FUNCTIONAL COMPARISON BETWEEN PREDICTIONS OF A CHINOOK SALMON MODEL AND MONITORING DATA IN THE TUOLUMNE RIVER, CALIFORNIA

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Functional Comparison between Predictions of a Chinook Salmon Model and Monitoring Data in the Tuolumne River, California

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Table of Contents

List of Figures

List of Tables

iv

Preface

The Public Interest Energy Research (PIER) Program supports public interest energy research and development that will help improve the quality of life in California by bringing environmentally safe, affordable, and reliable energy services and products to the marketplace.

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Functional Comparison between Predictions of a Chinook Salmon Model and Monitoring Data in the Tuolumne River, California is the final report for the Testing and Improvement of the ORCM Chinook Salmon Model project (contract number 500-02-004 MR035) conducted by Oak Ridge National Laboratory. The information from this project contributes to PIER's Energy-Related Environmental Research program.
For more information on the PIER Program, please visit the Energy Commission's Web site at www.energy.ca.gov/pier or contact the Energy Commission at (916) 654-5164.

1.0   Abstract

This study sought to reduce uncertainty in estimates of Chinook salmon outmigration in the Tuolumne River, California by 1) improving estimation of rotary screw trap (RST) estimates and 2) improving predictions of a particular salmon recruitment model, the Oak Ridge Chinook Model (ORCM). We developed two methods for improving estimates of outmigrants based on RST monitoring data. First, RST estimates were improved by avoiding extrapolation beyond the maximum flow that occurred during efficiency tests. Second, using empirical, Ricker models, we imputed rotary screw trap estimates for missing days.

We sought to improve ORCM predictions by comparing relationships between model predictions and environmental covariates (referred to here as "functional relationships") with relationships between RST monitoring data and environmental covariates. Although we were not able to improve model predictions significantly during this project, we made considerable progress both in developing the methods needed and in identifying processes where discrepancies are likely. The methods presented here for comparing model predictions with field monitoring-based estimates that can be used with missing data and data that are strongly autocorrelated. Our model-data comparison suggested two hypotheses about observed model-data discrepancies. The first hypothesis is that the density dependent mortality is weaker in the model than in the field. Examination of seining estimates of fry abundance is needed to determine whether this mortality occurs in the egg-alevin stage (i.e., redd superimposition) or the fry stage (i.e., predation). The second hypothesis is that fish kills associated with extreme events resulted in lower-than-predicted juvenile survival in years 2000-2004. This hypothesis could be partially addressed by examining extreme river conditions more closely.

Finally, we added the capability to simulate energy generation to the ORCM to permit simultaneous evaluation of the effects of flow regime on both salmon and energy. This capability will be important in order to quantify the flow-related trade-offs using the model.

2.0   Executive Summary

Introduction
Water agencies that generate hydropower and resource agencies in California are interested in better understanding how their decisions about seasonal and annual patterns in river flow will influence salmon production. The financial problems and energy deficits experienced by California during the late 1990's highlight the importance of understanding the loss of energy capacity associated with legal restrictions on flows. Better tools are needed to quantify the costs and benefits associated with hydropower production in California.

Purpose
Several models have been developed to predict the effects of hydropower operations on Chinook salmon production in California rivers, but have not had the opportunity to undergo a rigorous, iterative process of comparing predictions against field data, followed by model refinement and also improved collection and/or interpretation of field estimates. For example, when the Oak Ridge Chinook Model (ORCM) was developed in the mid-1990's, there was no program to monitor outmigrating Chinook salmon in the Tuolumne River. Since then, rotary screw trap (RST) data have been collected in this river and used to estimate salmon production. However, the true numbers of outmigrants are uncertain due to the low sampling efficiencies of RST data. The purpose of this project is to develop and apply methods to compare predictions of an existing model with new field data, with the goal of reducing uncertainty in both model predictions and field-based estimates. Our primary tool is a constructive "validation" that seeks to explain model-data discrepancies via empirical models involving environmental covariates.

Project Objectives
The three goals of this project were to: (1) improve methods for estimating numbers of outmigrating juveniles from RST data, (2) reduce uncertainty in ORCM predictions, and (3) add the capability to estimate hydropower generation in ORCM that will allow prediction of trade-offs between energy and salmon.

Project Outcomes
We highlight the following five project outcomes:
1) Two methods for improving estimated production based on RST data are presented.
2) Methods and tools for functional comparison between model predictions and field monitoring-based estimates are presented. These robust methods work for missing data and time series data that are autocorrelated.
3) Future directions for improving ORCM predictions during some years are recommended based on functional model-data comparisons. Results suggest differences may be due to higher density dependent mortality than simulated or to episodes of poor water quality with effects not represented adequately in the model.

4) ORCM now has the added capability to simulate energy generation, which will permit the simultaneous evaluation of the effects of flow regimes on production of salmon and energy.

5) The analyses presented illustrate the value of continued feedback between environmental monitoring design and predictive model development. Such an iterative process is an essential part of effective adaptive management.

Conclusions

Empirical modeling proved useful as a tool for imputing missing field measurements and functional validation of a Chinook salmon model, ORCM. The timing of smolt outmigration was similar between model and data. However, ORCM predictions of smolts per spawner were much higher than RST-based estimates for some years. Our analysis suggested two hypotheses to explain the differences in juvenile survival. Thus, a longer process of monitoring, comparison, and refinement is needed to improve our understanding of salmon smolt production in this river and to reap the benefits of the ORCM model as a predictive tool.

Benefits to California

Providing environmentally sound energy and reliable energy are two goals furthered by this research. This project started the process of testing and improving a model for quantifying the change in Chinook salmon production and the change in hydropower generation associated with regulated flow regimes, which could be used in future to consider maximizing both salmon and energy production as objectives. The improved methods presented here should also reduce uncertainty in estimates of Chinook production based on RST monitoring data.

3.0 Introduction

With its dry climate, California rivers serve many important functions and there is not always enough water available for all. This study focuses on two important functions: reproductive habitat for salmon and hydropower generation. The San Joaquin Basin in the Central Valley represents a southern extreme of the distribution for fall-run Chinook salmon. Although fall Chinook salmon are not currently listed as threatened or endangered by the federal government, this species has been declining for many years in the San Joaquin Basin (Yoshiyama 2000). Wetter years are considered good for California's salmon because, among other things, higher flows in fall and spring lower water temperatures. One strategy that salmon biologists claim will help to recover Chinook salmon is to allocate higher flows during times of year when they are needed to ensure successful reproduction.

On the other side of this picture, we see that the state of California has a significant need for hydropower. During the late 1990's, California experienced a sharp increase in energy prices and periodic rolling blackouts when the supply of energy failed to meet the state's demand. One of the causes of this crisis was drought conditions; others were regulatory. The energy deficits experienced by California highlight the importance of understanding

whether or not legal restrictions on regulated flows to benefit salmon would result in a significant loss of energy capacity for the state.

As part of a hydropower license for the New Don Pedro project, a 10-y study was instituted in the Tuolumne River to learn more about the influence of spring flows on Chinook production. Monitoring of outmigrating Chinook salmon was started around 1995, as a means of determining whether goals of increasing salmon production were being met. Rotary screw traps (RST) are were the primary monitoring devices used during the 10-year study. However, the traps do not operate every day and daily totals must account for flow-related changes in capture efficiency. Therefore, one goal of this study is to improve field estimates of Chinook salmon outmigration using statistical methods to impute estimates for missing days and to better account for flow effects on efficiency.

One promising way to quantify alternative strategies for allocating water is to use a model that can predict the effect of flow regimes on both salmon and hydropower. Several models, including the Oak Ridge Chinook Model (ORCM), have been developed to predict the effects of hydropower operations on salmon recruitment. Such models can help decision makers to understand how decisions about seasonal and annual patterns in river flow will influence salmon production (Jager and Rose 2003). However, none of these models also predicts the effects of flow regulation on hydropower generation. A second goal of this project is to test and improve a quantitative tool for those making decisions about California's water, aquatic resources, and energy.

3.1. Fall Chinook salmon in the Tuolumne River

Fall Chinook salmon spend their adult lives in the ocean. At some point between age 2 and 5, adults migrate into rivers during the fall to spawn. Each female digs a redd in the gravel river bottom. During courtship, she releases her eggs into her redd. She buries the eggs after they are fertilized by one or more males. Eggs incubate through the winter, hatch as alevins (non-feeding larvae) into inter-gravel spaces, and emerge from redds as fry (pre-smolt juveniles) in the spring. Fall Chinook salmon fry feed on invertebrates along river margins for the first month or two, and gradually move downstream. Fry may exit tributaries in winter or spring to rear in the lower main stem and estuaries prior to becoming smolts. During smoltification, juveniles become tolerant to saltwater and migrate to the ocean. This study focuses on the Tuolumne River, a tributary of the San Joaquin River (Figure 1). The LaGrange Dam, at 83.7 km above the confluence, blocks upstream migration of adult salmon returning to spawn. Flows are regulated by the much larger New Don Pedro Dam just upstream.
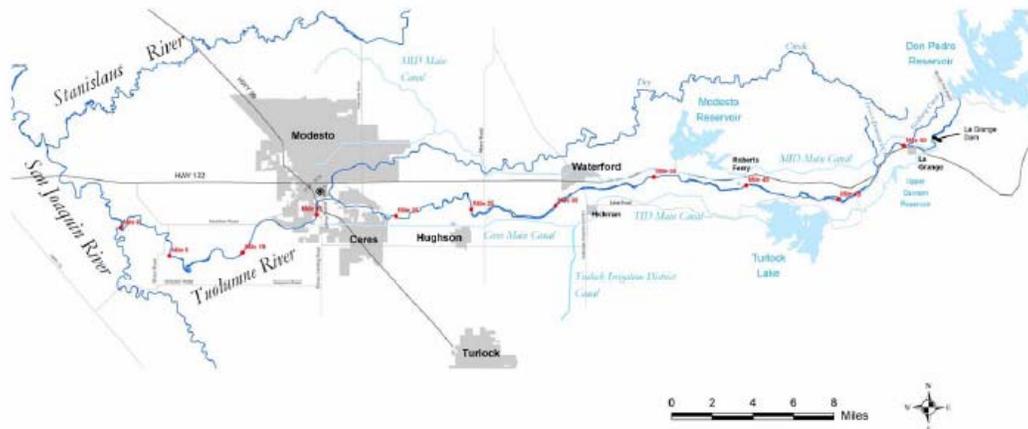
Figure 1. Map of the Tuolumne River (Source: TID/MID 2005).

3.2. Functional validation

The predictive value of ecological models increases greatly when modeling is coordinated with long-term field studies. This is especially true when the field studies focus on measuring variables used by the model as input, or those that it predicts. An iterative process of confronting models with data leads to reduced uncertainty in model predictions (Hilborn and Mangel 1997).

The most common approach to model validation is to compare model predictions with field observations and to test goodness of fit between them at different times or places (e.g., Smith and Rose (1995)). One problem with using formal statistical tests to compare models and data is that a model with highly uncertain predictions can never be rejected. Another is that such tests rarely suggest directions for future improvement in either the data or model. Thus, Jager et al. (2000) suggested that statistical testing is a non-constructive approach to model-data comparison.

Functional comparison, to see whether model and data follow similar relationships with environmental variables, is more constructive because it reveals processes that are poorly represented in the model (or measured in the field) and it suggests areas of improvement in modeling or measurement. For example, we used this approach to compare model predictions and field estimates of net primary productivity at the national (US) scale, which suggested that one of the models was exaggerating the response of net primary productivity to precipitation (Jager et al. 2000).

In this paper, we compare model predictions of Chinook salmon recruitment with those estimated from rotary screw trap (RST) data in a California river. We initially focus on two functional patterns that have already been described for juvenile Tuolumne River Chinook

salmon: relationships with flow and density. TID/MID (2005) concluded that the timing of downstream movements by fry, but not smolts, relate to flow. Earlier juveniles, called "fry," have not begun the transformation to tolerate saltwater, after which they are referred to as "smolts." Most juveniles captured in a low-flow year (2002) were captured after March, whereas most juveniles captured in higher flow years (1998 to 2001) were captured earlier, in February and March. TID/MID (2005) also reported a power relationship between fry density and spawner density the previous fall.

3.3.   History of the Oak Ridge Chinook Model

ORCM uses an individual-based modeling approach to predict the influence of seasonal flow releases on fall and late-fall Chinook salmon recruitment in the Tuolumne River, California (Appendix). Originally conceived as a tool for comparing alternative flow regimes proposed by stakeholders in the operation of New Don Pedro Dam (Jager et al. 1997), ORCM has been used to examine optimal patterns in seasonal flows from the perspective of Chinook salmon (Jager and Rose 2003). Both efforts yielded insights about the relationships between flow, temperature, and successful reproduction of the two salmon runs. Validation of some model predictions was possible; specifically growth patterns were compared against seining data. Growth predictions compared well with those observed in the field (Jager et al. 1997). Sensitivity analysis was used to identify critical variables for each of several model predictions (Jager et al. 1997). At that time, the primary response predicted by the model (the number of juvenile smolts outmigrating from the tributary) had not been measured in the field and, thus, could not be compared with model predictions. Since the initial model was developed, new monitoring data has become available.

