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Application of a Life Cycle Simulation Model to Evaluate Impacts of Water Management and Conservation Actions on an Endangered Population of Chinook Salmon

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Abstract Fisheries and water resource managers are challenged to maintain stable or increasing populations of Chinook salmon in the face of increasing demand on the water resources and habitats that salmon depend on to complete their life cycle. Alternative management plans are often selected using professional opinion or piecemeal observations in place of integrated quantitative information that could reduce uncertainty in the effects of management plans on population dynamics. We developed a stochastic life cycle simulation model for an endangered population of winter-run Chinook salmon in the Sacramento River, California, USA with the goal of providing managers a tool for more effective decision making and demonstrating the utility of life cycle models for resource management. Sensitivity analysis revealed that the input parameters that influenced variation in salmon escapement were dependent on which age class was examined and their interactions with other inputs (egg mortality, Delta survival, ocean survival). Certain parameters (river migration survival, harvest) that were hypothesized to be important drivers of population dynamics were not identified in sensitivity analysis; however, there was a large amount of uncertainty in the value of these inputs and their error distributions. Thus, the model also was useful in identifying future research directions. Simulation of variation in environmental inputs indicated that escapement was significantly influenced by a 10% change in temperature whereas larger changes in other inputs would be required to influence escapement. The model presented provides an effective demonstration of the utility of life cycle simulation models for decision making and provides fisheries and water managers in the Sacramento system with a quantitative tool to compare the impact of different resource use scenarios.

Keywords California · Delta · Life cycle model · Sacramento River · Simulation · Winter run Chinook salmon

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1 Introduction

Understanding what drives interannual variability in Chinook salmon (*Oncorhynchus tshawytscha*) populations is of considerable interest to resource managers because of the large number of salmon stocks that are currently listed as threatened or endangered [1, 14]. Declines in the number of salmon returning to spawn have triggered recovery plans intended to stabilize or increase population sizes. The success of these plans has varied considerably and many populations remain at risk [15]. The factors responsible for declines in Chinook salmon populations are generally known yet, the relative importance of each factor and the scale at which it operates is often unknown, which complicates attempts to effectively apply management actions to recover Chinook salmon stocks [7, 31, 37].

Both scientists and managers have increasingly recognized the utility of life cycle models for evaluating salmon population responses to management actions [28], and a recent review of salmon recovery efforts in California's Central Valley recommended their use [12]. Although there have been many studies and monitoring efforts focused on the ecology of salmon at the individual and population level, many of these data relate only to a single life stage, habitat type, or environmental variable. This has made it difficult to integrate these data into a traditional statistical framework to estimate interannual population dynamics or to identify specific bottlenecks to population recovery. Life cycle models utilize available time-series data as well as values taken from laboratory studies or other sources to parameterize model relationships, thereby utilizing the greatest amount of data available to dynamically simulate responses of populations across multiple life stages to changes in environmental variables or combinations of

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environmental variables at specified times and locations. Thus, these models are powerful tools that can be used by managers to plan and evaluate recovery actions for Chinook salmon. Here, we present a life cycle simulation model for an endangered winter-run Chinook salmon population in the Sacramento River, California, USA (Fig. 1).

Sacramento River Chinook salmon stocks have experienced severe declines over the last century resulting in extirpation of some populations [14] and a moratorium on commercial and sport harvest in recent years to protect extant populations. Winter run in the Sacramento River was listed as endangered under the Federal Endangered Species Act in 1994 [9]. Historically, winter run utilized high elevation stream habitats in the Upper Sacramento River and tributaries for holding, spawning, and rearing [36]. However, extensive dam construction in the early twentieth century restricted winter run to a single reach of the lower Sacramento River below Keswick Dam [35]. After leaving the spawning and rearing habitat, juvenile winter run migrate down the Sacramento River, through the Sacramento–San Joaquin Delta (hereafter referred to as the Delta) and spend from 2 to 4 years in the ocean before returning to their natal spawning grounds.

As pressure on Sacramento River water resources continues to increase from domestic and agricultural users, resource managers are in need of quantitative tools to compare the relative impact of future water use activities on the winter-run population and to select relevant life stages and environmental variables to focus on for recovery actions. Our goals for this study were to describe a stochastic life cycle simulation model for winter run in the Sacramento River: the Interactive Object-Oriented Simulation Model (IOS). Specifically, we: (1) present the structural and functional relationships of the IOS model, (2) conduct a sensitivity analysis that describes uncertainty in estimates of model parameters, and uncertainty due to inherent stochasticity of the population, and (3) examine the response of the model to variability in the four environmental drivers for which sufficient data were available including: temperature that affects egg and fry survival during early development, flow that affects survival and migration travel time during freshwater migration, water exports that affect survival in certain migration pathways, and ocean productivity that affects survival in the ocean.

2 Methods

2.1 Model Description and Structure

The IOS model uses a systems dynamics modeling framework, a technique that is used for framing and understanding the behavior of complex systems over time [6, 10]. System dynamics models are made up of stocks (e.g., number of fish) and flows (e.g., sources of mortality) which are informed by mathematical equations [10]. IOS was implemented in the software GoldSim, which enables the simulation of complex processes through creation of simple object relationships, while incorporating Monte Carlo stochastic methods [27]. Terms used in the model description are defined in Table 1.

The IOS model is composed of six model stages that are arranged sequentially to account for the entire life cycle of winter run, from eggs to returning spawners (Fig. 2). In sequential order, the IOS model stages are: (1) *spawning*, that models the number and temporal distribution of eggs deposited in the gravel at the spawning grounds; (2) *early development*, that models the impact of temperature on maturation timing and mortality of eggs at the spawning grounds; (3) *fry rearing*, that models the relationship between temperature and mortality of salmon fry during the river rearing period; (4) *river migration*, that estimates mortality of migrating salmon smolts in the Sacramento River between the spawning and rearing grounds and the Delta; (5) *delta passage*, that models the impact of flow, route selection, and water exports on the survival of salmon smolts migrating through the Delta to San Francisco Bay; and (6) *ocean survival*, that estimates the impact of natural mortality and ocean harvest to predict survival and spawning returns (escapement) by age. Below is a detailed description of each model stage.

