Scenario: Targeting river operations to the critical thermal window of fish incubation: Model and case study on Sacramento River winter-run Chinook salmon

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Abstract
Allocating reservoir flows to meet societal and ecosystem needs under increasing water demands and climatic variability presents challenges to resource managers. Often, rivers have been regulated to meet flow and temperature compliance points or mimic historical patterns. Because it is difficult to assess if this approach is efficient, process-based models are being used to design river operations. This paper describes a model for fish incubation survival based on the premise that mortality from thermal stress occurs over a critical window (CW) of embryo development. A model for the embryo CW based on metabolic studies of development is combined with density-dependent and background mortalities to describe salmonid survival from egg fertilization to fry detection downstream. The model is calibrated with a two-decade dataset of Sacramento River winter-run Chinook salmon egg-to-fry survival. The effects of temperature exposure over a range of CWs were explored. Based on statistical and biological support, two alternative CWs were identified for temperature control: the entire incubation period and a short duration window prior to hatching. Survival under different CW assumptions and temperature control operations were simulated with an internet-accessible form of the model. The analysis indicated that under years of limited cold-water resources, targeting water releases to the CW prior to hatching would yield the highest incubation survival.

Keywords
Chinook salmon, critical window, incubation, modeling, mortality, reservoir operation, Sacramento River, temperature

1 | INTRODUCTION

Through natural selection, fish species adjust their spawning strategies so their offspring experience favorable conditions. River regulation can disrupt these strategies and so a common approach of water regulators has been to mimic the natural patterns of flow and temperature (Olden & Naiman, 2010). However, increasing societal needs for water and climate-driven variability in supply make mimicking historical conditions difficult and are compelling ecologists and river managers to seek more mechanistic models for designing and managing rivers (Arthington, Kennen, Stein, & Webb, 2018). The Sacramento River presents a prime example of the challenge and possibilities of new approaches. The Sacramento River winter-run Chinook (SRWRC) salmon, which historically spawned in the cool headwaters of the...
McCloud and Pit rivers in the spring and summer, were displaced to the warmer Sacramento River habitat by the construction of Shasta Reservoir (1938–1945) (Fisher, 1994; Williams, 2006) (Figure 1). In most years, mimicking their historical conditions has been possible with cool water releases from the reservoir during the spring and summer (NMFS, 2009). (Seager et al., 2015) and with climate warming it has become increasingly difficult to control the river temperature (Beer & Anderson, 2013; CDWR, 2021; Hallnan, Saito, Busby, & Tyler, 2020; Thompson et al., 2011). In this paper we develop a mechanistic model for the effect of temperature on salmon incubation and survival. We calibrate the model with a two-decade time series of SRWRC data and then evaluate impacts of alternative Shasta

FIGURE 1  Upper Sacramento River showing reaches 1–5 of winter-run Chinook salmon spawning habitat. The study area is divided into five reaches: (1) Keswick Dam to A.C.I.D. Dam, 5.5 km, (2) A.C.I.D. Dam to Highway 44 Bridge, 3.3 km, (3) Highway 44 Bridge to below Clear Creek confluence, 7.7 km, (4) Below Clear Creek to Balls Ferry Bridge, 24.8 km, (5) Balls Ferry Bridge to Bend Bridge, 30 km [Color figure can be viewed at wileyonlinelibrary.com]
Reservoir operations on the annual survival from egg fertilization to fry passage at Red Bluff Diversion Dam (RBDD) downstream.

2 | METHODS

At the core of the system is a mechanistic model of the effects of temperature on the development and survival of individual embryos, which is expressed in terms of a critical window (CW) of temperature. Applying the CW framework at a habitat scale, the system predicts the effects of river temperature on population-level egg-to-fry survival. Thus, in this framework, reservoir operations shift from mimicking historical temperature patterns to operations that target cold-water releases to the transient appearance of embryo CWs across the riverine habitat. We first develop a model of a CW based on embryo metabolism and then use a simplified CW form to describe a population of embryos incubating across a river habitat.