In 1995, a settlement agreement was signed that modified the hydropower license for New Don Pedro Dam on the lower Tuolumne River. An adaptive monitoring program was implemented in 1996 that included monitoring of outmigrants for the period 1997-2004. Here, these data are used to compare functional responses to environmental variables with those followed by predictions of the ORCM.

4.0   Methods

Two goals of this project were: (1) to compare field and model results to reduce uncertainty in ORCM predictions, and improve RST estimates; and (2) to permit energy-salmon trade-offs to be quantified by adding the capability to estimate hydropower generation in ORCM.

Below, we first describe processing of field data and methods for ORCM model predictions. Next, we describe methods for comparing the magnitude and timing of smolt outmigration predicted by the ORCM model and estimated from RST data. This is followed by a description of methods to compare functional relationships between outmigrant counts and environmental variables. Finally, we describe methods for simulating hydropower generation.

4.1.   Field Data

A research program monitors the production of fall Chinook smolts from the Tuolumne River (see TID/MID 2005). This program includes monitoring of outmigrating juveniles using rotary screw traps (Figure 2), which were installed in the Lower Tuolumne River by the California Department of Fish and Game (CDFG) in 1995 (TID/MID 2005). Two 8-foot diameter rotary-screw traps were operated in the lower Tuolumne River at the Grayson (RM 5)/Shiloh Bridge (RM 3.5) locations to monitor the number, size, timing and rate of fry and/or juvenile Chinook salmon emigrating from the Tuolumne River (TID/MID 2005). The sampling gear is stationary in the river current and operates in the upper part of the water column (TID/MID 2005). Each trap has an eight foot diameter and capture any fish that swim downstream into the mouth of the trap. These traps operate on a subset of days, with a focus on what is believed to be the peak period of fall Chinook salmon outmigration in April and May. The number of juveniles captured is recorded for each time and date of operation, and the length is measured for a subset of individuals. Although measurements began in 1995, the first two years data were too sparse to include. Only one trap was used in 1998.

Figure 2. Grayson rotary screw trap installed on the Lower Tuolumne River to sample outmigrating Chinook salmon

Only a fraction of salmon juveniles that are moving downstream are captured in the traps. To estimate the trap's capture efficiency, a known number of hatchery juveniles are released during field trials on dates with different flows. Trap efficiency is the ratio of the number captured to the number released. This ratio has been found to decrease with river flow. In addition, an adjustment is made for the proportion of the day when the trap is operated.

In summary, two adjustments are made to the data to obtain daily RST estimates. First, the number counted during a given day is divided by the proportion of the day sampled to get a daily total, N_d. Second, N_d is divided by trap efficiency, E_t, which depends on flow, Q_t in cfs (Equation (1)).

$$E_t = a - b \, ln(Q_t)$$ (1)

Parameters a = 0.1464 and b = 0.0164 were fitted to data collected during field trials to assess trap efficiency (TID/MID 2005). The CDFG provided us with a spreadsheet, which calculated RST estimates for each day from flow.

Uncertainties associated with the RST estimates are high because the trap efficiencies in the Tuolumne River are low. A minimum efficiency of 10% is sometimes cited as a lower limit for reliability. In the Tuolumne River, efficiencies are below this, even at moderate flows.

In the comparisons reported here, we improved estimation of efficiency at high flows, incorporated juveniles with imputed lengths, and separated RST juveniles smaller than and greater than 70 mm. Each of these improvements is described below.

We accounted for the fact that the model predicts fry and smolts, where simulated juveniles become smolts when they reach 70 mm and have grown over a certain number of degree days (sum of degrees C). However, days with the highest counts included many juveniles that lacked length data. Because we now required length information, we imputed lengths for juveniles lacking length measurements by determining the length frequency distribution for each day from measured individuals and applying these to the unmeasured counts to assign fractions of unmeasured juveniles to each length class.

One problem with the linear model in Equation (1) is that it can produce very small, and even negative, estimates of trap efficiency when flows are higher than those used to estimate the parameters. Very small efficiencies, when used in the denominator, produce very high RST estimates. In the first comparison, efficiencies at flows high enough to produce negative efficiencies were set to one, which likely underestimated counts on these dates. In the second round, we set efficiency estimates smaller than the minimum efficiency observed during the trial, which occurred at a flow of 6,400 cfs (181 cms), to the observed minimum, E_{min} = 0.0027. An alternative solution would be to fit a logistic model rather than a linear one.

4.2. Model Predictions

The ORCM (Jager et al. 1997, see Appendix) is a spatially explicit and individual-based model of fall chinook salmon recruitment in a river below a dam. The model links a spatially explicit representation of river habitat with a biotic model of chinook salmon reproduction, development, growth, and mortality. The river habitat changes seasonally and includes important spatial gradients (e.g., temperature, predator densities) between upstream spawning areas and lower reaches inhabited by juvenile salmon during outmigration. The biotic component uses a daily timestep to simulate coexisting life stages, as individuals grow, develop from one life stage to the next, move, and die. The ORCM simulates the river phase of chinook salmon ecology, beginning with adults entering the river to spawn. For each redd, we simulate the daily development and mortality of egg and alevin lifestages. After emerging from redds, the daily development, growth, mortality, and downstream movement of individual juveniles (fry and smolts) is simulated, culminating in the migration of smolts from the river (i.e., recruitment).

The biotic events leading from upmigration of spawners to the outmigration of recruits are simulated in a spatially explicit river habitat represented by a series of adjacent 1.6-km segments differing in the proportion of riffle and pool habitat, temperature, and flow (at confluences with tributaries or diversions). Simulated average daily water temperature in each river segment is determined by allowing water released by the dam (about 12°C year-round; FERC 1996) to equilibrate to the air temperature as the water travels downstream. The simulated river temperature of each segment depends on daily air temperature, dam release temperature, and flow rate, which controls the rate of travel downstream. Daily flow in each segment is generated as part of the optimization procedure and used to drive the ORCM.

We began by improving the simulation of downstream variation in water temperature in the Tuolumne River using available data. The ORCM model requires daily average flow and temperature data (water and air), and predicted downstream water temperatures daily. We obtained temperature and flow data for a variety of locations in the Lower Tuolumne, using USGS daily data when and where available, but supplemented with averages calculated from hourly temperature data and recent data obtained from the California Data Exchange Center (see http://cdec.water.ca.gov/), which is maintained by the Department of Water Resources. We obtained recent, but incomplete, temperature data at a larger number of sites on the river. These data were used to calibrate a simpler model for spatial variation in temperature. We compared the fit of a variety of linear and non-linear regression models used to predict longitudinal temperatures (°C) at all downstream locations (T_x) from release temperature at LaGrange Dam (T_r), air temperature (T_a), distance downstream in km (x), and release flow in m³s⁻¹ (Q). Equation (2) fit the best and replaced the original equation in ORCM.

$$T_x = b_0 + T_r + b_1(T_{air} - T_r)\left(1 - e^{-b_2 x Q^{b_3}}\right)$$

(2)

Ideally, model validation is an iterative process in which feedback from comparison with field data leads to improvements in the calibration or structure of a model. Here, we completed two rounds of model-data comparison and iterated the process of making model predictions and comparing them to data. Our first objective is to adjust the average number of outmigrants predicted by ORCM to match field estimates. We started by using the same parameter values used in previous simulations (see Appendix). We determined that ORCM outmigrant numbers tended to be higher, and next, tried to determine during what lifestage survival was higher in the model than in the field. ORCM predictions of egg-to-fry survival in Round I were higher (average = 0.57; range: 0.21 to 0.79) than field estimates of survival to emergence and an empirical model based on gravel permeability, which varied from 0.34 to 0.51 (TID/MID 2000). Although other parameters influence egg-to-fry survival, we have no reason to modify mechanistic factors, and therefore focused on baseline egg mortality as the parameter to calibrate. For Round II, we increased baseline egg mortality, *eggm* = 0.012, to match the observed mortality. We also observed that juvenile survival was higher. Juvenile survival in the model is influenced by predation, temperature, and premature emigration. We are confident in our simulation of temperature-related mortality, and to a lesser extent in estimates of premature migration, but less so in predation rates. In addition, changes in the river have altered the density of warmwater predators (bass) and spatial overlap between predators and Chinook salmon juveniles (TID/MID 2005). We therefore increased the probability of capture for predators, *pcap* = 0.001 from 0.0001 using the simplified predation model (see Appendix). The equations in which these parameters are used are given in the Appendix. In the second round, we also modified ORCM to reading in the proportion of female spawners in each year rather than using the same sex ratio for all years. By doing this, we hoped to refine the predicted timing of outmigration.

4.3. Comparison of Outmigration Magnitude and Timing

We graphed the number of outmigrants on each day between the beginning of March and early June. Different graphs are presented for each year and for each of the two rounds. All sizes of juveniles, both fry and smolts, are included in these graphs.

4.4. Functional Comparison

Differences between the relationships observed in field data and model-predictions can provide guidance in further improving processes in the ORCM model. This approach was successfully used to evaluate three regional models for net primary productivity (Jager et al. 2000), and discovered that one model was over-responding to precipitation. Here, we developed empirical relationships to describe the daily number of outmigrating smolts for both the RST data and the ORCM predictions. We contrasted the coefficients of relationships between smolt numbers and key predictors, including degree-days, escapement (i.e., number of spawners counted the previous fall), and flows.

We fitted daily smolt numbers as a function of predictors that changed within and among years for the seven years between 1997 and 2004. The R software was used for statistical analyses reported here (http://www.r-project.org/). We fitted one set of models to all the data, keeping zero smolt counts (days when the traps were operating but caught no

salmon), and another set of models to the subset of days with non-zero smolt counts. We added the analysis with only non-zero counts, in part, to help satisfy distributional assumptions. Interpretation of these models is also slightly different: the set of models fitted to days with non-zero smolt counts predicts abundance, given that migration is occurring.

The annual production of saltwater-tolerant smolts that leave the river to migrate seaward depends on the number of spawners or "escapes", *Esc*, the previous fall. We expect more smolts to be produced when there are more spawners to product them up to a point. Beyond a certain number of spawners, "density dependent" factors cause the number of offspring that survive to migrate downstream as smolts to reach a limit or even to decrease. Examples of density-dependent mortality exist at all stages. Beginning with reproduction, adults may interfere with one another during spawning. Adults that arrive on the spawning grounds later might dig their nests (redds) for their eggs right on top of those of previous spawners, which causes mortality of the earlier eggs. This is called "superimposition" of redds. After hatching, larvae (called "alevins") reside in the interstices of the gravel riverbed. High alevin densities can reduce water quality by depleting dissolved oxygen and high levels of ammonia (waste products). After emerging from the gravels, juveniles (both fry and smolts), are exposed to predation. At high densities, smaller, later-emerging fry have trouble competing for feeding territories. Consequently, more fry remain small and vulnerable to predation when densities are high[1]. The Ricker function (below) is one function that is typically used to represent this dependence on spawner density. The equation below shows a general or extended form that includes other, potentially time-varying, environmental predictors, in linear function, $f_t(.)$, for calculating daily smolt outmigrants, $Y_{i,t}$ for each year i and day t.

$$Y_{i,t} = Esc_i \cdot e^{b_0 + b_1 Esc_i + f_t(.) + \varepsilon} \tag{3}$$

We linearized Equation (3) as shown below to obtain parameter estimates and to examine the evidence for density dependence in daily smolt outmigrants, $Y_{i,t}$, where in our case counts are daily (indicated by subscript t) and the number of escapes is the same within a year (indicated by subscript i). To avoid taking the log of zero on days when no smolts were observed and/or predicted, we added a one to the number of smolts in datasets that included zero counts. The error term, ε, is assumed normally distributed with zero mean and variance-covariance matrix $\sum$ for the linearized equation below.

$$\log_e\left(\frac{Y_{i,t}}{Esc_i}\right) = b_0 + b_1 Esc_i + f_t(\square) + \varepsilon, \quad \varepsilon \cap \square(\vec{0}, \Sigma) \tag{4}$$

---

[1] However, at high juvenile densities, predators become saturated and are unable to eat as large a fraction of available fry and smolts, an example of inverse density dependence.

We evaluated the residuals of the models for the RST data to determine the extent to which they follow an independent (i.e., no autocorrelation) normal distribution with zero mean and a constant variance were met, which is assumed by linear regression. For residuals with no autocorrelation, the expected correlation between two values separated by one day would be the same as the expected correlation between two values separated by one hundred days, which in both cases would be zero.

Analysis of the residuals indicated strong autocorrelation in the residuals of the models we examined. We therefore used generalized least squares to fit the Ricker models described below. Generalized least squares allowed us to model and incorporate the autocorrelation structure. We used the exponential covariance model shown in Equation (5) to model an exponential decay in autocorrelation over time. According to this model, the expected correlation between pairs of residuals is smaller when they are more days apart. Equation (5) was fitted to the residuals and used to construct the appropriate variance-covariance matrix, Σ, and solve for the parameters of Equation (4). The final estimate of λ in Equation (5) is reported. The same procedure was used to solve each of the extended Ricker equations to be described later.

$$C(\Delta t) = e^{-\lambda \Delta t} \tag{5}$$

The following information is presented for each model. First, a Pearson correlation between predictions of outmigrating smolts[1], Y_t, and either RST or ORCM-II predictions is reported. Squaring this value estimates the percent explained variance. We also present Akaike's information criteria[2] (AIC) to compare models and the residual standard error. We present estimated coefficients, and the probabilities associated with the T- test of a 2-sided hypothesis that each is zero. The estimated range of the exponential variogram model is also presented.