Spawning For the first four simulation years, the model is seeded with a fixed number of female spawners. In subsequent years, the number of spawners is determined by the model's probabilistic simulation of survival to this life stage. To ensure that developing fish experience the correct environmental conditions during each year, spawn timing mimics the observed arrival of salmon on the spawning grounds as determined by 8 years of carcass surveys (2002–2009) conducted by the United States Fish and Wildlife Service (USFWS). Winter run die after spawning which allows the size of the spawning population to be estimated from the number of carcasses observed. In each year, one of the eight spawning distributions is chosen at random. Eggs deposited on a particular date are treated as cohorts which experience temperature and flow on a daily time step during this stage. The daily number of spawners is calculated by multiplying the daily proportion of the total carcasses observed during the USFWS surveys by the total Jolly–Seber estimate of spawners [24].

$$S_d = C_d S_{JS} \tag{1}$$

where, S_d is the daily number of spawners, C_d is the daily proportion of total carcasses, and S_{JS} is the total Jolly–Seber

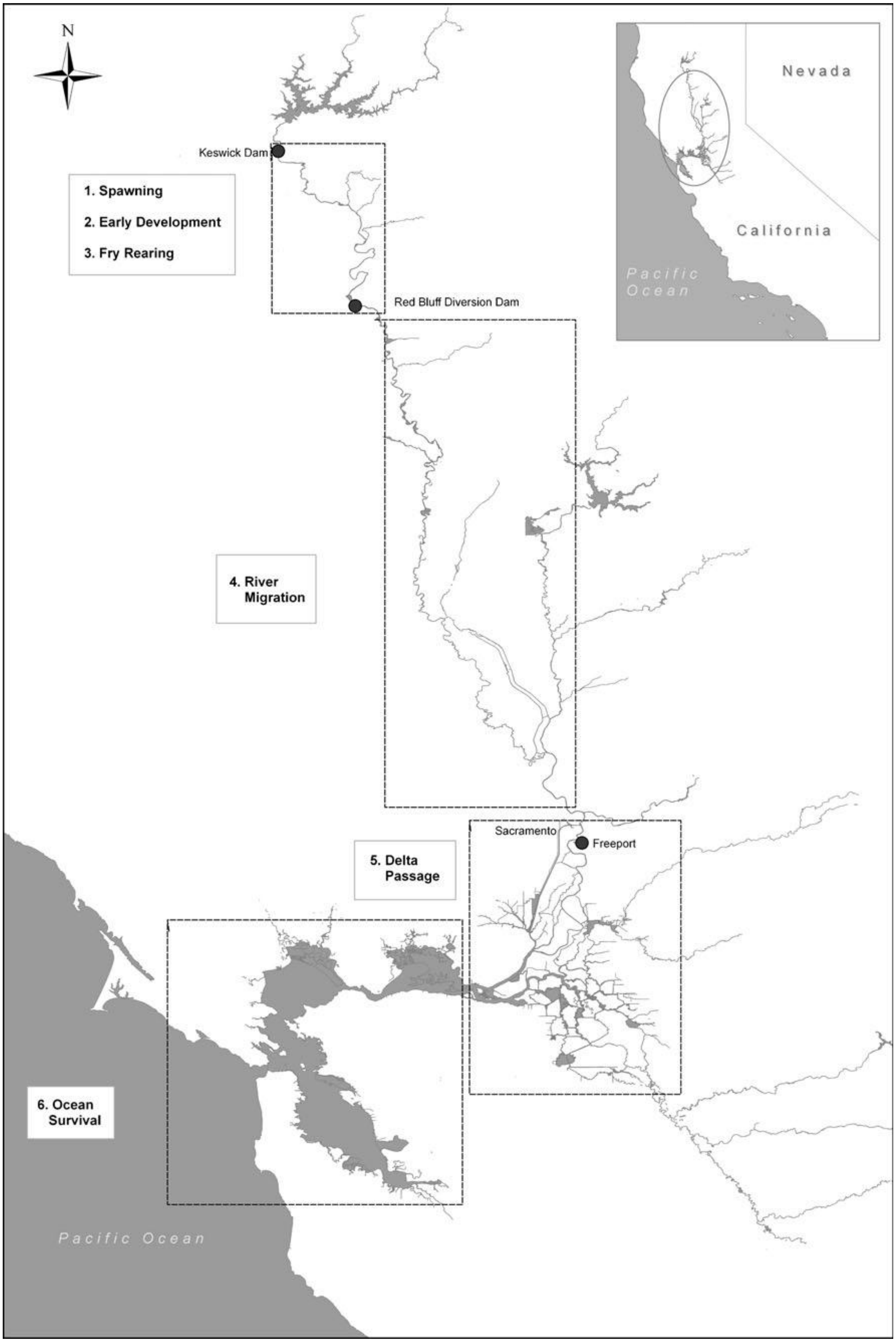

Fig. 1 Map of the Sacramento River and the Sacramento–San Joaquin Delta, including approximate areas defined by each model-stage

Table 1 Glossary of terms used to describe model functions, data sources, and relevant locations in the study area

Term	Definition
CDFG	California Department of Fish and Game
Delta	A freshwater tidal estuary formed by the Sacramento and San Joaquin Rivers that salmon juveniles must pass through on their way to the Pacific Ocean
Escapement	The total number of Chinook salmon that leave the ocean and return to the Sacramento River to spawn. This number includes 2-, 3-, and 4-year-old fish
Fry	Salmon life stage that occurs from the period of emergence from spawning gravels until the start of physiological changes in preparation for migration
Jolly_Seber estimate	A statistical method of estimating the size of a population using mark and recapture data
Screwtrap	A passive sampling devise that traps juvenile salmon as they migrate downstream
Smolt	Salmon life stage characterized by physiological changes in preparation for migration and ocean entry
Spawner	Salmon that leaves the ocean and returns to the Sacramento River to spawn. This can occur at age 2, 3 or 4. All fish die after spawning
USFWS	United States Fish and Wildlife Service
Winter-run Chinook salmon	A genetically distinct population of Chinook salmon that completes the freshwater portion of their life cycle in the Sacramento River. This population has been listed as endangered under the federal Endangered Species Act
Junction Geo/DCC	The combined junction of the Sacramento River, Georgiana Slough and the Delta Cross Channel. Both Georgiana Slough and the Delta Cross channel lead into the Interior Delta reach
Junction SS	The junction between two potential migration routes, the Sacramento River and Sutter/Steamboat Slough
Interior Delta	A reach that fish entering through Junction Geo/DCC must pass through on their way to the ocean. This reach is a network of tidal channels and a relationship between water exports and survival is present in this reach
Reach Geo/DCC	The combined reach of Georgiana Slough and the Delta Cross Channel
Reach Sac 1	The Sacramento River between the start of the Delta at Freeport and the junction with Steamboat/Sutter Slough
Reach Sac2	The Sacramento River between the reach Sac1 and the Junction of Georgiana Slough and the Delta Cross Channel
Reach Sac3	The Sacramento River between Sac2 and the confluence of Steamboat/Sutter Slough and the Sacramento River. A flow–survival relationship is present in this reach
Reach Sac4	The Sacramento River between the confluence of the Sacramento River and Sutter/Steamboat Slough and the end of the Delta Passage model stage
Reach SS	The combined reach of Sutter and Steamboat Slough. A flow–survival relationship is present in this reach.