2.1 | Embryo model

Several studies of freshwater and marine fish species assume that the CW for population viability includes all phases of embryogenesis, that is, fertilization to fry emergence (Dahlke, Wohlrab, Butzin, & Pörtner, 2020; Martin et al., 2017). However, physiological studies indicate that fish thermal sensitivity is most important at the end of organogenesis when internal organs and eyes are formed, and the embryo is about to hatch. Studies suggest that mortality associated with hatching involves hypoxia (Del Rio, Davis, Fangue, & Todgham, 2019; Greig, Sear, & Carling, 2007).

We focus on the duration of hypoxia as a surrogate for the level of mortality. Prior to hatching, the metabolic oxygen demand is proportional to the embryo mass while the cutaneous supply through membrane diffusion is proportional to egg surface area (Martin et al., 2020). As the mass-to-area ratio increases with age, the oxygen demand increases more rapidly than supply and at some point, demand can exceed supply resulting in hypoxia. This transition likely occurs over a few days because the oxygen demand increases exponentially while the supply increases linearly (Rombough, 1994). Upon hatching, branchial respiration augments the diffusive supply (Wells & Pinder, 1996) and the embryo can recover quickly from hypoxia (Rombough, 2007) even though the surrounding oxygen level remains unchanged. Also, because the gill surface area increases as the square of body mass, oxygen delivery can increase faster than demand after hatching. Additionally, alevin movement can enhance redd ventilation and decrease distance to the gravel-water interface (Dill & Northcote, 1970). After hatching, oxygen sensitivity is largely independent of temperature in salmonids (Rombough, 1986; Wood, Clark, Elliott, Frappell, & Andrewartha, 2019). Furthermore, SRWRC alevin are tolerant of temperatures up to 16.8°C, which is generally higher, than has been observed historically in salmonid habitats (Myrick & Cech, 2004; USFWS, 1999). Thus, metabolic information suggests a threshold-like onset and cessation of hypoxia is likely associated with hatching. We designate this to the hypoxia CW.

Because the respiration rate and hatch age are both functions of temperature, the CW duration can be modeled. First, the salmon embryo oxygen demand rate \( R (\mu g O_2/hr) \) is \( \log R = a_R + b_R \log y + c_R \log T \) where \( y \) is age (days post fertilization), \( T \) is temperature (°C), and the coefficients obtained from laboratory studies are \( a_R = -16.897, b_R = 2.873, \) and \( c_R = 3.840 \) (Rombough, 1994). Rearranging the equation, the CW onset, which is the age at which \( R \) first exceeds the oxygen supply rate \( F \), is \( y_T = \exp((\log F - a_R - c_R \log T)/b_R). \) Next, the hatching age, designating the end of the CW, can be approximated \( y_F = ATU_H/(T - c_H) \) where \( ATU_H = 515°C \cdot d \) is the accumulated temperature units (ATU) (°C · d) required for hatching and \( c_H \) is an empirical adjustment factor (Alderdice & Velsen, 1978), where the area is set to zero. The CW of hypoxia duration is then

\[
y = y_F - y_T = ATU_H/(T - c_H) - \exp((\log F - a_R - c_R \log T)/b_R).
\]

This equation does not predict the mortality rate, only days of hypoxia. Nor does it imply that the temperature \( T \) fully defines the window duration. Studies indicate that temperature stress weeks before hatching, in the gastrulation phase (Irvine, 2020; Mueller et al., 2015) could alter the efficiency of respiration and cellular development, which in turn could affect the coefficients in Equation (1).

2.2 | Habitat scale egg-to-fry model

At the population level, survival between egg fertilization to fry detection downstream is described with three processes: temperature-dependent mortality (TDM) occurring during egg incubation; density-dependent mortality (DDM) characterizing the competition between spawners for suitable habitat; and background mortality (BGM) mainly characterizing predation on fry after emergence and prior to detection downstream (Table 1).

To describe TDM, first denote \( \beta_i \) as the daily mortality rate associated with temperature where \( y \) is age and fry emerge at \( y = E \). Thermal survival is then \( S = \exp(-\beta_i E) \). The daily mortality rate changes with both temperature and developmental phase and is unknown. However, the rate over a specific CW can be expressed using a modification of a model (Martin et al., 2017) in which the thermal mortality rate depends on the differential between the daily temperature \( T_i \) and a critical temperature \( T_{crit} \) as \( \Delta_y = \max(T_i - T_{crit}, 0) \) where temperature at age \( y \) is specific to redd \( i \) and depends on redd location and date of fertilization \( d \) such that the daily temperature for redd \( i \) is \( T_i = T_{d+i} - d \).