We expanded the function, f, in Equation (4) to include predictor variables that represent within- and among-year variation in smolt counts. We hypothesize that within-year variation in smolt counts (i.e., timing) is related to the cumulative temperature (degree days) since the beginning of the current year, $DD_{i,t}$, and $DD_{i,t}^2$, as shown in Equation (6). Degree days reflect the physiological time that juveniles have to develop into smolts, which is largely controlled by temperature.

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[1] Note that these are estimates of median outmigration, back-transformed from the log-transformed ratios predicted by Equation 4. The mean can be estimated by adding half the estimated error variance to the linear equation before taking its exponent and dividing by Esc_i.

[2] Akaike's information criterion (AIC) is an index that penalizes for the number of predictors included in a model (Akaike 1974). In contrast, the R^2 always increases as more predictors are added.

$$\log_e\left(\frac{Y_{i,t}+1}{Esc_i}\right) = b_0 + b_1 Esc_i + b_2 DD_{i,t} + b_3 DD_{i,t}^2 + \varepsilon \qquad (6)$$

In addition to temperature and escapement, flow could also explain variation in smolt production. We considered a variety of models involving lagged flows, with lags between 5 and 21 days. However, we focused mainly on the following flow variables which have one value for each year, i:

(1) $Qfall$ - fall flow (that from the previous October or November),
(2) $Qwinter$ - winter flow (December to February),
(3) $Qspring$ - spring flow (March to June),
(4) $Qcum$ - cumulative flow between Feb 15 of the current year and the date of outmigration,
(5) Qsd - standard deviation in flow between Feb 15 and the date of outmigration.

$$\log_e\left(\frac{Y_{i,t}+1}{Esc_i}\right) = b_0 + b_1 Esc_i + b_2 DD_{i,t} + b_3 DD_{i,t}^2$$
$$+ b_4 Q_{fall,i} + b_5 Q_{winter,i} + b_6 Q_{spring,i} + b_7 Q_{cum,i} + b_8 Q_{sd,i} + \varepsilon \qquad (7)$$

We considered models with flow at all lags up to 21 days (but no other flow variables) and one lag at a time. The dynamic linear modeling package, available in the R software, was used for time-series regression analysis of models involving temporally lagged flows. These lagged-flow models were not predictive and results are not shown here. In the model with all lags, we found only one or two lags to be significant, with little overall predictive power. The particular lags that were significant depended highly on which other lags were included, suggesting high autocorrelation in flow. Considered individually, flow lagged by 10 days was the most significant when added to Equation (6) for the RST data (zero counts included).

We identified a different "best" model for the RST data by removing predictors from Equation (7) that were not significant and examining correlations among parameter estimates. We favored models with the lowest AIC. The model in Equation (8) was selected for RST data with dates having zero counts removed.

$$\log_e\left(\frac{Y_{i,t}}{Esc_i}\right) = b_0 + b_1 DD_{i,t} + b_2 DD_{i,t}^2 + b_3 Q_{spring,i} + b_4 \left(\sum Q_t\right)_i + b_5 \left(\sum Q_{sd}\right)_i + \varepsilon \qquad (8)$$

Our functional validation compares the fitted models for RST data to the corresponding models for ORCM predictions. Our goal is to identify differences in coefficients that reflect differences in environmental responses of model-predicted and field-estimated smolt numbers.

4.5. Imputing RST Estimates

The date of peak outmigration clearly changes from year to year, and appears to be driven by temperature-related development of smolts more than by flow and other environmental variables. Predicting this more precisely might be useful for tailoring the dates of pulse flow releases, which are costly in terms of foregone energy production. The significant degree-day relationship in Equation (4) can be used to find the degree days (DD) when outmigration is at a peak by calculating the derivative of Y with respect to DD for coefficients for the RST data. The derivative was set to zero, and solved for $DD^* = -b_2 / (2 b_3)$, which holds for the general case also (i.e., where the Escapement term is replaced by $f(\cdot)$). For demonstration purposes, we estimated DD^* using coefficients from Equation (6) fitted to RST data excluding zero counts.

In addition, any of the empirical relationships could be used to impute smolt counts for days when the rotary screw traps were not operating. We obtained imputed totals using Equation (6) fitted to RST data excluding zero counts. Imputed values obtained in this manner were used to obtain annual totals, but not for functional validation.

4.6. Energy Generation

Our final task was to add the capability to estimate hydropower generation in ORCM, making it possible to evaluate tradeoffs between hydropower generation and salmon production. We combined annual flow data for the Tuolumne River below LaGrange Dam (USGS gage 11289650) with annual generation data from the Department of Energy's EIA-860 database (generator id's pcode = 439 and 440 for LaGrange and the New Don Pedro). A linear relationship between river flow and electricity generation is suitable for dams that produce electricity with a fixed hydraulic head (Kotchen et al. in press). We fitted a linear model to explain annual generation as a function of total annual river flow. The coefficients were then input to the ORCM model and used to estimate daily generation from daily flows.

5.0 Results

5.1. Comparison of Outmigration Magnitude and Timing

ORCM-I predictions were much higher than RST estimates of smolt outmigration for all years. After reducing egg survival and increasing predation on fry, ORCM-II predictions were closer to RST estimates for three years: 1998, 1999, and 2004, but the totals for 2000-2003 remain much higher (Figure 3). RST estimates suggest fewer than 10 smolts emigrated per spawner in all years, whereas ORCM predicted a much more variable numbers of smolts per spawner, from 1 to 62 (Figure 3). Spawner abundance measured in the Tuolumne River was highest in the fall of 2000 (17,873), lowest in 2003 (2,961) and similar in other years (7,125-9,222) (TID/MID 2005).
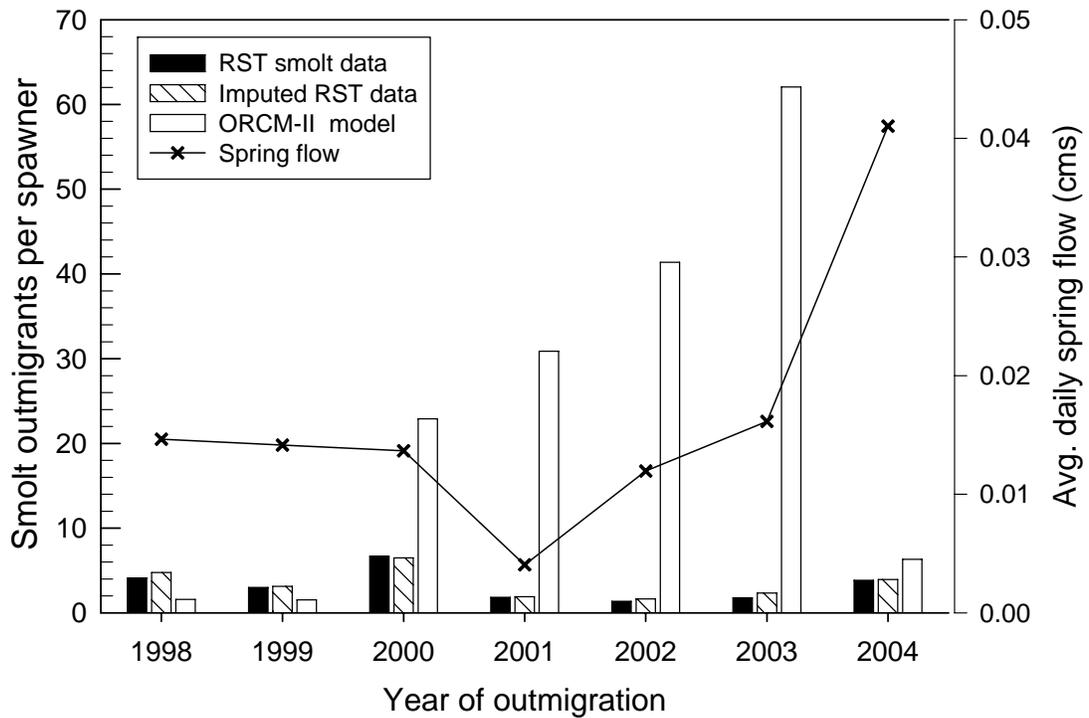
Figure 3. Comparison of total smolt outmigrants (bars) predicted by ORCM in rounds I and II and those estimated from rotary screw trap (RST) data during the spring of 1998 to 2004. The line depicts average spring flow.

The simulated peak date of smolt outmigration compared well (within a week) with RST data for four of the seven years (the spring of 1998, 2002-2004). During the period 1999-2001, predicted average outmigration date differed by up to 17 days, with no clear bias earlier or later. The average outmigration julian date, weighted by numbers of smolts, are shown in Table 1, and include all ORCM predictions. Statistics in Table 1 include ORCM predictions for all dates. ORCM-II predicted outmigration peaked earlier than RST in the spring of 1999 and 2000, later in 2001, and during a similar timeframe in the later years. Timing did not change much between the two rounds of validation, except for the spring of 2000.

Table 1. Average julian date of smolt outmigration for rotary screw trap (RST) data and ORCM-II predictions, which included all dates (not just those with RST data).

Year of spring	Rotary screw trap data	ORCM-II predicted	Difference (d)
1998	103	106	3
1999	115	101	-14
2000	112	96	-16
2001	108	125	17
2002	116	116	0
2003	115	110	-5
2004	110	116	6

5.1.1. Functional comparisons

First, we compare results for the non-flow model (Table 2). Next, we compare results for a "complete" model that includes flow variables (Table 3). Finally, we show parameters for the "best" model for RST data, as determined by AIC and examination of correlations among the predictors.

5.1.2. Functional responses to degree days and escapement

Functional relationships produced by the ORCM-II model and RST data showed similarities and differences. The regression analysis of RST data and ORCM-II predictions using Equation (6) showed several similarities. Both model and field data showed a significant quadratic (parabolic) response to degree-days when zero counts were included (Table 2). Degree days (cumulative temperature) are an important predictor, presumably because of its ability to predict the onset of smolt outmigration and daily variation in smolt outmigration (timing).

Autocorrelation was also a persistent feature of both field estimates and model predictions of outmigration, and residuals of regression models to predict outmigration. However, the range of the exponential correlation function, which measures the length of time within which residual errors are autocorrelated, error differed, with autocorrelation over a shorter range for RST data than for ORCM-II predictions (1.4 and 15.5 days, respectively).

An important feature of the Ricker model is its ability to represent density dependent effects, i.e., a decrease in smolt production at high spawner densities due to superimposition of redds and other mortality risks that increase with density. We consider density dependence to be significant when the coefficient b_3 (Table 2) is significantly less than zero ($p \leq 0.05$). RST and ORCM-II showed different responses to spawner density (Table 2). When fitted to Equation (6), the "Escapement" coefficient fitted to the RST data showed the expected negative sign, whereas this term had a positive sign model for ORCM-II predictions. This indicates a decrease in RST outmigrants at high spawner densities, but a stronger-than-linear positive response to escapement in ORCM-II predictions over the range of densities simulated.

Table 2. Comparison of empirical regression models for $\log_e$(smolts / escapement) shown in Equation (6) for RST-estimated and ORCM-predicted smolt outmigrants in the lower Tuolumne River with and without zero counts included.

Coefficient	Variable	RST (zeroes included)	P<|T|	RST (zeroes excluded)	P<|T|	ORCM-II (zeroes included)	P<|T|	ORCM-II (zeroes excluded)	P<|T|
b_0	Intercept	-12.7922	0.0000	-5.7428	0.0000	-7.0344	0.0000	-2.9171	0.3712
b_1	DD	0.01250	0.0002	0.00550	0.0002	0.00325	0.0332	0.00066	0.8845
b_2	DD^2	-0.000004	0.0001	-0.000002	0.0001	-0.000001	0.0342	0.0000004	0.8081
b_3	Escapement	-0.000013	0.7285	-0.00010	0.0123	-0.00011	0.2765	0.000027	0.7309
	Correlation	0.2286		0.2287		0.2217		0.5466	
	Residual SE	1.1308		1.1308		3.209		1.8171	
	Residual df	542		388		1102		312	
	AIC	2114.0		1075.43		3385.25		896.02	
	Range (d)	1.1		2.2		16.5		7.1	

Table 3. Comparison of the full empirical regression models for $\log_e$(smolts / escapement) shown in Equation (7) for RST-estimated and ORCM-predicted smolt outmigrants in the lower Tuolumne River with and without zero counts included.