estimate of spawners. In order to better match the timing of carcass observations to the deposition of eggs, the date of egg deposition is shifted 14 days before the carcasses were observed (Kevin Niemela, personal communication).

To obtain an estimate of juvenile production, a Ricker stock-recruitment curve [26] was fit between the number of fry produced each year (R) and the number of spawners (S) as estimated by the California Department of Fish and Game screw trap sampling (juveniles) and USFWS carcass surveys (spawners) for years (1996–1999, 2002–2007):

$$R = \alpha S e^{-\beta S} + \varepsilon \tag{2}$$

where, R is the estimate of juvenile recruitment, α is a parameter that describes recruitment rate, and β is a parameter that measures the level of density dependence. The density-dependent parameter (β) did not differ significantly from zero (95% CI=-6.3×10^{-6}–5.5×10^{-6}). Therefore, β was removed from the equation and a linear version of the relationship was estimated. The number of spawners explained 86% of the variation in fry production ($F_{1,9}$=268, p<0.001) in the data, so the value of α was taken from the regression:

$$R = 1043 \bullet S \tag{3}$$

This linear relationship is used to predict values for mean fry production along with the confidence intervals for the predicted values. These values are then used to define a normal probability distribution, which is randomly sampled each year to determine the annual fry production. Although the Ricker model accounts for mortality during egg incubation, the data used to fit the Ricker model were from a limited time period (1996–1999, 2002–2007) when water

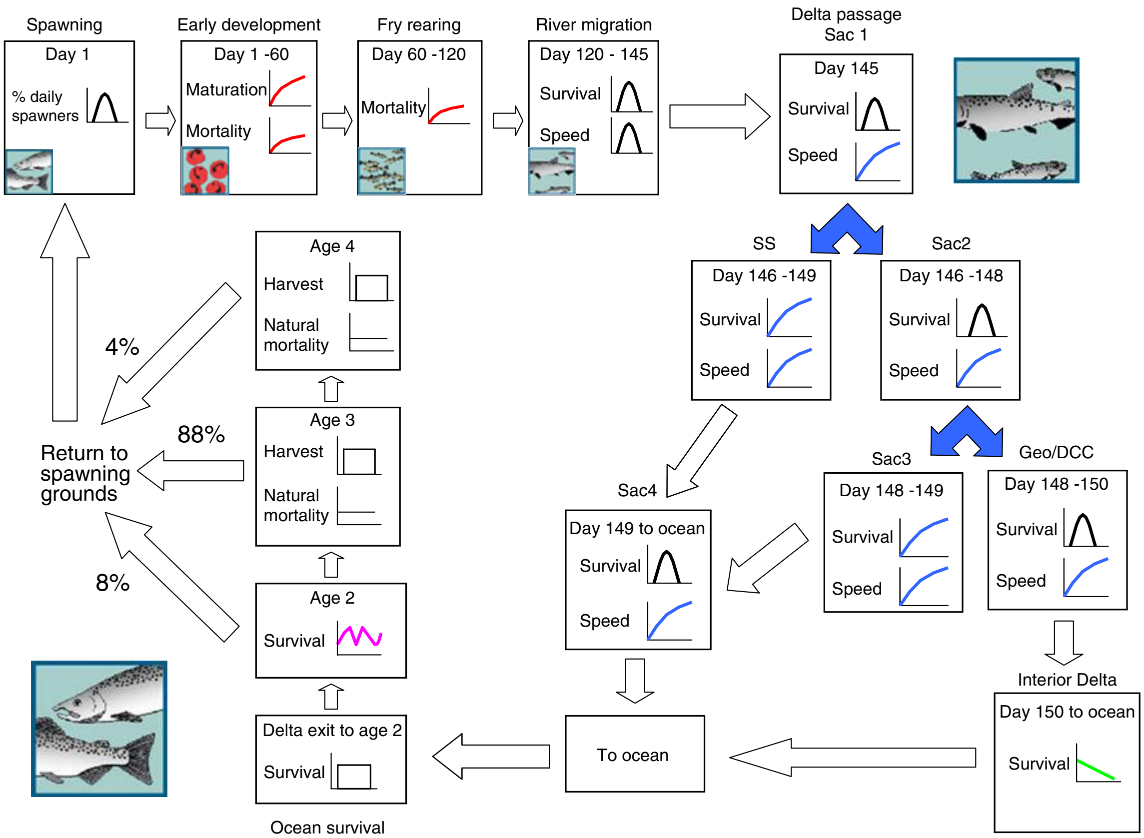

Fig. 2 Conceptual diagram of IOS model stages and environmental influences on functional relationships at each stage. *Colors* indicate the environmental driver influencing each relationship where *red* temperature, *blue* flow, *green* water exports, and *pink* ocean productivity. Relationships in *black* indicate that values are drawn from a normal distribution, a uniform distribution, or are constants

temperatures during egg incubation were too cool (<14°C) to cause significant temperature-related egg mortality [32]. Thus, additional mortality was imposed in the model when temperatures exceeded those experienced during the years used to construct the Ricker model.