The CW is now characterized by a square wave that is zero everywhere except within the interval \( Y < \delta \) to \( Y > Y \) where \( Y \) is the end date of the CW. The mortality rate coefficient within the window is \( b_s \) and thermal survival in redd \( i \) is then

\[
S_i = \exp\left(-b_s \sum_{Y_i - \delta}^{Y_i} \Delta_y \right)
\]

Thus, thermal mortality only occurs within the CW and is defined by the embryo age \( Y_i \) at the CW end, the window duration \( \delta \), the
TABLE 1  Parameter definitions for Embryo and Egg-to-Fry models

| Symbol | Description                      | Symbol | Description               |
|--------|----------------------------------|--------|---------------------------|
| $R$    | Egg oxygen consumption rate ($\mu$O$_2$/hr) | $F$    | Egg membrane oxygen flux ($\mu$O$_2$/hr) |
| $a_R$, $b_R$, $c_R$ | Respiration coefficients | ATUY | ATU at hatching (°C-d) |
| $\gamma$ | Duration of hypoxia (d) | ATUH | ATU at hatching (°C-d) |

| Egg-to-fry model | |
|------------------|------------------|
| $B$              | Background survival |
| $U$              | Density-dependent survival |
| $V$              | Thermal survival |
| $S$              | Egg to fry survival |
| $\rho$           | Carrying capacity (#/km) |
| $D$              | Carrying capacity (#/km) |
| $A$              | Total number of carcasses (#) |
| $\delta$         | CW size (d) |
| $d$              | Fertilization day of year (d) |
| $y$              | Embryo age in days (d) |
| $Y$              | Embryo upper CW boundary age (d) |
| $E$              | Embryo age at emergence (d) |

| Symbol | Description                      |
|--------|----------------------------------|
| $Ty$  | Temperature over the window |
| $\Delta_y$ | Temperature differential at $y$ |
| $b_y$ | Intrinsic thermal mortality rate (1/d) |
| $\beta_y$ | Age-specific thermal mortality rate (1/d) |
| Opt   | Error of logit fitting |

The ATU at the beginning and middle of the CW are defined

$$ATU_i = \frac{y_i}{X} T_{x,i}.$$  (4)

The ATU at the beginning and middle of the CW are defined

$$ATU_0 = ATU_V - T_\delta \delta$$  
$$ATU_M = ATU_V - T_\delta \delta / 2,$$  (5)

where $T_\delta$ is the mean temperature over the CW.

The density-dependent mortality follows the Beverton-Holt model (Beverton & Holt, 2012), where the effect of population density on mortality depends on a habitat carrying capacity $D$ expressing the density of spawners at which survival is half the maximum level as

$$U_i = 1/(1 + \rho_i / D),$$  (6)

where $\rho_i$ designates the density of redds surrounding redd $i$ and is calculated for each river reach segment by dividing the number of redds in a reach by its length. Correspondingly, $D$ has units of redds/km. Note the mortality determined from Equation (6) is not a function of redd deposition date, temperature or flow.

Any additional mortality not associated with temperature or spawner density is designated background mortality and the corresponding background survival, $B$ is a free fitted parameter that is assumed to be constant for all years and redd locations.

The total population level incubation survival in year $j$ is the product of the three survivals as

$$S_j = B \frac{A_j}{X_j} \sum_{i=1}^{A_j} U_i V_i,$$  (7)

where $A_j$ is the total number of redds produced in year $j$.

2.3 Calibration strategy

The model parameters $[\delta, b_R, ATU_V, T_{crit}, B, D]$ were estimated by fixing $\delta$ and estimating the free parameter set $P = [b_R, ATU_V, T_{crit}, B, D]$ by minimizing the logit objective function

$$\text{opt} = \sum_{i} \left( \log \left( \frac{S_{obs,i}}{1-S_{obs,i}} \right) - \log \left( \frac{S_i}{1-S_i} \right) \right)^2.$$  (8)
where $S_{obs,j}$ is survival in year $j$ and $S_j$ is estimated from Equation (7) as implemented in the Egg-to-Fry model available at (Beer & Anderson, 2021) (Appendix S1A). $S_j$ was estimated with observed daily temperature, $T_{ij}$, and spawning date, $d_{ij}$. $P$ was fit using the derivative-free optimization Nelder–Mead simplex nmkb in the dfoptim package of the R® programming language (R Core Team, 2018) where parameter search limits were set.