Coefficient	Variable	RST (zeroes included)	P<|T|	RST (zeroes excluded)	P<|T|	ORCM-II (zeroes included)	P<|T|	ORCM-II (zeroes excluded)	P<|T|
b_0	Intercept	-16.491	0.0000	-8.8638	0.0000	-15.1496	0.0000	-6.9706	0.2804
b_1	DD	0.0178	0.0000	0.00724	0.0000	0.01714	0.0001	0.00789	0.2817
b_2	DD^2	-0.0000006	0.0000	-0.000002	0.0001	-0.000006	0.0000	-0.000002	0.3259
b_3	Escapement	0.0000017	0.8644	-0.000027	0.7411	0.000030	0.8609	0.000464	0.0011
b_4	Fall flow	0.000082	0.9390	0.000376	0.6633	-0.001114	0.6350	-0.00592	0.0010
b_5	Winter flow	-0.000023	0.4218	-0.000026	0.3165	-0.000244	0.7206	-0.000643	0.2454
b_6	Spring flow	0.000077	0.1741	0.000190	0.0001	-0.000033	0.9000	0.000166	0.3187
b_7	Cum. flow	-0.000112	0.4755	-0.000329	0.0071	-0.000312	0.4280	-0.000341	0.5447
b_8	SD flow	0.00452	0.8501	0.01507	0.4610	0.07642	0.1721	0.16636	0.0014
	Correlation	0.2363		0.3414		0.6785		0.7672	
	Residual SE	1.737		1.0657		3.1815		1.3237	
	Residual df	436		380		669		301	
	AIC	1849.33		1135.76		2424.0		926.31	
	Range (d)	0.9		1.9		10.7		3.6	

5.1.3. Functional responses to flow variables

Next, we examined Equation (7), which included a set of summary flow variables in addition to degree days and escapement. These models cannot be compared with those in Table 2 using AIC because a subset of days are dropped when variables "Cum flow" and "SD flow" are added.

In the models with zero counts included, none of the flow variables was significant for either the RST data or ORCM-II predictions (Table 3). In models fitted to data with zero counts excluded, a few flow variables became significant, suggesting that flow variables influence the number migrating on a given day, but not whether or not migration occurred. Equation (7) includes some predictors that are significant for one and not the other (RST vs. ORCM-II). These differences are the focus of our validation. Spring flow and cumulative spring flow were significant predictors for RST outmigrants, but not for ORCM-II (Table 3). Fall flow and the standard deviation in flow since Feb. 15 (SD flow) were significant predictors for ORCM-II, but not for RST outmigrants (Table 3). Finally, we note that escapement, which played a significant role in Equation (6), was not important in the full models that included flow variables (Table 3). This suggests that the effects of escapement were correlated with, and replaced by, other predictors (e.g., the correlation between parameter estimates for escapement and fall flow was -0.764).

The "best" RST model included degree-days, spring flow (total and cumulative), and variation in flow (Table 4). Note that the three flow variables do not greatly increase the predictive capability, as measured by the correlation, over that in the model with just degree days and escapement (Table 2).

Table 4. "Best" empirical regression models for loge(smolts / escapement) shown in Equation (8) for RST-estimated smolt outmigrants in the lower Tuolumne River (zero counts excluded).

Coefficient	Variable	RST	P<|T|
b_0	Intercept	-8.2961	0.0000
b_1	DD	0.006633	0.0001
b_2	DD^2	-0.000002	0.0002
b_4	Spring flow	0.000173	0.0000
b_5	Cum. flow	-0.000267	0.0033
b_7	SD flow	0.013277	0.1263
	Correlation	0.3079	
	Residual SE	1.038	
	Residual df	380	
	AIC	1081.54	
	Range (d)	1.9	

5.2. Imputing RST Estimates

First, we propose that the correction for catchability as a function of flow can be improved by using the maximum flow that occurred during efficiency tests. In addition, there is some question about the Modesto flow data, which are quite a bit higher than those provided by USGS. We applied the first correction (but not the second) before running these analyses. Second, we estimated the degree days at peak outmigration from fitted parameters for RST data as 1,563 degree days by solving for the optimal value in Equation **Error! Reference source not found.**(6) with coefficients derived from RST data with zeroes included (Table 2). Third, we used one of the models developed as part of our validation, a Ricker model involving previous-fall escapement and degree-days, to impute rotary screw trap estimates for missing days (Figure 4). Using the same model as above, we estimated the following annual totals: 5,244 in 1997; 35,510 in 1998; 27,954 in 1999; 51,025 in 2000; 36,253 in 2001; 14,695 in 2002; and 15,264 in 2003.
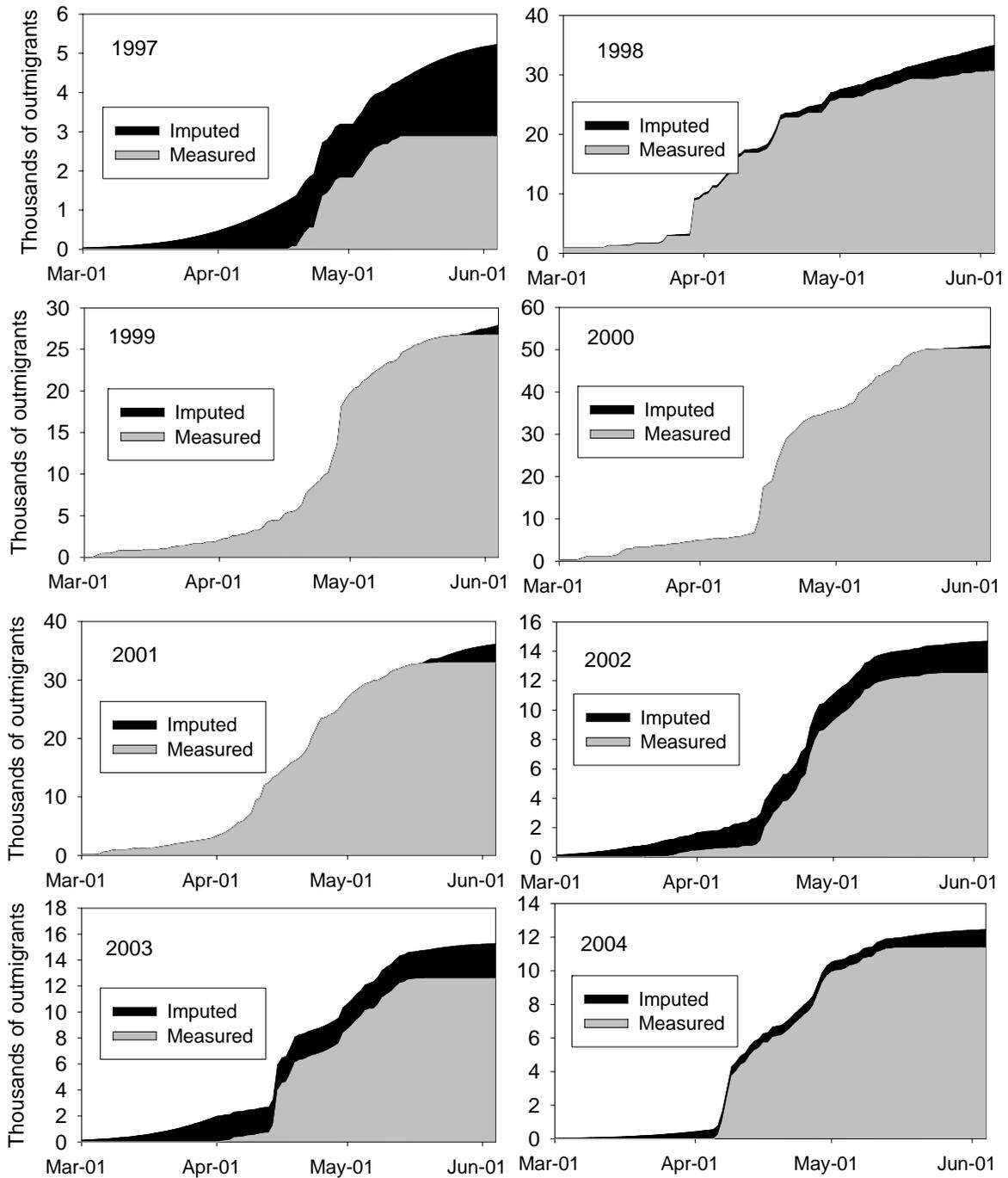
Figure 4. Cumulative estimates of outmigrants > 70 mm in size based on rotary screw trap data collected by the California Department of Fish and Game. The black shaded area shows the additional estimated Chinook smolt production using the imputation method described here, and the grey shaded area shows the cumulative production without imputing missing dates.

5.3. Energy Generation

The linear relationship, Generation (mwh) = 295,807 + 7814.1 Flow (cms) explained 77% of variation in annual generation at the New Don Pedro and La Grange projects between 1970 and 2003. We incorporated this relationship in ORCM to allow simultaneous prediction of salmon production and hydropower generation. To scale from annual to daily flows, we divided the intercept by 365 days. For linear relationships such as the one above, disaggregation does not introduce error (O'Neill 1979). Figure 5 shows the relationship between flow and generation over the period of study, where summer dates after outmigration of smolts were excluded.
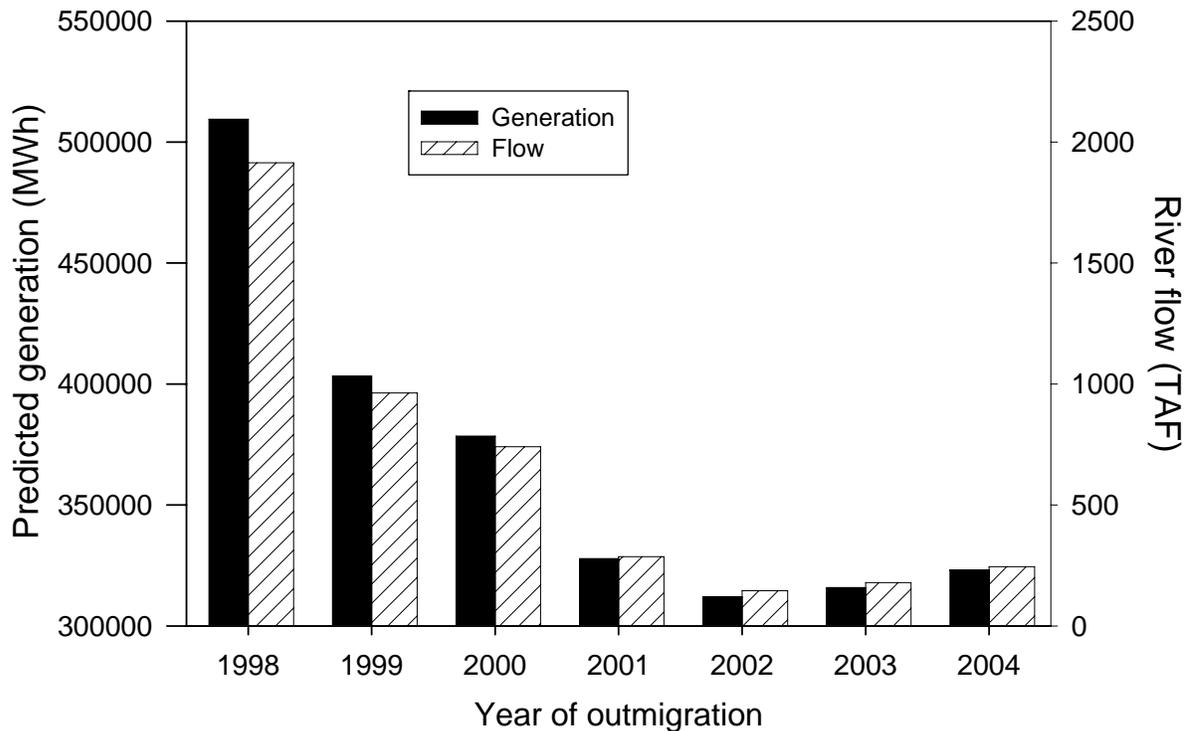
Figure 5. Relationship between ORCM-simulated generation and cumulative river flow over the 330 days simulated by the model in each year.

6.0 Discussion

Three objectives of this study were: (1) to improve RST estimates of outmigrating juveniles, (2) to reduce uncertainty in ORCM predictions, and (3) to add the capability to estimate hydropower generation in ORCM, which will allow trade-offs between energy and salmon to be predicted.

Our first objective was to reduce uncertainty in RST estimates of annual numbers of outmigrants. The empirical relationships presented earlier as part of our functional validation were useful for pursuing this objective. First, we used one relationship to solve

for the degree-days at peak smolt outmigration, which could be used to fine-tune the timing of pulse flows. Second, we used one relationship to impute outmigrant counts on dates when the rotary screw traps did not operate. In practice, these relationships should first be verified using cross-validation against new data not previously used to estimate parameters.

Our second objective was to reduce uncertainty in ORCM predictions. Because we only completed two rounds of model comparison, we did not fully accomplish this objective. However, we have made a start and developed methods needed to continue the effort. Discrepancies between model-predicted survival and that suggested by field sampling remain unacceptably large for some years. Our comparison of timing of outmigration showed differences in some years, but not others. Because ORCM uses the same temporal distribution of spawners in fall of each year, timing of outmigration in the model does not reflect year-to-year differences that are likely to be observed in the field.

The consequences of extreme weather events and density dependent mortality are two possible reasons for the discrepancy between the model and data. Our functional analysis suggests that density dependent mortality is higher in the field than simulated in the model. Another line of evidence suggesting that the "missing" mortality must be density dependent is that increased density independent mortality would result in no smolt outmigrants in the three years now predicted reasonably well, 1998, 1999, and 2004. Two sources of density dependent mortality that are now simulated by ORCM are redd superimposition and predation on fry. However, the parameters controlling the strength of each of these density dependent factors may need tuning.