Early Development Data from three laboratory studies was used to estimate the relationship between temperature, egg mortality, and development time [4, 19, 32]. Using data from these experiments, a relationship was constructed between maturation time and water temperature. First, we converted *maturation time* (days) to a daily *maturation rate* (1/day):

$$\text{daily maturation rate} = \text{maturation time}^{-1} \tag{4}$$

A significant linear relationship between maturation rate and water temperature was detected using linear regression ($F_{1,15}$=2,188, p<0.001):

$$\text{daily maturation rate} = 0.00058 \bullet \text{Temp} - 0.018 \tag{5}$$

Each day, the mean maturation rate of the incubating eggs is predicted from the daily temperature using the above linear function; the predicted mean maturation rate along with the confidence intervals of the predicted values are used to define a normal probability distribution, which is then randomly sampled to determine the daily maturation rate. A cohort of eggs accumulates a percentage of total maturation each day from the above equation until 100% maturation is reached.

Data from the USFWS [32] was used to inform the relationship between temperature and mortality of developing winter-run eggs. This study utilized a small number of treatments (three temperature treatments) and although studies from other regions could have been used, we chose to use data specific to winter run. Salmon populations are adapted to local temperature regimes and use of data from outside of the Sacramento River may not conform with the requirements of winter run. The functional form of the temperature–mortality relationship was similar to data from other regions suggesting that USFWS data on winter run was sufficient to parameterize the model-predicted mortality over the entire incubation period was converted to a daily mortality rate to apply temperature effects in the model. This conversion was used to calculate daily mortality using the methods described in [3]:

$$\text{mortality} = 1 - (1 - \text{total mortality})^{(1/\text{development time})} \tag{6}$$

where, *total mortality* is the predicted mortality over the entire incubation period observed for a particular water temperature and *development time* was the time to develop from fertilization to emergence.

The following exponential relationship was fitted between observed *daily mortality* and observed water temperatures [32]:

$$\text{daily mortality} = 1.38 \bullet 10^{-15} e^{(0.503 \bullet \text{Temp})} \tag{7}$$

Each day, the mean mortality rate of the incubating eggs is predicted from the daily temperature measured at Bend Bridge on the Sacramento River using the above exponential function. The predicted mean mortality rate along with the confidence intervals of the predicted values is used to define a normal probability distribution, which is then randomly sampled to determine the daily egg mortality rate.

Fry Rearing Data from USFWS [32] was used to model fry mortality during rearing as a function of water temperature. The following exponential relationship was fitted between observed *daily mortality* and observed water temperatures [32]:

$$\text{daily mortality} = 3.92 \bullet 10^{-12} e^{(0.349 \bullet \text{Temp})} \tag{8}$$

Each day, the mean proportional mortality of the rearing fish is predicted from the daily temperature using the above exponential relationship; the predicted mean mortality along with the confidence intervals of the predicted values are used to define a normal probability distribution, which is then randomly sampled to determine daily mortality. Temperature mortality is applied to rearing fry for 60 days that is the approximate time required for fry to transition into smolts [32] and enter the next stage.

River Migration In this model stage, survival of smolts from the spawning and rearing grounds to the Delta (City of Freeport on the Sacramento River) is a normally distributed random variable with a mean of 23.5% and a standard error of 1.7%. Mortality in this stage is applied only once and occurs on the same day that a cohort of smolts enters the model stage rather than being applied daily as in the *Early Development* stage because there was no data to support a relationship with flow or temperature. Smolts are delayed from entering the next model stage to account for travel time. Mean travel time (20 days) is used along with the standard error (3.6 days) to define a normal probability distribution, which is randomly sampled to determine the total travel time of migrating smolts. Survival and travel time means and standard deviations were acquired from an acoustic study of late-fall run Chinook smolt migration in the Sacramento River [18].

Delta Passage Smolt migration is evaluated based on four major functional relationships: (1) route selection by smolts at river junctions, that is a function of the proportion of flow entering each route; (2) reach specific and flow-survival relationships, where survival in two reaches is a function of flow and a normally distributed variable in all other reaches; (3) flow–migration speed, which is a function of reach specific flow; and (4) export mortality, which is caused by entrainment into State and Federal water pumping facilities. Daily cohorts of smolts enter the first reach of the Delta on a day of the year determined by timing in the previous model stages. In reaches with a flow–survival relationship, mean flow on the day smolts enter the reach is used to calculate a survival value and a migration speed for that reach. The survival value is applied once to all smolts that entered the reach on that date. Then, smolts are delayed from entering the next reach by a number of days determined by the calculated migration rate and the length of the reach. In reaches without a flow–survival relationship, survival values are drawn from a normal probability distribution and migration speed is calculated as a function of flow on the day of entry into the reach. When smolts reach a junction, a daily cohort will split according to the relationships described below, based on the flow on the day smolts reach the junction.

Fish route selection at junctions is based on acoustic tagging studies in the Delta by Perry et al. [23]. At the junction of the Sacramento River and Steamboat/Sutter Slough (Junction SS, Table 1), smolts consistently entered downstream reaches in proportion to the flow being diverted. For the Sacramento River–Geo/DCC junction (Junction Geo/DCC, Table 1), there was a linear, nonproportional relationship between flow and fish movement:

$$y = 0.22 + 0.47x \tag{9}$$

where, y is the proportion of fish diverted into Geo/DCC and x is the proportion of flow diverted into Geo/DCC.

Reach-specific survival and associated error estimates also were obtained from Delta acoustic tagging studies [23] where mean reach survival is used with reach-specific standard deviation to define a normal probability distribution sampled daily to determine the survival rate. There was a significant relationship between survival and flow for two Delta reaches (SS and Sac3; [23]) and we used a logit survival function to predict mean reach survival (S) from reach flow (*flow*):

$$S = \frac{e^{(\beta_0 + \beta_1 \text{flow})}}{1 + e^{(\beta_0 + \beta_1 \text{flow})}} \tag{10}$$

where, β_0 (SS=−0.175, Sac3=−0.121) is the reach coefficient and β_1 (0.52) is the flow coefficient. All the benefits of increased flow are accounted for the in relationships we have applied for reaches SS and Sac3.