In setting search limits, our goal was not to find a global fit but to identify parameter sets for biologically plausible CWs, specified by duration $\delta$ and endpoint ATU$_F$. To this end, we first estimated $P$ across the possible range of $\delta$ (1–79 days) using parameter limits: $0.01 < b_2 < 2$, $0.4 < b < 0.6$, $50 < D < 100$, $11 < T_{crit} < 13$, and $100 < ATU_F < 947$. Initial search values were taken as midpoints of ranges except for $b_2$ which from Equation (3) was set as $b_2 = 2/\delta$. The fitted ATU$_F$ represents a CW endpoint for the associated $\delta$. The window start ATU$_D$ and middle ATU$_M$ were then approximated with Equation (5) with $T_{\delta} = 11.54^\circ$C as derived from observed temperatures. Next, we conducted finer-scale searches over selected $\delta$ and ATU$_F$ endpoints corresponding to organogenesis (400–550°C · d), and then to the entire incubation (850–950°C · d).

To validate the model, we used a leave-one-out (LOO) cross validation approach in which the survival time series (2002:2015, 2017:2020) was sliced into 18 unique sets, each consisting of a 17-year learning set and 1-year testing set. Cross validation was expressed as the mean absolute deviation, $\text{MAD} = \sum_{j} \text{mean}[S_{obs,j} - S_{est,j}]/18$, where $S_{est,j}$ is the predicted survival for slice $j$.

### 2.4 Model application

We use the model to evaluate the effects of alternative Shasta Reservoir operations on the survival of SRWRC from egg fertilization to fry passage at RBDD (Figure 1). In the spring and summer, the reservoir operation goal is to maintain cool temperatures during embryo incubation, but the control ability depends on the available volume of cold water in the reservoir prior to fish spawning. Consequently, the US Bureau of Reclamation plans the operations based on the cold-water pool and total reservoir volume expected on May 1. Other factors considered include the flows required to avoid dewatering the redds and meet water delivery obligations for downstream users. Additionally, the assessment uses long-term weather forecasts and current reservoir levels to assess the probability of refilling the reservoir the following year. Using this information, the planned operation is set into one of four Tiers (Table 2) which are designed to best allocate the available cool water to a Critical Egg Incubation Period (CEIP) (NMFS, 2019). However, the Tier plan does not specify the CEIP properties. The Egg-to-Fry Model predicts survival outcomes under biologically based definitions of the CEIP. Thus, reservoir operations can be linked to specific biological criteria defining a CW.

### Table 2 Description of Shasta operations for water-year Tiers

| Tier         | Year type | Notes                                                                 |
|--------------|-----------|----------------------------------------------------------------------|
| 1            | Wet       | Target 53.5°F (11.9°C) or lower, starting May 15 through October 31 |
| 2            | Normal    | Target 53.5°F during critical egg incubation period (CEIP) and do not exceed 56°F during the management period ending October 31 |
| 3            | Dry       | Target 53.5–56°F (11.9–13.3°C) during CEIP and do not exceed 56°F during the management period ending October 31 |
| 4            | Extremely dry | Target 53.5–56°F during CEIP and do not exceed 56°F during the management period ending October 31 |

### Figure 2 Isolines of days of incubation hypoxia as a function of diffusive flux and temperature (Equation 1). Dashed lines (---) depict diffusive oxygen flux for comparisons with temperature [Color figure can be viewed at wileyonlinelibrary.com]

### 2.5 Data

The model was calibrated with SRWRC salmon spawning dates and locations from carcass surveys conducted by the California Cooperative Anadromous Fish and Habitat Data Program (Killam, 2021). Survival to RBDD was determined by expanding fry passage estimates at RBDD divided by estimates of female spawner carcass counts (Poytress, 2016; Rea, 2019, 2021). Spawning information was also available from coarser-grained aerial surveys of redds. In this paper we apply the carcass data because it was used to calculate survival above. Temperature was calculated by linear interpolation between the daily temperatures at Keswick Dam (rkm 483) and Clear Creek (rkm 470) (Figure 1) sourced from the California Data Exchange Center (CDEC, 2021). All data are accessible on the Egg-to-Fry model webpage (Beer & Anderson, 2021) which is linked to the SacPAS.
database (Itlis, Holmes, & Anderson, 2021). The calibrations based on carcass surveys covered years 2002–2015 and 2017–2020. The year 2016, a significant outlier, was excluded from the analysis (Appendix S1C for details).