It is difficult to say from the RST data whether the additional, unpredicted mortality occurs during the egg or fry life stage. The RST data are not useful for addressing this question because fry outmigration was not sampled in most years. The most complete early sampling occurred in 2000 and 2002. During these two years, ORCM-II predicted 5-times (in 2000) and 100-times (in 2002) more fry outmigrants than were estimated based on the rotary screw trap data. Thus, higher egg and alevin mortality may have occurred during these two years than the average value estimated in the field and used by us as input to the model. Increasing egg mortality in the model to correspond to those in field tests was not sufficient to produce such low numbers (simulated egg-to-fry survival ranged from 0.06 to 0.20).

Juveniles in the Tuolumne River might grow slower at high densities, and thus risk higher exposure to predation for a longer period. To test the hypothesis that density dependent mortality is caused by slower growth, we could compare growth rates in the different years to see whether there is evidence in the RST and seining data of slower growth at high densities, and whether density-related differences in growth are tracked by growths simulated in ORCM. Preliminary comparison of an annual growth index and seined juvenile densities do not suggest an inverse relationship (TID/MID 2005; Figure 6).
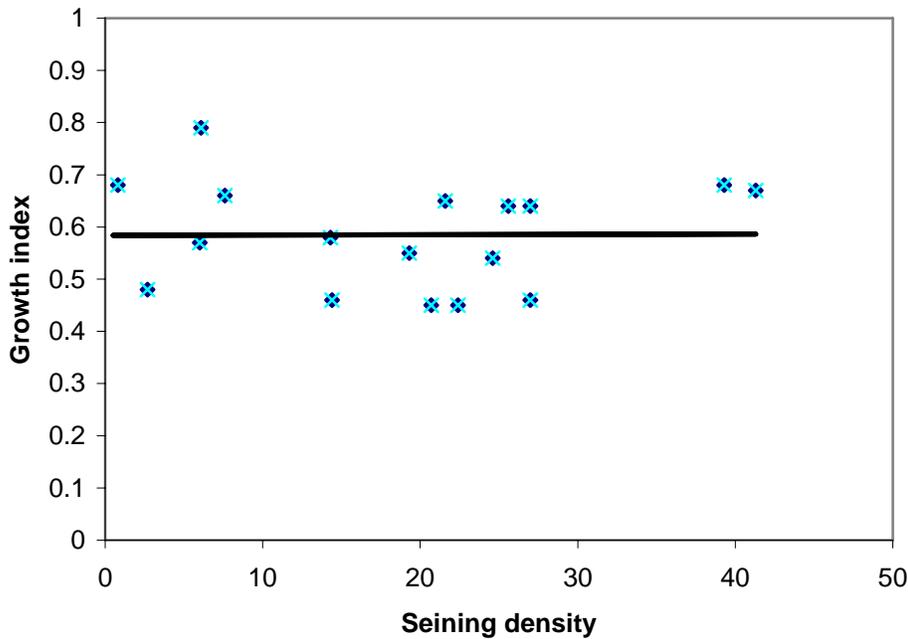
Figure 6. Juvenile growth index (mm/d) showed no relationship with seining density.

Another possibility is redd superimposition, which is known to occur in this river (TID/MID 2005). To address superimposition, we could consider whether the spatial distribution of spawners is more concentrated near the upstream dam, leading to higher levels of superimposition that we currently simulate in ORCM.

If we were to continue the process of iterative improvement, identifying density dependent influences would be our next focus. The most powerful test of density dependence requires approximately 16 years of population estimates (Dennis and Taper 1994).

Flow influences salmon directly through velocity and depth (i.e., physical habitat), and indirectly, through temperature – water released by the dam is, in general, colder than air in fall and spring and warmer than air in winter. Our results suggest that temperature-related effects of flow are more important than the direct effects of flow as predictors of outmigration time. Neither model nor data showed a large increase in predictability after including flow variables, none of which were significant in models fitted to data including zero counts. However, patterns in the models fitted to data excluding zero counts suggest that flow variables correlate better with overall abundance than with timing. In these data, we did observe differences between the RST estimates and model predictions: ORCM-II predictions showed a weaker response to spring flow and cumulative spring flow, and a stronger response to fall flow and variation in spring flow, than we observed in the RST data. In a next round of model validation, these differences might be examined for clues to model improvement. In addition, there is always the possibility that observed effects of spring flow on RST data reflect the effects of correcting RST counts for low efficiency at high

flow. In future efforts, it would be instructive to include an index of maximum temperature as an additional predictor to determine whether ORCM predictions of temperature-related mortality are sufficiently accurate.

Analysis of residuals revealed that the episodic nature of outmigration, combined with the presence of many small (and zero) counts makes prediction difficult. One would think that a hierarchical model including a logistic function for presence-absence of outmigrants and a separate model to predict counts, given the presence of outmigrants, would improve prediction, but we found this not to be the case in our preliminary assessment. Even residuals of the "best" linearized equation for RST data show the difficulty of predicting many small counts and few large counts using the predictors available (Figure 7).   This suggests that the extended Ricker model does not represent the error structure of these data particularly well. Others have encountered the same problem in dealing with Chinook migration data (e.g., Zabel et al. 2005).
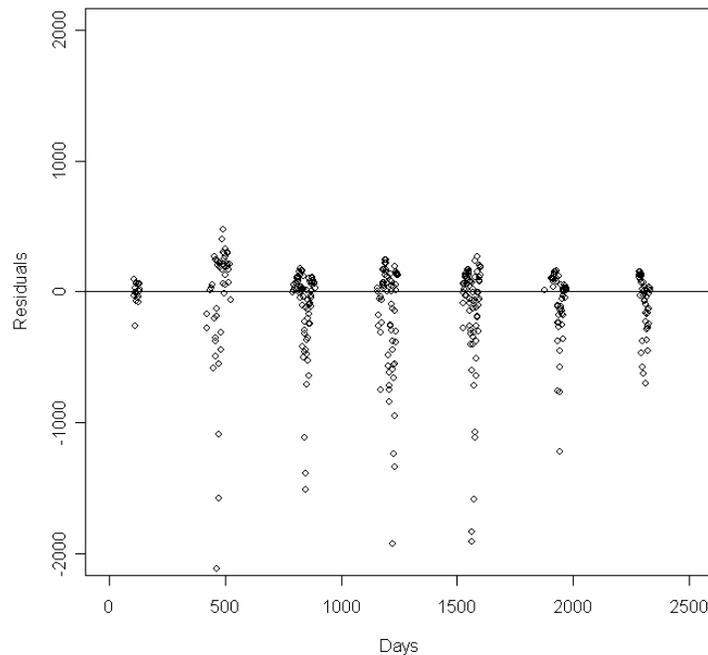
Figure 7. Residuals from the model shown in Equation (8) for $\log_e$(RST-estimated smolt outmigrants/Escapement) over time (1997-2004).

Several studies have quantified relationships between Chinook salmon migration rate and river conditions, including flow, temperature, and turbidity (Conner et al. 2000, Smith et al. 2003). However, we identified only one other study that attempted to predict the numbers migrating at different times (i.e., timing of migration). Trapanier et al. (1996) developed a time-series model to predict the upstream migration of landlocked Atlantic salmon as a function of river discharge and water temperature. The authors argued for a need to include autocorrelation in prediction and demonstrated the facts that model significance and the significance of individual predictors are overestimated by ordinary least squares models that assume residuals are uncorrelated. The residuals in our study also showed

considerable autocorrelation: Figure 8 shows the average correlation between pairs of values separated by the number of days on the x-axis. We were able to account for autocorrelation in the analysis by using generalized least squares. Our analyses of time series models with lagged variables suggested that models including earlier counts could substantially improve predictions and, consequently, whiten (i.e., reduce autocorrelation among) the residuals. In our opinions, it is unlikely that such feedback could be provided quickly enough to be useful in practice, and model-data differences in autocorrelation would not be easy to interpret for purposes of functional validation.

Figure 8. Temporal autocorrelation in residuals from the model given by Equation (8) for RST data excluding zero counts. The x-axis shows the lag in days and the y-axis shows the autocorrelation function, ACF.

Our third objective was to calculate energy production in the ORCM model. We met this objective by developing an equation that predicts energy generation from flow based on historical data from the USGS and EIA. This was incorporated into the ORCM model and will make it possible to quantify the flow-related trade-offs between salmon production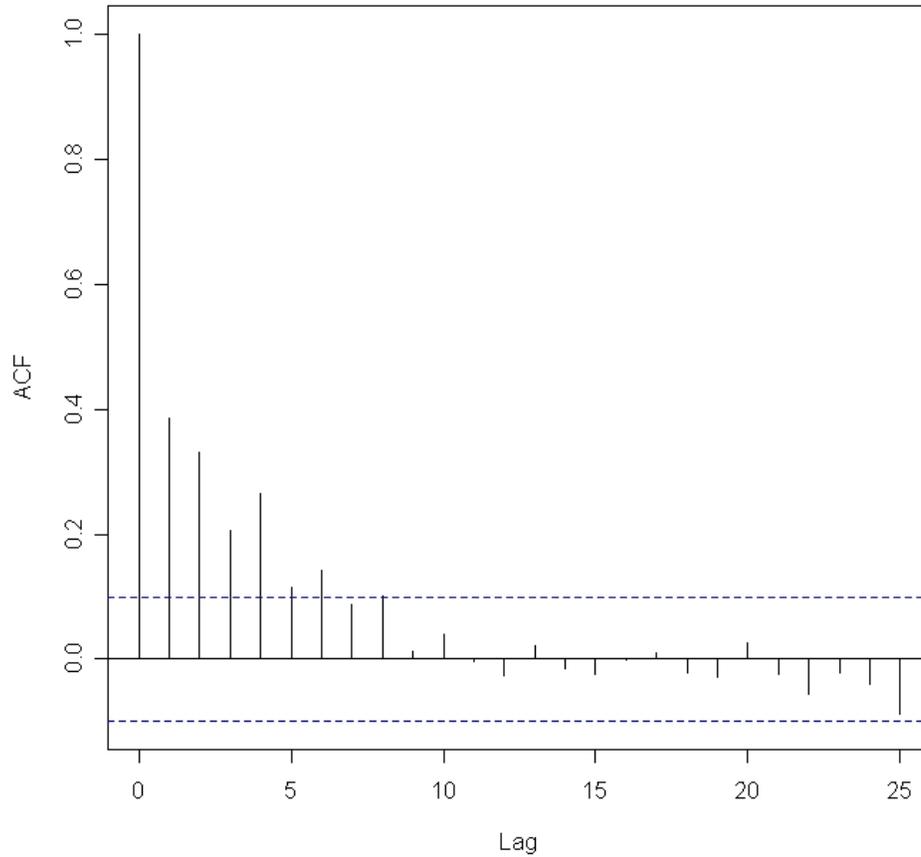 and energy production. Flow-based predictions of generation could be refined by incorporating reservoir elevation, which determines the "head" – or vertical distance between the water surface and the turbines. The relationship presented here predicts well on an annual basis, and we are confident that distributing the energy generation across days based on flow results in accurate predictions.

We did not attempt to estimate the value of hydropower generation. Stewart (1997) estimated that each acre-foot of water diverted through turbines in the Sierra-Nevada region of California produces $15 of electric power valued at a wholesale power rate of 2.5 cents/kWh. It would be difficult to incorporate such a fixed conversion because of the temporal variation in markets and demand-driven variation in price. Hydropower is typically of higher value during hours of peak demand (daytime) to offset the cost of buying power from fossil fuels or other sources. In future, seasonal variation in price could be incorporated to estimate hydropower revenue.

7.0 Conclusions

We conclude that the approach used by this study will eventually reduce uncertainty in model predictions and field estimates by improving our understanding of model-data discrepancies. Both the model and data involved in this study are characterized by high uncertainty. Low capture probabilities increase the uncertainty in RST-based estimates, which are obtained by statistically cloning one captured fish to represent hundreds that were not caught. This makes it difficult to know with confidence how many outmigrants exited the river in a given year. On the model side, ORCM predictions vary considerably from year to year, a phenomenon not observed in the RST estimates. Because only two rounds of comparisons were completed, this study has reached the stage of highlighting uncertainties in model predictions, while somewhat reducing uncertainty in RST estimates.

As one result of this study, we provided guidance for the next steps in iterative model improvement. Two hypotheses that may explain why observed survival in the field was lower than predicted in half the years are (1) under-representation of density dependent mortality in the model, and (2) fish kills due to factors not represented, or not adequately represented, in the model (e.g., episodes of low dissolved oxygen, high temperature, or contaminants). The first hypothesis can be tested using other sources of information, in particular seining survey data. Average sizes of salmon in the seining data should indicate when migration is likely to occur, and the relationship between fry and smolt abundance in the river and the number of outmigrating smolts captured in RST traps. A decoupling between these two could indicate a high, density dependent mortality acting on fry, whereas a strong positive relationship between fry and smolts, combined with a weak relationship with spawner abundance, would suggest that density dependent mortality

during the egg stage is important. One could begin to examine the second hypothesis by adding maximum temperature over some previous time interval as a predictor in the functional comparison. Although temperature-related mortality is simulated by ORCM, the lethal thresholds used may not adequately account for associated changes in dissolved oxygen. Scouring mortality acting on redds during extreme flow events is another possible factor that may be underrepresented.