Daily downstream smolt movement occurs as function of reach-specific length and migration speed as developed from acoustic tagging results. We used flow and migration speeds reported by Vogel [33] to create a best-fit logarithmic relationship:

$$y = 16.59\ln(x) - 76.79 \tag{11}$$

where, y is migration speed (kilometer per day[1]) and x is flow (cubic meter per second). Due to assumed strong tidal influences in reach Sac4, migration speed in this reach is independent of flow; set at 22.6 km·day^{-1}, the average speed of acoustic tagged smolts [33]. Migration speed variance from acoustic study data is used along with mean migration speed to define a normal probability distribution that is sampled from each day to determine the daily migration speed in each reach.

Fish that enter the DCC/Georgiana Slough junction enter the interior delta that is a complex network of tidal freshwater channels where smolts are exposed to natural mortality as well as entrainment in large water diversions. To apply water export-related effects, we used the export–mortality relationship described by Newman and Brandes [22]:

$$S = -0.000024 \bullet \text{exports} + 0.625 \tag{12}$$

where, S is mean survival and the slope (−0.000024) is from the relationship between survival and Delta exports in cubic meter per second. The intercept was adjusted from 0.58 to 0.625 so the regression line passes the point (184, 0.47), where 184 is the mean export level (cubic meter per second) and 0.47 is the mean survival rate observed during the acoustic studies we used to estimate survival in the Interior Delta. In effect, we used the slope of the relationship between survival and exports estimated by Newman and Brandes [22] as a scalar on the survival rates observed from acoustic tagging studies. Mean survival is then used along with the standard deviation to inform a normal probability distribution that is sampled from each day to determine Interior Delta survival.

As each cohort of smolts exits the final reaches of the Delta, they accumulate until all cohorts from that year have exited the Delta. After all smolts have arrived, they enter the *Ocean Survival* stage as a single cohort and the model begins applying mortality on an annual time step.

Ocean Survival This model stage utilizes equations for smolt-to-age-2 mortality, winter mortality, ocean harvest, and spawning returns to predict yearly survival and escapement numbers (i.e., individuals exiting the ocean to spawn). Ocean Survival model stage elements are listed in Table 2 and discussed below.

Relying on ocean harvest, mortality, and returning spawner data from Grover et al. [13], we applied a uniformly distributed random variable between 96% and 98% mortality for winter run from ocean entry to age 2 and we developed functional relationships to predict ocean survival and returning spawners for age 2 (8% return), age 3 (88% return), and age 4 (4% return), assuming that 100% of individuals which survive to age 4 return for spawning. Ocean survival to age 2 is given by:

$$A_2 = A_i(1 - M_2)(1 - M_w)(1 - H_2)(1 - S_{r2}) \bullet W \tag{13}$$

survival to age 3 is given by:

$$A_3 = A_2(1 - M_w)(1 - H_3)(1 - S_{r3}) \tag{14}$$

and survival to age 4 is given by:

$$A_4 = A_3(1 - M_w)(1 - H_4) \tag{15}$$

where, A_i is abundance at ocean entry (from the Delta Passage model stage), $A_{2,3,4}$ are abundances at ages 2–4, $H_{2,3,4}$ are harvest percentages at ages 3–4 represented by uniform distributions bounded by historical harvest levels, M_2 is smolt-to-age-2 mortality, M_w is winter mortality for ages 2–4, and $S_{r2,r3}$ are returning spawner percentages at ages 2 and 3. Age 2 survival is multiplied by a scalar W that corresponds to the value of Wells' Index of ocean productivity. This metric was shown to significantly influence growth and maturation of age 2 fish [34]. The value of Wells' Index is a normally distributed random variable that is resampled each year. In our analysis, we used the following values from Grover et al. [13]: H_2=0%, H_3=0–39%, H_4=0–74%, M_2=94–98%, M_w=20%, S_{r2}=8%, and S_{r3}=96%.

The number of adult fish in the ocean that will return to the spawning grounds is determined on day 334 of each year according to the percentages described above. Returning fish are assumed to be 65% female and are assigned a prespawn mortality of 5% to determine the final number of female returning spawners [30].

2.2 Environmental Input Data

Daily flows and temperatures experienced by salmon (Table 3) are determined by selection of a water year type in the Sacramento River as classified by the California Department of Water Resources (critical, dry, below normal, above normal, and wet). The probability of each type of water year being selected is represented by a discrete distribution based on the previous 100 years of data. With the exception of flow into the State Water Project (SWP) and Central Valley Project (CVP) pumping plants, flow is modeled using daily (tidally averaged) flow output from the hydrology module of the Delta Simulation Model II (DSM2-HYDRO; http://baydeltaoffice.water.ca.gov/modeling/deltamodeling/). Export flow into the CVP and SWP pumping plants is modeled using monthly flow output from the hydrologic simulation tool CALSIM II

Table 2 Functional relationships in the IOS model during each model stage and environmental variables associated with each relationship

Model Stage	Parameter	Environmental variable	Function
Spawning	Daily proportion of total spawners	None	Equation 1
Early development	Daily egg mortality	Temperature	Equation 7
	Egg-to-fry development time	Temperature	Equation 5
Fry rearing	Daily fry-to-smolt survival	Temperature	Equation 8
River migration	Downstream survival	None	Normally distributed random variable
Delta passage	Reach-Sac1 survival	None	Normally distributed random variable
	Reach-Sutter/Steamboat	Flow	Equation 10
	Reach-Sac2	None	Normally distributed random variable
	Reach-Sac3	Flow	Equation 10
	Reach-Sac4	None	Normally distributed random variable
	Reach-Geo-DCC	None	Normally distributed random variable
	Interior Delta	Water exports	Equation 12
	Junction-Sac2-Sutter/Steamboat	Flow	Proportional to flow in each reach
	Junction-Sac3-Delta Cross Channel	Flow	Equation 9
	Migration duration	Flow	Equation 11
	Migration duration (Sac4)	None	Constant
Ocean survival	Smolt-age 2 survival	None	Uniform random variable
	Age 2 ocean survival	Well's Index of ocean productivity	Equation 13
	Age 3 ocean survival	None	Equation 14
	Age 4 ocean survival	None	Equation 15
	Age 3 harvest	None	Uniform random variable
	Age 4 harvest	None	Uniform random variable

that are "disaggregated" into mean daily flows based on historical patterns. Mean flow and temperature was averaged each day over the entire period of record for each of the five water year types to create a single flow and temperature regime for each water year type. Daily temperature in the Sacramento River at Bend Bridge from 1989 to 2010 was obtained from the California Data Exchange Center (http://cdec.water.ca.gov/).