### 3 | RESULTS

#### 3.1 | Embryo model

From Equation 1, isopleths of the duration of hypoxia were generated over ranges of incubation temperature and diffusive oxygen flux (Figure 2). In general, the hypoxia duration increases with lower oxygen fluxes and higher temperatures, but the responses are not equal. For a fixed oxygen flux of 25 μgO₂/hr a change in temperature from 11 to 13°C increases the hypoxia duration by 2 days, while a drop in oxygen flux from 25 to 20 μgO₂/hr over the same temperature range increases the duration by 3–4 days. At lower fluxes, temperature has no effect on hypoxia duration.

#### 3.2 | Egg-to-fry model

A main goal of the calibration was to characterize the model fit over a range of CWs defined by the window boundaries ATU₀ and ATUₓ. Functionally, these boundaries were determined by fitting ATUₓ for selected $\delta$ and calculating ATU₀ with Equation (5). We focused on two CW types covering different phases of embryo development (Velsen, 1980). The O-type CW depicts late phase of organogenesis prior to hatching (ATU range 400 to 520°C · d) and the E-type CW depicts spawning to alevin emergence (ATU range 0–950°C · d). Table 3 gives the representative parameters for these window types. Figure 3, showing the model responses versus $\delta$ depict the CW types by colors and circles the parameters points in Table 3.

To explore the effect of model fits across the range of CW types we first derived P sets in Figure 3 by limiting the ATUₓ search to the range 100 to 947°C · d (Figure 3). This encompassed the hatch stage, although the search algorithm was not constrained to that stage. The fitted ATU₀ versus $\delta$ has a hockey stick shape with a break at $\delta^* = 33$ days (Figure 3a). The lower boundary, ATU₀, for the O-type CW clusters at approximately 400°C · d for $\delta < \delta^*$ and thereafter declines to zero corresponding to the E-type CW (Figure 3b). The ATUₓ peaks at $\delta^*$ and then declines resulting in the O- and E-type CWs locating below the hatching range (Figure 3c gold region), ATUₓ = 515 ± 22°C · d @ 10–12°C (Alderdice & Velsen, 1978). Between $\delta_1$ and $\delta_2$ the ATUₓ is within or above ATUₓ. Note, the $\delta^*$ break in ATU₀ and ATUₓ graphs (Figure 3a,b) corresponds to the peak ATUₓ, which is also above the range of ATU₀ (Figure 3c). The critical temperature for the onset of TDM, $T_{\text{crit}}$, has a hockey stick shape with a breakpoint at $\delta_1$ (Figure 3d). The density-dependent carrying capacity $\delta$ varies between 70 and 90 redds/km for these model runs (Figure 3e) and exhibits high variability, as does the background survival $B$ (Figure 3f).

The model fit measure, opt, increases with $\delta$ up to $\delta_1$, is relatively flat between $\delta_1$ and $\delta_2$ and thereafter decreases and spreads (Figure 3g). The region between $\delta_1$ and $\delta_2$ largely corresponds to ATUₓ points within the hatch region. Notably, characteristic parameters for O- and E-type CW, which yield good model fits, occur 50–100°C · d below the range of ATUₓ (Figure 3c).

The parameters $D$ and $B$ (Figure 3h) associated with DDM and BGM co-vary such that estimates of background survival vary inversely with estimates of carrying capacity as $B = 0.6939 - 0.0022D$ with $R^2 = 0.781$. As a result, predictions of non-TDM survival are constrained. For example, with carcass density 50% of carrying capacity, that is, $\delta = D$, and estimated $D$ between 70 and 90 the non-TDM survival varies between 0.26 and 0.28.