We found empirical models to be useful, both as a means of functionally validating and improving the model, and as tools for imputing missing field measurements. We used one empirical model to impute missing RST estimates, and the same could be done for dates on which flows are high, leading to very low capture efficiencies. The methods demonstrated here can be used in future to evaluate other recruitment models against rotary screw trap data for this river and other rivers in California.

Development of predictive models of salmon populations is a very challenging task, because the dependent variables are responding to multiple environmental drivers in space and time. Long-term environmental monitoring data are essential to the development process. However, if monitoring data are to be useful to model development, they should be designed with that use in mind. An ongoing process of iterative improvement in both models and monitoring can be achieved if they are seen as interconnected and managed as such. The Tuolumne River and other tributaries of the San Joaquin River offer important opportunities for improved fish management if we can learn from our monitoring and modeling experiences and integrate them more closely.

8.0 References

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9.0   Glossary

ACF	Autocorrelation function
AIC	Akaike's information criteria
CDC	California Data Center
CDFG	California Department of Fish and Game
DD	degree days
DOE	U.S. Department of Energy
Energy Commission	California Energy Commission
EIA	Energy Information Agency (U.S. Department of Energy)
GLS	generalized least squares
MID	Modesto Irrigation District
ORCM	Oak Ridge Chinook salmon Model
PIER	Public Interest Energy Research
RD&D	research, development, and demonstration
RST	rotary screw trap
TID	Turlock Irrigation District
USGS	U.S. Geologic Survey (Department of Interior)

Appendix A

**Designing Optimal Flow Patterns for Fall Chinook Salmon in a
Central Valley, California River**

Designing Optimal Flow Patterns for Fall Chinook Salmon in a Central Valley, California, River

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Abstract.—Widespread declines in stocks of Pacific salmon in the genus *Oncorhynchus* highlight the need for research to find new and effective management strategies for recovery. Two recovery objectives are (1) to ensure that recruitment is adequate to rebuild self-sustaining populations and (2) to maintain phenotypic diversity. This study seeks to understand how seasonal flow patterns in a flow-regulated California river might be managed to attain each of these recovery objectives, specifically for the fall and late-fall runs of chinook salmon *O. tshawytscha*. We ask two questions: (1) Does the optimal pattern of seasonal flows change as the amount of water available is constrained by droughts or diversions of flows? and (2) How do optimal flow regimes designed for the two conservation objectives differ? We coupled simulated annealing with a recruitment model to find flow regimes that maximize either the number of smolt out-migrant ''recruits'' (MR) or the variation in spawning times among recruits (MV). Optimal flow regimes identified for both the MR and MV objectives changed as we increased the annual quantity of water available, allocating higher flows during the spring and fall seasons. Flow regimes that optimized the MR and MV objectives were different. For example, the MV flow regime with unlimited annual flow provided a pulse of high flow 2 weeks before the peak spawning date of the minority late-fall run. Simulated recruits produced by MV flow regimes were fewer in number—and had parents that spawned later and over a wider range of dates—than recruits produced by MR flow regimes. Although these results have not been verified by empirical studies, they demonstrate the potential for managing species with special conservation status by combining state-of-the-art numerical optimization methods with mechanistic ecological models.

Anadromous salmonids play a significant role as keystone species in the river ecosystems draining to the Pacific coast of North America (Willson and Halupka 1995; Cederholm et al. 1999). Historically, Pacific salmon in the genus *Oncorhynchus* permeated coastal rivers and streams from Alaska to southern California. A tendency to return to spawn in their natal river allowed salmon populations to adapt to local environmental conditions (Waples 1995) and led to an adaptive radiation in life history traits for chinook salmon *O. tshawytscha* (Healey 1994). Collectively, salmon populations diversified into an array of populations (also known as ''runs,'' ''races,'' or ''stocks'') with life histories distinguished by spawning time and place. The temporal diversity and geographic distribution of salmon populations resulted in the presence of one life history type or another during most seasons of the year in coastal rivers throughout their range. These spawning aggregations support dozens of bird, mammal, and fish predators, and decomposing salmon carcasses provide a significant nutrient subsidy to the surrounding terrestrial ecosystem (Bilby et al. 1996).

Today, the majority of Pacific salmon stocks have declined, and healthy stocks (those exceeding one-third of their historical abundances) are outnumbered by stocks that are either currently at risk or recently extirpated (Nehlsen et al. 1991; Huntington et al. 1996). Life history diversity among salmon species has also declined because habitat degradation has differentially affected some races. This loss of life history variation is of particular concern for Pacific salmon, both from a conservation biology (i.e., single species) perspective and from an ecosystem perspective. From a conservation biology perspective, salmon species are defined by an evolutionary biology that promotes diversity in life history, and by a meta-population structure that requires diversity to per-

sist. Homing to natal streams and infrequent straying rates promote local adaptation, and therefore phenotypic diversity. This diversity of adjacent populations in time and space increases the likelihood that straying adult spawners will recolonize locally extinct runs and thereby enhance the long-term persistence of the metapopulation (Li et al. 1995; Stanford et al. 1996). One might consider salmon as having a temporal, as well as a spatial, metapopulation structure supported by straying from populations with different spawning times. From an ecosystem perspective, Pacific salmon represented a relatively stable component of ecosystems because of the temporal and spatial partitioning of river spawning habitat among populations. Efforts to restore salmon populations typically focus on two recovery objectives: (1) rebuilding the size of salmon populations, and (2) protecting salmon populations with unique genetic and phenotypic qualities.

Flow regulation is an important policy tool available for meeting these two conservation objectives for salmon (National Research Council 1996). Salmon declines have been attributed to many factors, including the "4Hs": harvesting, hydropower, habitat, and hatcheries (Lackey 1999). The alteration of natural river flows, by diverting water for hydropower and for other social uses, has contributed to decreases in salmon spawning habitat, both in quality and quantity. River flow is viewed by Poff et al. (1997) as a master variable that regulates the ecological integrity of rivers. Flow manipulations will only be effective as a tool for restoring salmon populations if the relationship between seasonal patterns of instream flow and salmon recruitment is understood.

Flow effects differ during different life stages and seasons. For example, elevated flows during the alevin life stage has been linked with reduced survival of salmonids (Jensen and Johnsen 1999), whereas higher spring flows may increase survival of spring out-migrants (Kjelson and Brandes 1989; Kope and Botsford 1990; Cada et al. 1993; Speed 1993; but see Williams and Matthews 1995). Reduced temperature-related mortality and reduced predation are two possible factors producing a positive survival–flow relationship in spring. Because juvenile salmon have low tolerance for elevated stream temperature, high spring flows provide an indirect benefit by slowing the rise in river temperatures during late spring and early summer. Predation on migrating juveniles may be lower during higher flows for two reasons. First, predation ef-

ficiency is curbed at high river flows by higher turbidity, higher water velocities, and an increased tendency for prey to form aggregations (Peterson and DeAngelis 1992). Second, faster downstream migration at high flows shortens the duration of exposure to predation risk (Berggren and Filardo 1993), but it may also hasten exposure to high predation risk in the estuary.

The effect of river flow on salmon recruitment at times of year other than spring is less clear. Higher flows in fall attract adults waiting to migrate upriver to spawn (e.g., Fleming and Gross 1994). Elevated flows may facilitate swimming past natural and artificial barriers, or they may merely serve as a cue for migration. High fall flows are correlated with lower temperatures that benefit females migrating upriver by ensuring that eggs are not damaged before spawning (Independent Scientific Group 1996). The flow level during the building of redds influences later exposure to dewatering at lower flows and to scouring during flood events, favoring stable fall and winter flows (Becker et al. 1982; Stevens and Miller 1983). Summer flows can be very critical for the juvenile life stage of spring races because they remain in the river over summer before migrating to sea.

In this paper, we use a numerical optimization technique coupled with a recruitment model to design optimal seasonal flow patterns for salmon. Our analysis builds on earlier work linking flow management to chinook salmon recruitment (Bartholow and Waddle 1995; Jager et al. 1997). We use a slightly modified version of the Oak Ridge Chinook Model (ORCM) to simulate the main linkages between salmon biology and instream flow (Jager et al. 1997). We focus on the fall and late-fall runs of chinook salmon at the southern extreme of their range in the lower Tuolumne River, a tributary of the San Joaquin River, California.

We used optimization methods to identify the optimal pattern of seasonal flow for two different management objectives: (1) maximizing overall recruitment and (2) maximizing variation in run times among recruits. Recruitment is defined here as the number of individuals that successfully reach the smolt stage and emigrate from freshwater to saltwater. The run time of a recruit is defined as the date that a recruit was spawned by its parents. For each of the two objectives, we determined how the optimal pattern of seasonal flow changes in response to changes in the annual amount of water available. Decision-makers can use this information to adjust instream flow policies to the

hydrologic conditions (e.g., wet versus dry) in a given year.

Our analysis uses chinook salmon, a well-studied species, to demonstrate how optimization methods can be coupled with a biologically detailed recruitment model to identify optimal flow conditions. We recognize that our understanding of how flow affects the growth, survival, reproduction, and movement of salmon is incomplete, and the specific recruitment model we used is one of many possible model formulations. Despite these limitations, our approach can yield insights into optimal flows for chinook salmon and illustrate the general approach of coupling optimization methods to mechanistic models. Our method should be applicable to many other species for which environmental effects on recruitment are complex and for which it is important to identify optimal environmental conditions for recruitment.

Central Valley Chinook Salmon

The Central Valley of California historically supported substantial numbers of both spring- and fall-run chinook salmon (Myers et al. 1998; Yoshiyama et al. 2000). Although spring chinook salmon were historically more abundant than fall chinook salmon, they now represent a much smaller fraction of the fishery. Fall chinook salmon still support a significant ocean fishery due, in part, to hatchery production (Moyle 1994). The spring and winter runs have been extirpated from the San Joaquin River. Dams blocking access to headwater and spring-fed streams have resulted in population declines and federal listing of the spring and winter runs in the Sacramento River as endangered under the Endangered Species Act (Fisher 1994; Healey 1994; Myers et al. 1998).

Fall chinook salmon actually include two runs: a fall run and a late-fall run. Genetic differences between these two runs indicate that they were reproductively isolated, probably by temporal and spatial segregation of spawning (Nielsen et al. 1994). Fall-run adults spawn between October and December, whereas late-fall adults spawn between January and April. Historically, both fall runs occupied the Sacramento and San Joaquin river basins (Hatton and Clark 1942; Fisher 1994). Adults of the late-fall run spawned in upper main-stem rivers, where summertime water temperatures remained low enough for juvenile growth (Fry 1961; Fisher 1994). In the Central Valley, late-fall spawners lost access to their historical spawning habitat following construction of the Friant Dam on the San Joaquin River and the Shasta Dam on

the Sacramento River. The two runs and the two river basins are regulated jointly as the Central Valley fall-run Evolutionarily Significant Unit (ESU; National Marine Fisheries Service 1999), which is not currently listed by the federal government as threatened or endangered. Three lines of evidence suggest that the late-fall run has a considerably greater risk of extinction than the fall run: (1) population sizes are smaller (Yoshiyama et al. 2000), (2) population sizes are declining faster (Yoshiyama et al. 2000), and (3) two races (spring and winter runs) that also used spawning habitat above dams are now listed or extirpated. Both fall runs are considerably more depressed in the San Joaquin River basin than in the Sacramento River basin (Myers et al. 1998). According to Huntington et al. (1996), both the fall and late-fall runs are at risk of extirpation from the San Joaquin River basin.

Fall chinook salmon spend their adult lives in the ocean. At some point between ages 2 and 5, adults migrate into rivers during the fall to spawn (Table 1). Each female digs a redd in the gravel river bottom. During courtship, she releases her eggs into her redd. After fertilization of the eggs by one or more males, the female buries the eggs. Eggs incubate through the winter, hatch as alevins (nonfeeding larvae) into intergravel spaces, and emerge from redds as fry (defined here as presmolt juveniles) in the spring. The emergent fry of fall chinook salmon feed on invertebrates along river margins for the first month or two and gradually move downstream. Fry may exit tributaries in winter or spring to rear in the lower main stem and upper estuaries before becoming smolts. The process of smoltification enables them to tolerate salt-water and migrate to the ocean.

This study focuses on the Tuolumne River, a tributary of the San Joaquin River. The LaGrange Dam, at 83.7 km above the confluence, blocks upstream migration of adult salmon returning to spawn. The average natural annual flow estimated below LaGrange Dam between 1897 and 1923 was 2,390 hm^3 (1 hm^3 = 10^6 · m^3; McBain and Trush 2000). The average impaired annual flow measured below LaGrange Dam between 1971 and 1999 was 952 hm^3 (McBain and Trush 2000; Paterson 1987:20–23). The difference between natural and impaired flow is accounted for by upstream water diversions.