2.3 Sensitivity Analysis

Sobol' indices were used to evaluate the sensitivity of model output to input parameters. Sobol' indices are a variance-based global sensitivity method that produces main indices (effects independent of other input parameters) and total indices (effects accounting for first-order interactions with

Table 3 Environmental variables used to inform functional relationships in the IOS model

Location	Variable	Model stage	Source
Sacramento River at Bend Bridge	Temperature	Early Development	CDEC
Sacramento River at Hood	Flow	Delta migration	DSM2
Sutter-Steamboat Slough	Flow	Delta migration	DSM2
Delta Cross Channel	Flow	Delta migration	DSM2
Georgiana Slough	Flow	Delta migration	DSM2
Sacramento River at Rio Vista	Flow	Delta migration	DSM2
Interior Delta	Exports	Delta migration	CALSIM2
Ocean	Ocean productivity	Ocean survival	Wells et al. 2007

other input parameters). This method does not require a linear relationship between model output and input parameters and thus is superior to other global methods, such as multiple regression, when relationships are nonlinear or nonmonotonic [5, 8, 29].

For the sensitivity analysis, 1,000 bootstrap resamples were used to calculate 95% confidence intervals for Sobol' main and total effects. The number of female spawners returning (escapement) was used as the response variable and model inputs included as independent variables for each age class are listed in Table 4. Each group of returning spawners is composed of three age classes (age 2, 3, and 4) that experiences a different set of environmental conditions during their life. Thus, sensitivity analyses were conducted separately for each year class. Certain parameters were not included in all sensitivity analyses because they did not apply to all year classes. For example, age 2 fish are not exposed to harvest.

Latin Hypercube sampling was used to generate 1,000 Monte Carlo iterations of the IOS model for use in calculation of the Sobol' indices. For each iteration, the first 4 years of the model was seeded with 5,000 returning spawners and allowed to run for 5 years. The fifth year of output data was used for the sensitivity analysis because this is the first year that the number of returning spawners is a function of model parameters. Fish returning to the spawning grounds are mix of 2-, 3-, and 4-year-old fish that account for 8%, 88%, and 4% of the total, respectively. Input parameters were considered sensitive if their confidence interval did not include zero and were then ranked based on their absolute values. Sobol' indices were calculated using the package "sensitivity" within the R statistical program [25].

To explore how uncertainty in parameter estimates influenced model output, we conducted five additional sets of 1,000 Monte Carlo simulations where the variation around the mean of selected parameters was increased by 10%, 20%, 30%, 40%, and 50%. The parameters we chose to examine were those that could potentially be addressed by management actions including: egg mortality, fry-to-smolt survival, river migration survival, Delta survival, age 3 harvest, and age 4 harvest. Coefficients of variation were calculated for each set of simulations to examine how the sensitivity of model output changed with increased uncertainty in input parameters estimates.

2.4 Influence of Environmental Parameters

To understand the influence of environmental parameters on model output, we examined the response of escapement to variation in the four environmental parameters: flow, exports, temperature, and ocean productivity. For each parameter, we performed three sets of 100 Monte Carlo simulations. All simulations ran for four winter-run generations (16 years) and included a baseline condition, a 10% increase in the parameter and a 10% decrease in the parameter. A one-way analysis of variance and a Tukey's multiple comparisons test was then used to determine which treatments resulted in escapement estimates that were significantly different from baseline conditions. All statistical tests were performed with the R statistical program [25].

3 Results and Discussion

3.1 Sensitivity Analysis

Sobol' sensitivity indices suggested that escapement was sensitive to different input parameters depending on the age class examined (Table 4). For age 2 fish, main indices indicated

Table 4 Sobol' sensitivity indices (standard deviation in parentheses) for each age class of returning spawners based on 1,000 Monte Carlo iterations

Input parameter	Age 2		Age 3		Age 4	
	Main	Total	Main	Total	Main	Total
Water year	0.300[a] (0.083)	0.306[a] (0.079)	0.181[a] (0.091)	0.150 (0.091)	0.073 (0.067)	0.012 (0.065)
Egg mortality	0.030 (0.016)	−0.006 (0.016)	0.222[a] (0.081)	−0.021 (0.081)	0.102[a] (0.044)	−0.072 (0.044)
Fry-to-smolt survival	0.039 (0.020)	−0.009 (0.020)	0.166 (0.090)	0.091 (0.092)	0.079[a] (0.017)	−0.071 (0.017)
River migration survival	0.007 (0.034)	0.135[a] (0.034)	0.164 (0.084)	0.062 (0.085)	0.079 (0.018)	−0.07 (0.018)
Delta survival	0.010[a] (0.002)	−0.009 (0.002)	0.404[a] (0.180)	0.643[a] (0.177)	0.313[a] (0.134)	−0.009 (0.132)
Smolt to age 2 survival	0.734[a] (0.118)	0.454[a] (0.113)	0.015 (0.016)	−0.006 (0.016)	0.057[a] (0.017)	−0.052 (0.017)
Ocean productivity	0.003 (0.009)	0.009 (0.009)	0.034[a] (0.015)	−0.034 (0.015)	0.061[a] (0.030)	−0.048 (0.029)
Age 3 harvest	N/A	N/A	0.029[a] (0.001)	−0.028 (0.001)	1.48[a] (0.306)	0.188 (0.293)
Age 4 harvest	N/A	N/A	N/A	N/A	0.055[a] (0.003)	−0.054 (0.003)

[a] Index value was statistically significant at α=0.05

escapement was sensitive to smolt-to-age-2 survival, water year type, and Delta survival (Table 4). Main and total indices were similar for water year whereas the main index value for smolt-to-age-2 survival was considerably larger than the total value (Table 4). Additionally, age 2 escapement was sensitive to river migration survival when interactions were accounted for in the total index. This suggests that there were strong interactions between certain input parameters for fish returning to the spawning grounds at age 2 and confirmed that Sobol' sensitivity measures were the best choice for this sensitivity analysis, as interactions are difficult to deal with using other global analysis techniques [5]. The main index for Delta survival was significant yet the total index value was negative. Negative numbers are possible for Sobol' indices [2] and we considered negative values to indicate zero sensitivity [8]. Main indices for age 3 escapement suggested that model output for this age class was sensitive to many of the input parameters examined (Table 4). However, total index values indicated there were strong interactions between inputs, and age 3 escapement was only sensitive to Delta survival after accounting for these interactions. Similarly, main indices for age 4 escapement indicated that output was sensitive to many parameters (Table 4) whereas after accounting for interactions in the total index, none of the input parameters significantly influenced model output.