The relationship of the mortality rate coefficient and CW width is highly linear (Figure 3i). A regression of Equation (3) gives the intrinsic mortality rate coefficient as $\alpha = 1.8527$ ($SE = 0.0058$) with $R^2 = 0.9999$. We further investigated the model fits of the CW types using a leave-one-out correlation analysis and found median absolute deviation (MADs) for O- and E-types CW of ~20% of the average survival of 0.23. Figure 4a illustrates that survivals from the CW types are nearly identical and Figure 4b depicts survival resulting for individual mortality processes for an O-Type CW. The BGM process is constant while TDM and DDM contributions to survival vary across years.

#### 3.3 | Reservoir operation simulation

Because all CW types reasonably fit the data, we simulated the effects of alternative reservoir operations paired with their associated factual and counterfactual CEIP assumptions (Figure 5). Factual simulations for Operation I, which targets cold water over the entire incubation, assume an E-type CEIP and simulations for Operation II, which targets cold water between the hatch of the first and last redds, assume an O-type CEIP. Counterfactual simulations reversed the CEIP assumptions. We compared results by normalizing Tier 2–4 survivals to the

| CW type | $\delta$ | ATU₀ | $T_{\text{crit}}$ | $b_3$ | $B$ | $D$ | Opt | $R^2$ | MAD |
|---------|---------|------|-------------------|------|-----|-----|-----|-------|-----|
| O       | 4       | 400  | 11.82             | 0.4361| 0.503| 85  | 1.438| 0.843 | 0.040 |
| E       | 75      | 859  | 12.04             | 0.030 | 0.531| 76  | 1.436| 0.857 | 0.068 |

**Table 3** Egg-to-Fry model results for two critical window (CW) types

Note: Model predicted to observe survival fit is depicted by the linear regression coefficient $R^2$. Cross validation fits measure MAD was determined with a leave-one-out method.
respective Tier 1 survivals because the model fits for the CW type's partitioned mortality differently between TDM, DDM, and BGM.

For Operation I, the relative survivals are independent of the CEIP assumption. Operation II generally gives higher survivals under an O-type CW than under an E-type CW. However, the effects are variable and depend on how many of the population CWs are targeted with cold water.

4 | DISCUSSION

In this study, we modeled the effect of temperature during CWs on embryo development and survival. While a CW may be of any duration and centered at any phase of development, the model fit to the two-decade time series of SRWRWC salmon incubation resulted in two CW types fitting the data best. The E-type CW covers all incubation, and the O-type covers the pre-hatch period of organogenesis.

Notably, the selection of the CW types has little effect on the predicted TDM. To explore a possible underlying reason for this insensitivity note that \( b_\delta \) is related to \( \delta \) by Equation (3) such that Equation (2) simplifies to \( V = \exp(-\alpha \Delta) \), where the mean temperature differential over the CW, \( \Delta \), is essentially independent of \( \delta \) (details in Appendix S1B). Thus, the TDM largely is a function of \( \alpha \), which depends on the oxygen flux to the redd, and \( \Xi \), which depends on mean temperature over the critical window. Furthermore, we postulate that variability in \( \Xi \) increases when ATUM is outside the range of the actual TDM processes. Exceeding the range is exemplified by the interval between \( \delta_1 \) and \( \delta_2 \) in which the highest opt (Figure 3d) corresponds to the region in which ATUM ≥ ATUH (Figure 3c). In this

FIGURE 3 Plots of parameters P (Table 1) for 111 fitting delimited by pairs of critical window widths (\( \delta \)) and accumulated temperature units (ATUY). In panels a-h critical window (CW) types are shown as clusters O-type (○) and E-type (▲) with other points not in clusters (⊙). Circled points depict Table 3 parameters. Vertical line \( \delta^* \) demarks CW width with largest opt (poor model fit) and slope change in ATU versus \( \delta \) plots (panels a–c). Vertical lines \( \delta_1 \) and \( \delta_2 \) demark CW widths where middle of the CW (ATU0) is equal to or larger than the ATU range for hatching depicted by gold band (panel c). Critical temperature (\( T_{\text{crit}} \)) increases with \( \delta \) (panel d) while background survival (\( \beta \)) and density-dependent carrying capacity (\( D \)) exhibit no clear pattern (panels e, f). Pattern of model fits (opt) vs \( \delta \) (panel g). Regression lines \( B \) versus \( D \) (panel h) and \( b_\delta \) versus 1/\( \delta \) (panel i) [Color figure can be viewed at wileyonlinelibrary.com]
situation Δ is expected to include temperatures not associated with TDM processes and therefore introduces more noise in the model fit. Notably, the best fits correspond to $\text{ATUM} < \text{ATUH}$. Additionally, the Embryo model reveals that longer durations of hypoxic CW are dependent on oxygen flux, not temperature (Figure 2), which supports the observation of similar model fits with different $T_{\text{crit}}$.