Methods

The Oak Ridge Chinook Salmon model.—The Oak Ridge Chinook Salmon model (ORCM; Jager

TABLE 1.—Timing of events leading to recruitment of fall-run and late-fall-run chinook salmon in the Central Valley, California, and the main factors influencing the growth, development, and survival of each early life stage simulated by the Oak Ridge Chinook Salmon Model (FERC 1996).

Life stage	Fall run	Late-fall run	Influences on growth and development	Influences on survival
Egg	Oct–Dec	Jan–Apr	River temperature	Temperature Weighted usable area Density of spawners
Alevin	Dec–Mar	Mar–May	River temperature	Weighted usable area Density of spawners
Fry	Jan–Apr	Apr–Jun	River temperature Fish weight Fish size (rank)	Fish size Predator density Juvenile density Temperature
Smolt	Mar–Jun	Oct–May	River temperature Fish weight	Size of smolt Predator density Juvenile density Temperature

et al. 1997) is a spatially explicit and individual-based model of fall chinook salmon recruitment in a river below a dam. The model links a spatially explicit representation of river habitat with a biotic model of chinook salmon reproduction, development, growth, and mortality. The river habitat changes seasonally and includes important spatial gradients (e.g., temperature, predator densities) between upstream spawning areas and lower reaches inhabited during out-migration. The biotic component uses a daily time-step to simulate co-existing life stages, as individuals grow, develop from one life stage to the next, move, and die (Table 1). The ORCM simulates the river phase of chinook salmon ecology, beginning with adults entering the river to spawn. For each redd, we simulate the daily development and mortality of egg and alevin life stages. After emerging from redds, the daily development, growth, mortality, and downstream movement of individual juveniles (defined here as fry and smolts) is simulated, culminating in the migration of smolts from the river (i.e., recruitment). The values and definitions of model parameters are listed in Table 2.

Habitat component.—The biotic events leading from upriver migration of spawners to the out-migration of recruits are simulated in a spatially explicit river habitat represented by a series of adjacent, 1.6-km segments differing in the proportion of riffle and pool habitat, temperature, and flow (at confluences with tributaries or diversions). Simulated average daily water temperature in each river segment is determined by allowing water released by the dam (about 12°C year-round; FERC 1996) to equilibrate to the air temperature as the water travels downstream. The simulated river temperature of each segment depends on daily air temperature, dam release temperature, and flow rate, which controls the rate of travel downstream. Daily flow in each segment is generated as part of the optimization procedure and used to drive the ORCM.

Each river segment is assigned a habitat capacity for each life stage (numbers/m²) that depends on empirical relationships between the amount of suitable habitat (weighted usable area or WUA) and daily average flow. The WUA relationships were estimated from results of an instream-flow study conducted in the Tuolumne River for each life stage and for two mesohabitats: riffle habitat and run–pool habitats, where runs and pools are treated as one mesohabitat (EAEST 1992b). The total capacity of each segment is a weighted sum of that provided by its riffles and that provided by its runs and pools.

Upriver migration and spawning.—Simulations begin with the migration upstream of 5,000 adults (4,673 fall run and 327 late-fall run) to the tributary represented by the model. This is roughly the average annual number of spawners counted between 1971 and 1988 in the Tuolumne River (EAEST 1992a). Individual spawner sizes are drawn from a normal distribution. The initial distribution of spawning times of migrating adult spawners follows a triangular distribution with a start date, peak date, and end date for each run. However, model spawners delay upstream migration if the water temperature at the mouth of the tributary or discharge from the tributary is below a threshold. The number of migrants on each day includes the proportion calculated from this distribution, plus those unable to migrate on previous days.

On the day of spawning, each female spawner

TABLE 2.—Parameter values used in the Oak Ridge Chinook Salmon Model simulations for the Tuolumne River, California. Parameter sensitivity is measured by the standardized regression coefficient, which varies from −1 to +1 and reveals both the direction and magnitude of a parameter's effect. We present sensitivities to two model predictions separated by commas: the simulated number of out-migrants and the peak date of out-migration. Those parameters excluded from the Jager et al. (1997) analysis are indicated by a blank, and those with a coefficient smaller than 0.05 are shown as zeroes.

Name	Value	Sensitivity	Parameter definition
a_{fec}	3,200.2		Intercept of fecundity relationship with fish length
al	0.0005		Intercept of relationship between fry length and weight
a_{move}	0.25	+0.05, 0	Movement rate at zero flow for fry (d/km)
a_{move}	0.16	0, 0	Movement rate at zero flow for smolts (d/km)
A_{rat}	250	0, 0	Scaling ratio for river size against Columbia River
A_{redd}	216	0, 0	Average defended redd area (4× actual redd area; m^{-2})
A_{terr}	0.00148	0, 0	Coefficient in relationship between territory and fish length
B_{terr}	2.61	0, −0.13	Exponent in relationship between territory and fish length
b_{fec}	109.4		Slope of fecundity versus fish length (cm)
bl	2.136		Exponent of relationship between length and weight for fry
bq_{temp}	0.5	0, 0	Power function exponent relating velocity to flow
c_{move}	-6.0×10^{-6}	0, 0	Slope between travel time (d/km) and flow (m^3/s)
DD_{alv}	395.8		Degree-days required from hatching to emergence (°C)
DD_{eggs}	500		Degree-days required from egg laying to hatching (°C)
DD_{smo}	1,082	0, +0.15	Degree-days required to develop into a smolt (°C)
F_{spawn}	0.5	0, 0	Minimum flow needed to upmigrate and spawn (m^3/s)
K_{temp}	−0.0006	0, 0	Temperature equilibration rate coefficient (s^{-1})
L_{min}	70		Minimum size required to develop into a smolt (mm)
L_{s_avg}	688		Average length of adult spawners (mm)
L_{s_sd}	74		Standard deviation of spawner lengths (mm)
L_{s_min}	400		Minimum length of spawning adults (mm)
L_{s_max}	1,400		Maximum length of spawning adults (mm)
L_{segsp}	40.5		Stream distance below dam used for spawning (km)
N_{esc}	5,000	+0.05, 0	Fall-run escapement (number of adults)
P_{cap}	0.0001		Maximum probability of successful prey capture
P_{late}	0.07		Fraction of total chinook spawners in late-fall run
P_{pock}	0.125	0, 0	Average fraction of egg pockets superimposed
P_{smo}	0.6	0, 0	Fraction of maximum intake obtained by smolts
P_{up}	0.4	0, 0	Probability of upstream movement at low temperatures
P_{min}	0.08	0, 0	Minimum fraction of maximum ration at feeding station
P_{max}	0.6	0, 0	Maximum daily ration (obtained by largest juveniles)
S_{min}	0.9997	+0.85, −0.34	Daily survival rate in marginal habitat
S_{rat}	0.44	0, 0	Fraction of adult spawners that are female
S_{wait}	14		Period from egg laying to female departure (d)
t_{avg}	Apr 4		First date that air temperature reaches T_{avg}
T_{avg}	16		Average annual air temperature (°C)
T_{avoid}	22	0, 0	Lower threshold for behavioral avoidance (°C)
T_{max}	30		Maximum annual air temperature (°C)
T_{spawn}	17.8	0, 0	Upper temperature threshold for chinook salmon spawning (°C)
T_{ULT}	25	+0.12, −0.34	Upper lethal temperature for chinook salmon (°C)
UP_{max}	Apr 20		Latest date of late-fall spawning migration
UP_{max}	Dec 22	+0.16, +0.70	Latest date of fall spawning migration
UP_{min}	Jan 1		Earliest date of late-fall spawning migration
UP_{min}	Oct 1	+0.11, +0.16	Earliest date of fall spawning migration
UP_{peak}	Mar 1		Peak date of late-fall spawning migration
UP_{peak}	Oct 27	0, 0	Peak date of fall spawning migration

is assigned to a spawning location that is identified by its river segment and its site within the segment. The river segment is chosen at random from a triangular probability distribution that imposes a preference for segments closer to the dam. Segments with a larger proportion of riffle habitat contain more habitat suitable for spawning and incubation, as measured by the weighted usable area on day t (WUA$_t$; EAEST 1992a). The site within the segment points to a randomly selected entry in a ranked list of potential redd sites, where the total number of suitable sites varies daily in response to changing flows. Each river segment has a maximum number of suitable spawning sites available under optimal flow conditions. The model assigns sequential habitat quality ranks to these sites. On a given date, the number of suitable spawning sites, N_s, may be less than the number

available under optimal flow conditions, causing sites with higher ranks to become unsuitable (Figure 1).

$$N_s = \frac{\text{WUA}_t}{\text{average quality} \times A_{\text{redd}}}, \qquad (1)$$

where average quality is estimated as the midpoint of minimum and maximum suitability index assigned to suitable redd sites in the model, and A_{redd} is average redd area. This approach captures the effects of changing flow on survival of eggs and alevins at both ends of the spectrum (i.e., scouring during high flows and dewatering during low flows).

Survival and development of eggs and alevins.—The model tracks the number of eggs in each redd over time. At the time of spawning, the female deposits her eggs; the number of eggs increases linearly with female length, with intercept a_{fec} and slope b_{fec}. Daily flow-related survival of eggs and alevins is 0 at sites with rank values exceeding the number of suitable sites. Daily survival among suitable sites increases from $S_{\min}$ at the lowest quality site (site with rank N_s) to 1 at the highest quality site (the site with rank 1; Figure 1C). Two other sources of mortality of early life stages are superimposition and temperature-related mortality. When a later spawner in the model selects the same site as a previous spawner with offspring that have not yet emerged, superimposition causes a binomial fraction of older eggs to be killed. Superimposition of previous redds occurs most often when redd densities are high and spawning habitat is scarce. Temperature-related survival is highest at moderate temperatures (8°C for eggs; 5°C for alevins) and drops to zero at extremes temperatures (below 0°C or above 17.2°C; Murray and McPhail 1988).

Incubation and development of eggs takes place over the period required to accumulate a fixed number of degree-days (Murray and McPhail 1988). The duration of the alevin stage is determined by the number of posthatching degree-days required to achieve the alevin stage (Murray and McPhail 1988). For both these life stages, we discount degree-days accrued at temperatures below 5°C by 50%.

Growth and development of fry and smolts.—Alevins emerge from redds at 30–40 mm in length (Murray and McPhail 1988; EBMUD 1992). The model simulates each juvenile chinook salmon as an individual after it emerges from the redd. Each model fry develops into a smolt when it has accumulated sufficient degree-days after emergence and has reached a minimum length (Jager et al. 1997).

On each day, t, the model simulates juvenile growth (weight gain is ΔW in g wet weight) using the bioenergetic model developed by Stewart et al. (1983):

$$W_{t+1} = W_t + \Delta W, \qquad (2)$$

where wet weight gain, ΔW, equals consumption minus energetic costs (egestion, excretion, specific dynamic action, and respiration).

The length, L_{t+1}, of a juvenile chinook salmon increases only when it is in good physiological condition and experiences a positive weight gain:

$$L_{t+1} = \max\left[L_t, \left(\frac{W_t}{\text{al}}\right)^{1/\text{bl}}\right]. \qquad (3)$$

Daily consumption is modeled by calculating ration as a proportion of maximum daily intake, which depends on water temperature and fish weight. The ration obtained by an individual depends on its rank (i.e., the number of larger, competing juveniles in its river segment). Energetic costs depend on temperature and fish weight.

Growth rates vary among individuals because of differences in their locations and sizes. We simulate variability among individual fry growth rates by assigning higher quality feeding stations to larger fish. Each day, fry living in a segment are ranked by size. Feeding stations are reassigned daily, such that the larger fry receive the higher quality stations that provide a higher rate of prey intake (Figure 1C). If there are more fry than stations, those fry lacking a suitable feeding station do not grow. A resident fry may be shifted to a lower- or higher-ranked feeding station as larger or smaller fry immigrate into the segment, as new fry emerge, or as resident fry die or leave.

We assume that a site with quality X ($P_{\min} \leq X \leq P_{\max}$) provides a fish with fraction $P = X$ of its maximum daily feeding ration. The same procedure used to define the number of spawning sites from spawning habitat capacity, WUA_s, is used to define the number of feeding sites based on juvenile habitat capacity, WUA_{juv}. The number of suitable feeding sites is the current WUA_{juv} divided by the average size of feeding "territories" for individuals in the segment (Figure 1A). Feeding stations are allocated to individual fry in inverse order of size (larger individuals first) until the total area of stations reaches WUA_{fry} for the river seg-

ment. Territory size, T_{size} (m^2), is derived for each fry from a relationship with fish length, L (mm) from Grant and Kramer (1990):

$$T_{size} = A_{terr}L^{B_{terr}}, \qquad (4)$$

We assume that each smolt obtains a fixed proportion of maximum ration and does not compete for a feeding station, focusing instead on downstream migration.

Juvenile movement.—The ORCM allows each juvenile to disperse from the river segment of birth to other river segments and, eventually, out of the river. We assume different motivations for movements by fry and smolts. Smolt movements are directed toward migration out of the river, which progresses each day. Fry are motivated by the search for unoccupied rearing habitat with low predation risk and good conditions for growth, which can result in continued occupation of a single site. Simulated fry movement depends on fry density, habitat availability, and river flow and has a tendency to progress downstream. The probability of upstream movement was calibrated so that predicted rate of downstream movement matched the observed rate of downstream movement at different locations in the Tuolumne River. At temperatures above T_{avoid}, model fry tend to move upstream to avoid lethal temperatures (EPA 1971). The probability of upstream movement increases from P_{up} at temperature T_{avoid} to 1.0 at T_{ULT}.