Although there were differences among age classes in the sensitivity of input parameters, each age is not represented equally among returning spawners. Thus, sensitivity should be viewed in terms of the contribution of each age class and the relationship among age classes. Age 3 fish comprised the largest proportion of returning spawners (88%) thus, inputs driving variability in this age class should have the largest effect on total escapement. Delta survival, water year, and egg mortality were significant drivers of variability in age 3 escapement, however, water year and egg mortality were not significant after accounting for interactions. The Delta passage portion of the model has flow–survival relationships in two reaches, thus, it is not surprising that there are interactions between water year type and Delta survival. Similarly, temperatures were higher in critical and dry water years and there was an exponential relationship between temperature and egg mortality.

Age 2 and age 4 fish accounted for 8% and 4% of total escapement, respectively. Age 4 escapement was most sensitive to harvest of age 3 fish. This is an intuitive result as harvest at age 3 has a direct influence on the number of fish that survive to age 4. Age 2 escapement was most sensitive to smolt-to-age-2 mortality and this relationship remained strong after accounting for interactions with other inputs (Table 4). This is a critical period of the salmon life cycle when fish are transitioning from freshwater to saltwater habitats and a large portion of total mortality occurs during this time [16]. Water year also was an important driver of variability in age 2 escapement with significant main and total effects where as Delta survival was not significant when interactions were accounted for. This is likely a result of interactions with water year as discussed above for age 3 fish.

As variability in input parameters was increased, escapement ranged from 2,806±984 fish (mean and standard deviation) in the baseline treatment to 2,337±904 fish in the 50% treatment suggesting that model output was robust to parameter uncertainty (Fig. 3). Coefficients of variation differed among input variables yet, CVs for individual input parameters did not vary much among treatments (Fig. 3). Ages 3 and 4 harvest had the greatest CVs of any variable (0.55–0.60) and both of these parameters were represented by a uniform distribution due to limitations in the data available to inform the relationship. The use of uniform distributions to represent parameter uncertainty has been identified as a limitation in other sensitivity analyses [11]. Harvest may have a profound effect on salmon population dynamics [17, 28] and the IOS model could be improved by further research on harvest of winter run that would reduce uncertainty in the true levels of harvest. All other input parameters were represented by normal distributions and CVs were less than 0.30 (Fig. 3).

There is a tendency to identify sensitive parameters as most important to model output. However, Fullerton et al.

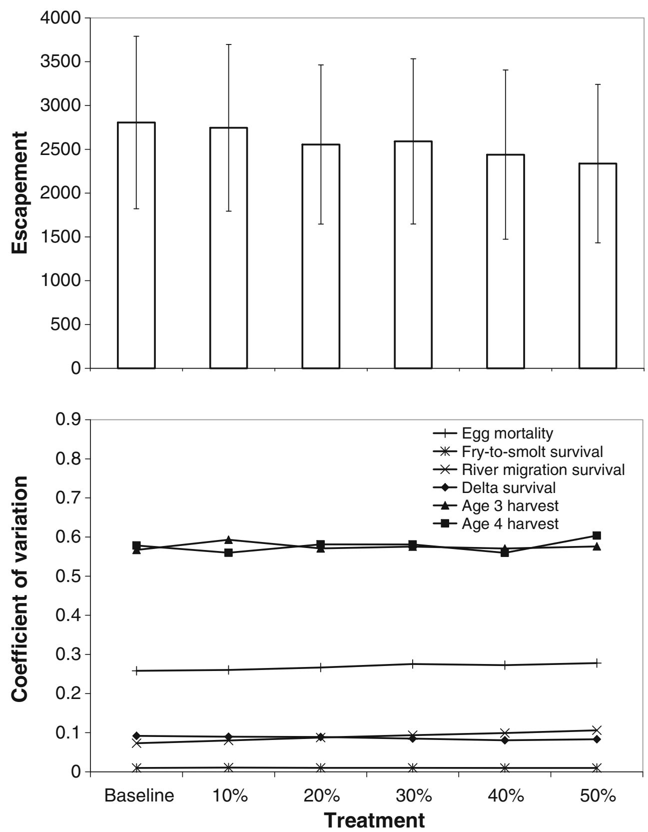

Fig. 3 Mean salmon escapement values (*top panel*) and coefficients of variation for input parameters (*bottom*) when variability of each input was increased by 10%, 20%, 30%, 40%, and 50%. All calculations are based on 1,000 Monte Carlo iterations

[11] recognized the importance of distinguishing between sensitivity and ecological relevance. For example, several of the relationships in the IOS model are based on limited data that influence the estimate of input parameters and the form of uncertainty distributions associated with those estimates. For example, river migration survival has been hypothesized to be influenced by flow [21], yet survival during the *river migration* stage is not influenced by flow in our model because the values we used to inform the relationship were taken from a field study conducted over three low-flow years [18]. Thus, the data available do not cover the range of potential conditions that may be experienced by out migrating salmon. A similar situation exists for other relationships such as smolt-to-age-2 mortality that is hypothesized to be an important determinant of year class strength but is difficult to estimate in the field and is thus represented by a uniform distribution. This is in contrast to laboratory studies of temperature–mortality relationships applied in the *early development* and *fry rearing* model stages where one of the goals was to examine biological responses over a range of environmental conditions. One of the strengths of the IOS model is that it can be used to identify where knowledge gaps exist and the model is flexible enough to allow the integration of new data and functional relationships as they become available.