While model fits do not clearly support one CW type over another, biological information better supports an O-type
CW. Studies demonstrate a rapid increase in respiration rate prior to hatching and a quick return to normoxia after hatching favor a short CW (Rombough, 1994). Also, the model fit improves with declining $\delta$ (Figure 3a). In contrast, no direct mechanism is readily identified for mortality processes across an E-type CW extending from fertilization to fry emergence. However, an E-type CW could involve post hatching hypoxic stress associated with microbial degradation of the redd environment (Sear et al., 2016) or unspecified high temperatures heat stress, for example, >16.8°C (USFWS, 1999). Also, we note that an E-type CW does not require continued mortality over the window and readily captures the effects of an embedded O-type window, that is, both CW types can have the same ATU$_{50}$.

We evaluated the outcome of reservoir operations when the CEIP assumption matched or mismatched the operation strategy. In general, optimum incubation survival required targeting the cold-water resources to the maximum number of CWs possible. However, determining the balance between the numbers of CWs targeted and temperature requires model simulations constrained on expected cold water volumes, the spawning distribution, and using the appropriate CW assumption.

5 | SUMMARY

The paper had three goals; fit the pattern of SRWRC salmon survival over the two-decades of data, explain the pattern in terms of fish embryogenesis and use the framework to guide design and evaluation of Shasta Reservoir operations.

Using the CW framework, we found that both short and long durations CWs better fit the survival data when the window middle was located several days before hatching. Notably, CWs centered in the hatching stage itself yielded lesser fits.

We sought to explain the effect of the CW on model fits using principles of embryogenesis. Literature and the results of this work together suggest the duration of hypoxia and mortality may be a few days to a week prior to hatching. Surprisingly, the models suggest that hypoxia persisting greater than a week would be largely independent of temperature and this insensitivity may account for the low variability in $T_{\text{crit}}$ with CW type. Additionally, the CW framework arises in physiological and ecological studies (Mueller et al., 2015; Uchida, Uesaka, Yamamoto, Takeda, & Irie, 2018) and is implicit in studies that consider cross life-stage effects (Del Rio et al., 2021; Gosselin et al., 2021; Stoks & Córdoba-Aguilar, 2012). We suggest that further studies in a CW framework will provide new insights into embryogenesis and population regulation in a warming climate.

The third goal has been to move beyond journal publications and open-source software distribution as the endpoint of model development. We advocate those models actively used in resource management are most useful if implemented as real-time web-based systems available to managers and the public. As described in Appendix S1A, the model presented in this paper is part of the Sacramento River Fish model that is linked to a database (SacPAS: Central Valley Prediction & Assessment of Salmon) containing information from multiple historical and real-time river and fish data sources (e.g., CDWR, 2021) as well as real-time information on reservoir operations and forecasts (CVTEMP, 2022).

In a brief analysis, we explored benefits and risks of applying alternative CW hypotheses with different reservoir operations. The exercise illustrates the flexibility and advantages of viewing operation targets, not at the level of the population, but at the level of multiple and transient CW events experienced by the individuals in the population. This shift in perspective we argue should allow more flexibility and insights, especially when decisions on resource allocations become decisions of triage between competing individuals and species (Council, 2012; Zarri, Danner, Daniels, & Palkovacs, 2019).

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DATA AVAILABILITY STATEMENT

All data used in the analysis are available on the website Fish Model website http://www.cbr.washington.edu/sacramento/fishmodel/ under the heading “Download CSV file after run.” Additionally, data are available at http://www.cbr.washington.edu/sacramento/data/.

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