawning activity (*horizontal dashed gray line*) is predicted to occur about one week earlier under mean McCloud temperature conditions than under mean Keswick temperature conditions.

DISCUSSION

We have presented a mechanism for winter-run Chinook spawn timing as a function of early spring (April-May) water temperatures below Keswick Dam. While the start date of spawning remains relatively constant from year to year, there is annual variability in when the bulk of spawning occurs, as well as when spawning activity ends. Cool springtime temperatures trigger fish to spawn earlier; warm temperatures trigger fish to spawn later. The mechanism we describe has the opportunity to act as follows: migration timing of winter-run Chinook leads to their arrival at the base of Keswick Dam starting in January or February, followed by a lengthy (up to several months) staging period before spawning (Moyle et al. 1989). Because nearly all winter-run spawning sites are concentrated in the 20 km below Keswick Dam, the majority of fish

are exposed to a similar set of temperatures that can affect their reproductive timing.

Spawn timing in salmon is a trait under strong genetic control (Ricker 1972; Quinn and Adams 1996; Smoker et al. 1998; Quinn et al. 2000; Neira et al. 2006) and is critical to the success of fry at emergence. It allows for optimization of emergence timing, so that fry are met with environmental conditions favorable to growth and survival (Quinn 2018). In winter-run Chinook, the relationship between spawn timing and spring temperature developed in spring-fed cold-water streams—a different ecosystem than that which is currently accessible to SRWC. A genetic trait linking annual variation in winter-run spawn timing to spring temperatures would have ensured that the vast majority of fish emerged before low October and November temperatures. To a lesser extent, coupling of winter-run spawn timing to spring temperatures may have also led to embryonic-stage benefits in the historic spawning habitat. The embryonic stage is the most sensitive to elevated temperatures in the Chinook life cycle (McCullough 1999), with thermal tolerance of winter-run embryos likely set by oxygen availability (Martin et al. 2017). As salmonid embryos develop, their metabolic rate ($\mu\text{gO}_2 \cdot \text{h}^{-1}$) increases 7-fold from fertilization to hatching (Alderdice et al. 1958), with a further 5-fold increase from hatching through most of larval (alevin) development, and then a slight decrease before emergence (Rombough 1986; Rombough 1994). Because water temperature has a determinant effect on dissolved oxygen levels, the timing of temperature sensitivity should be highest in the later stages of egg development and the first half of larval development (Anderson 2018).

Within the context of historic spawning streams (e.g., McCloud River), a genetic trait that caused delayed spawning (June 30–Aug 8; *p19*–*p22*) during warm years would have resulted in late-stage embryonic and larval development occurring predominantly after the end of July, thereby protecting these sensitive stages from summer temperatures exceeding 12.5 °C, where temperature-related mortality may begin to occur (Martin et al. 2017). In the current spawning

habitat below Keswick Dam, late spawning during warm years is significantly reducing survivorship of embryos and alevin, acting in opposition to the competitive advantage that this genetic trait may have conferred in the natal spawning habitat.

With the insight that spawning winter-run Chinook respond to water temperatures in April and May, potential management actions could improve egg-to-fry survival, particularly under drought conditions. Water temperature below Keswick Dam depends on management of the limited cool-water pool behind Shasta Dam (14km above Keswick Dam), which varies in size from year to year. This cool-water pool is depleted as summer progresses, leading to increasingly warm temperatures downstream during winter-run Chinook egg and alevin incubation. Management of the cool-water pool affects the timing and availability of suitable temperatures for winter-run Chinook (NMFS 2018; USBR 2018). Although suitable temperatures can be achieved in years with a large cool-water pool, dry or critically dry water years result in a smaller cool-water pool that is depleted much earlier. Drought conditions between 2013 and 2015 reduced the size of the cool-water pool behind Shasta Dam and severely affected survival rates of incubating eggs and alevin (NMFS 2016; Anderson 2018). During this period, over 73% of winter-run Chinook spawned on or after June 30 (Figure 2), resulting in the majority of eggs and alevin developing through September (e.g., 2014; Figure 5), when temperatures below Keswick Dam exceeded suitable thermal conditions for development. Climate predictions for California indicate increasing risk of drought intensity and impact (Mann and Gleick 2015), suggesting that temperature-related egg mortality in SRWC is likely to be a persistent problem in the future. To mitigate winter-run Chinook egg and alevin mortality during drought years, two possible strategies for cool-water management are: (1) release cool water early (April-May) to drive the peak of winter-run spawning earlier in an attempt to achieve emergence from gravel before temperatures increase; or (2) hold cool water until later in the season, when the bulk of spawners begin to deposit eggs. There are

trade-offs involving the timing of cold water releases for winter-run Chinook and other species (e.g., Green Sturgeon; Zarri et al. 2019), and, ultimately, models that combine reservoir management dynamics with SRWC spawning and egg incubation will be necessary to understand how reservoir management might affect spawn timing, egg and alevin development, and egg-to-fry survival under various climate conditions.

To ensure the survival of winter-run Chinook, we must consider the run distribution and how to protect the bulk of the spawning distribution with cool water in drought years. In 2014 and 2015, for example, cool water was released relatively early to meet the requirements for early spawners. This resulted in a lack of cool water for the eggs of later spawners, which formed the bulk of the run. The few juveniles that survived to emergence in these years were likely offspring of adults that spawned early. Repeated application of these types of selective pressures on SRWC has had unknown consequences; however, truncation of genetic diversity can have deleterious effects on population persistence, particularly for populations confined to a single breeding area (Quinn 2018).

CONCLUSION

In conclusion, our analysis indicates a correlation between winter-run Chinook spawn timing and water temperatures in April and May. While the start date of spawning remains relatively constant regardless of water temperature, the peak and end of spawning shifts earlier during cool years and later during warm years. Further, we have shown that spawn timing curves can be approximated using a proportional-odds logistic regression model with April and May temperatures as cofactors. The model presented here may prove valuable for structuring management of cool-water releases from Shasta Dam and increasing survival of developing embryos and alevin during dry or critically dry water years.

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