3.2 Influence of Environmental Variables

Escapement was significantly affected by both the 10% increase and 10% decrease in temperature ($F_{2,297}$=346, p< 0.001). However, the increase in temperature had a much greater effect producing a 95.7% reduction in escapement whereas the decrease in temperature yielded a 11% increase in escapement (Fig. 4). Varying flow produced a 6.2% increase and 4.7% decrease in escapement yet these differences were not statistically significant ($F_{2,297}$=2.19, p= 0.113). Similarly, variation in exports and ocean conditions did not yield statistically significant differences in escapement with p values of 0.656 and 0.114, respectively (Fig. 4).

The lack of significant changes in escapement with a 10% change in flow, exports and ocean conditions may reflect the type of data used to parameterize these relationships. The functions utilizing these inputs were constructed from data obtained from observational studies that had large error estimates associated with responses. Thus, large changes in these variables are required to produce a significant response in escapement. Temperature functions were parameterized with data from controlled experiments that produced small error estimates. Additionally, temperatures in the spawning and rearing area are close to the upper tolerance limit of Chinook salmon and even small changes have the potential to significantly affect the population.

Management of temperatures in the Sacramento River is a priority for stabilizing or increasing Chinook salmon populations. The Sacramento–San Joaquin Rivers represent the southern limit of Chinook spawning and stream temperatures can often approach the thermal tolerances for certain life stages [20]. Historically, Chinook salmon could avoid sub-optimal temperatures by utilizing higher elevation habitats [36]. However, these areas have been eliminated by the

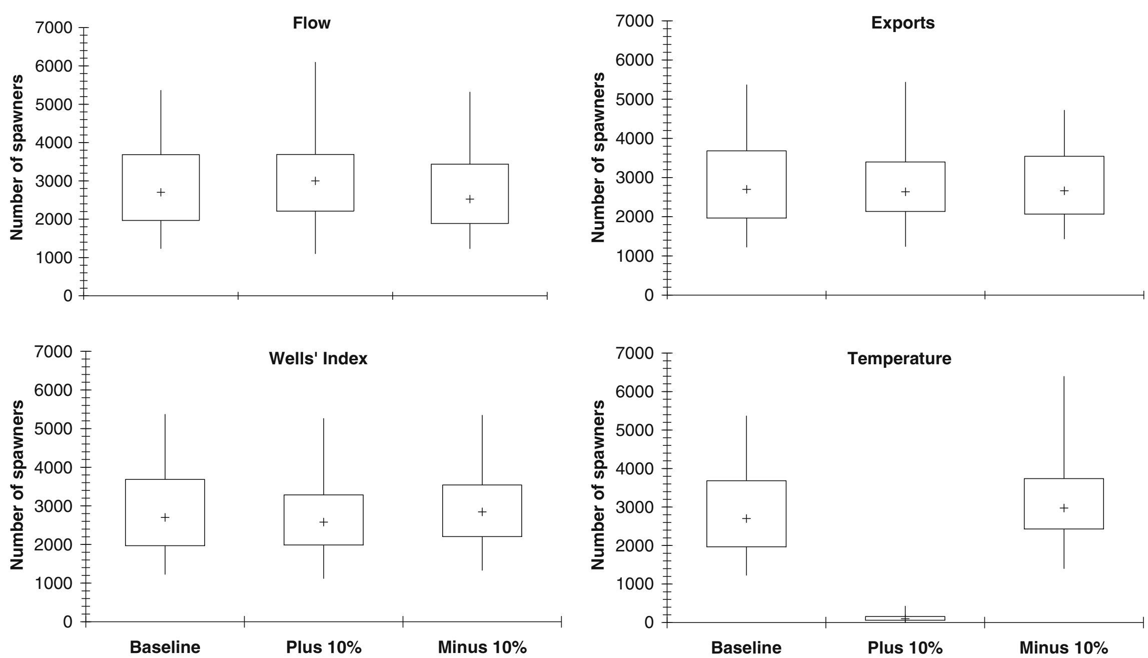

Fig. 4 Box and whisker plots of winter run escapement under baseline conditions, a 10% increase, and a 10% decrease in the four environmental inputs used in the IOS model

construction of impassable dams in the foothills of the Cascade and Sierra Nevada mountains [35]. Thus, understanding how population dynamics of Chinook are influenced by temperature-related mortality is essential for understanding how populations may be impacted by management actions or natural climate variations that may result in higher stream temperatures. The simulations conducted here do not represent any potential management or climate scenario, but instead demonstrate the utility of the IOS model for understanding this important driver of Chinook salmon population dynamics.

4 Summary and Conclusions

Our study developed and used a stochastic life cycle simulation model of winter-run Chinook salmon. The model brought together field monitoring data and laboratory studies to create six model stages that represent distinct salmon habitats and life stages. The model was created using GoldSim software and a free player version is available that will allow anyone to easily run and explore the IOS model. The model can be used to simulate population dynamics and mortality at each life stage for a period of years specified by the user. Our emphasis in developing this model was to allow managers a means to test and compare among alternative water management or restoration scenarios. A persistent problem in the management of anadromous salmonids has been the use of professional opinion in place of quantitative data to identify the life stages and/or habitats that will be affected by management actions [28]. The development of the IOS model provides a significant step such as recommended by Good et al. [12] to provide managers with the tools necessary for managers to make decisions based on the best quantitative data available. This was demonstrated by our simulation of variation in environmental parameters that revealed significant differences in escapement in response to higher and lower temperatures.

Sensitivity analysis revealed that uncertainty could be reduced by improving estimation of the mean values and uncertainty distributions of certain inputs and functional relationships between environmental variables and biological processes. This was particularly apparent for smolt-to-age-2 survival and ocean harvest that were uniform random variables. These variables had greater CVs than any other input and Sobol' indices indicated they could significantly influence model output. Additionally, river migration survival was not related to any environmental variables despite hypothesized relationships with flow because the data used was collected under a narrow range of conditions. Greater certainty in these relationships would improve model performance and reduce uncertainty in management and recovery actions based on IOS simulations. Although this model was specifically developed for winter run, the IOS model structure could easily be adapted for other salmon populations in the Sacramento-San Joaquin River system and serve as an example of how life cycle models can improve management of anadromous salmonids throughout their range. The IOS model will provide a much needed tool for resource managers and will continue to improve as more quantitative data becomes available.

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