Once a simulated juvenile decides to move, its movement occurs at a rate that depends weakly on river flow in the segment, Q (m^3/s). The model uses a linear relationship between mean travel time (d/km) during downstream movement and Q:

$$\text{travel time} = a_{move} + c_{move} \cdot A_{rat} \cdot Q, \qquad (5)$$

where c_{move} is the flow coefficient fitted to data reported by Berggren and Filardo (1993) for subyearling chinook in the Columbia River and A_{rat} accounts for differences in river size between the Columbia and the Tuolumne rivers. To adapt this relationship for fry in the Tuolumne River, a_{move} was adjusted so that a maximum of 30 d was required for fry to travel 122 km (Berggren and Filardo 1993). For upstream movement of fry, the sign of c_{move} is reversed.

To simulate out-migration, the ORCM assumes that environmental influences indirectly act on migration times by hastening or delaying development into smolts. For smolts, a variety of cues (e.g., flow, change in flow, water temperature, precipitation, turbidity, photoperiod, smolt density, the phase of the moon) can produce pulses of emigration (EBMUD 1992). The ORCM assumes that the necessary cues are present and that out-migration begins when fry become smolts. The daily distance traveled by a given smolt depends on flow (equation 5) and is always in a downstream direction.

Juvenile mortality.—The ORCM simulates mortality resulting from exposure to extreme water temperatures, premature emigration, and predation. Juveniles that remain in a segment with water temperatures above T_{ULT} (Brett 1952) die after 1 d of exposure. The model allows juveniles to avoid high, sublethal temperatures by increasing the likelihood of upstream movement.

Mortality may occur when fry leave the spawning tributary before smolting. Premature emigration is a more significant source of mortality when fry densities exceed the number of feeding stations because slower growth causes individuals to move downstream more frequently.

Fish predators, including smallmouth bass *Micropterus dolomieu*, largemouth bass *M. salmoides*, and Sacramento pikeminnow *Ptychocheilus grandis*, forage on chinook juveniles. Predator densities are specified for each of three river reaches defined by tributary confluences. Within each reach, predator densities are lower in segments with a high proportion of riffle habitat.

The original version of the ORCM simulated individual predator–prey encounters (Jager et al. 1997). This approach was computationally intensive, and sensitivity analysis indicated that ORCM model results were insensitive to the predation-related parameters (Jager et al. 1997). In the analyses here, we used a computationally more efficient option to simulate predation by replacing the individual encounters simulated between juvenile salmon (X = number of prey) and their predators (Y = number of predators) with the type II functional response (Holling 1959) shown in equation (6). We calibrated the probability of capture to obtain the same average level of predation as in the simulations that used individual encounters:

$$\text{Predation risk} = \frac{P_{cap} \cdot XY}{1 + P_{cap} \cdot XY}. \qquad (6)$$

Testing and sensitivity analysis of the ORCM.—Jager et al. (1997) reported on the results of corroboration and sensitivity analysis of the ORCM. We summarize the results here. Corroboration consisted of comparing model predictions of juvenile growth and population size to field data collected
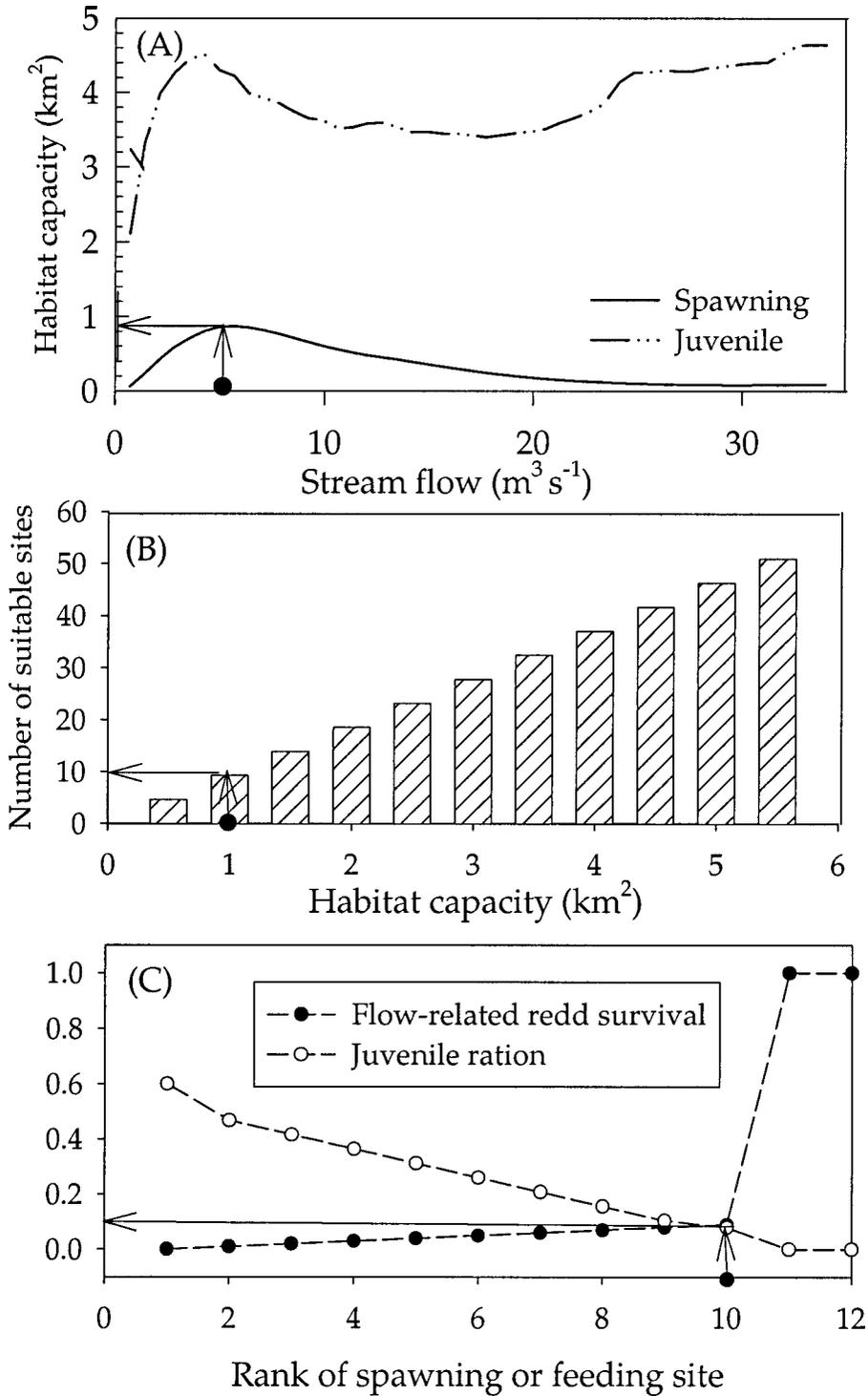
FIGURE 1.—Model representation of habitat effects on survival in redds and juvenile foraging. The model **(A)** represents habitat capacity as a function of river flow; **(B)** specifies a proportional relationship between the number of suitable sites and habitat capacity; and **(C)** specifies an inverse relationship between daily habitat-related survival in redds (ration) and the rank of the redd site (feeding station). To determine survival (ration) at a flow of 5 m³/s, follow the arrows in panel A to calculate habitat capacity from stream flow, then calculate the number of suitable sites

in the Tuolumne River. Jager et al. (1997) compared the length distribution of simulated fry to the observed average, minimum, and maximum sizes from weekly seining catches in the Tuolumne River from January to May 1987. The average predicted and measured juvenile lengths had a maximum difference of 6 mm. Both the model predictions and the field data showed a great deal of variation among individuals. Although the maximum length increased as spring progressed, the minimum length remained constant at around 30 mm, suggesting the continual appearance of newly emerged fry. A second comparison was made between simulated population size at one date and a temporal and spatial snapshot of population size obtained using mark–recapture in early May 1987. An estimated 3,341 ± 935 (95% confidence limits) juvenile chinook salmon inhabited the 360-m stretch of river included in this study. We extrapolated that estimate to 14,920 ± 4,174 for our 1,609-m-long river segment. This extrapolated field estimate was similar to ORCM's prediction of 15,443 juveniles in segment 3 on May 4, 1987. Although model predictions were deemed sufficiently similar to observed values, there is extremely high variability in population size during this period when juveniles are leaving the system. Direct corroboration of the predicted number of out-migrants was not possible because emigrating smolts were not counted.

To evaluate parameter sensitivities of the ORCM, model parameters were varied and used to simulate recruitment under flow and temperature conditions for the 1986–1987 year. Jager et al. (1997) identified a subset of important parameters by excluding those with a strong basis in field data, and therefore low uncertainty, and those redundant in their effects with other parameters. Jager et al. generated 5,000 parameter combinations drawn by Latin-hypercube sampling from truncated Gaussian distributions with specified mean values, a coefficient of variation of 1%, and no correlations among parameters. For each set of parameter values, ORCM predicted a number of responses, from which we have selected the two most relevant to this optimization: number of recruits and the peak date of emigration. The standardized regression coefficient obtained by regression between 5,000 model predictions and the

parameter values that produced them provided an index of sensitivity. The same parameters tended to influence both predictions (Table 2); redd mortality in marginal habitat had the largest effect on the number of recruits, and the final date of upstream migration had the largest effect on the peak date of out-migration. The earliest date of upstream migration by spawners and the upper lethal temperature for juveniles also had important effects on both the number of recruits and the peak date of out-migration.

Seasonal flows that maximize recruitment.—We used simulated annealing (Metropolis et al. 1953) to find a seasonal flow regime that maximized model-predicted salmon recruitment in hydrologic years ranging from wet to dry. Our first objective was to maximize the predicted number of out-migrating smolts (i.e., recruitment). The freshwater portion of the chinook salmon life cycle between upstream migration in the fall and out-migration in the spring was divided into 20 periods, each 2 weeks, characterized by a fixed average daily river flow. The flow assigned to each period is one value in a vector, **Q**, of 20 decision variables manipulated to maximize the simulated number of emigrating smolts. The optimization program found the flow vector that maximized $Z = F(\mathbf{Q})$, where Z is the number of predicted recruits and F denotes ORCM's prediction of the objective function (i.e., recruitment).

This optimization problem is of limited practical interest because it assumes that the annual quantity of river flow is unlimited. Therefore, we also sought optimal flow regimes that maximized Z, subject to a constraint on the total amount of water available annually, Q_{tot}. We repeated the optimization for Q_{tot} values that increased geometrically: 122, 245, 489, and 979 hm³. The threshold values above correspond to the 20th, 45th, 60th, and 78th percentiles of distribution of historical annual flows (e.g., 20% of years had annual flows of 122 hm³ or less and 60% of years had annual flows of 489 hm³ or less). In addition, we assumed that flows within each 2-week period were only constrained by the annual total and not by short-term constraints, such as daily demands by irrigators, that might restrict daily flows. Summer flows between July 8 and September 30 were not considered relevant for fall chinook salmon because most

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from habitat capacity in panel B, and finally calculate the survival (ration) at the site from its rank in panel C. Sites with a rank exceeding the number of suitable sites (e.g., 10) have zero survival (ration).

juveniles emigrate by then and water temperatures are too high for survival of those remaining. Therefore, we set daily average flows for July 8 through September 30 to be 1.42 m^3/s for the purpose of calculating an annual total flow.

All optimizations assumed 5,000 adult spawners, which is roughly the average historical number of returning adults in the Tuolumne River. This assumption is more likely to be a concern in extrapolating to higher abundances that are influenced by density-dependent effects, than for lower abundances (Jager 2000).

Seasonal flows that maximize spawning-time variation.—In addition to the objective of maximizing smolt recruitment for the combined fall and late-fall chinook salmon runs, we also used simulated annealing to find flow regimes that maximized variation in spawning times. We calculated the standard deviation (SD) in the parental spawning dates of recruits for each simulation. The parental spawning time is the integer number of days after October 1 that a given smolt emigrant was spawned by its parents. For the optimization of variation in spawning-run times, we considered two cases: unlimited annual flow and annual flows of 489 hm^3 or less. The optimization program found the vector Q of daily flows, during the 20 2-week time periods, that maximized the objective function, $Zv = Fv(Q)$. For a given flow regime Q, Zv is the standard deviation in spawning run times of out-migrating smolts predicted by the ORCM model, Fv.

Simulated annealing.—We used simulated annealing (SA) as our solution method because it is flexible and has a high probability of finding the optimal or a near-optimal solution for a wide range of optimization problems (Kirkpatrick et al. 1983). Simulated annealing has theoretical assurance of finding a globally optimal solution for problems with finite solution spaces (Geman and Geman 1984). Simulated annealing performed better than other methods in at least one comparison of heuristic algorithms for an optimal reserve design problem (Pressey et al. 1997). However, the solution method that works best for one problem is not guaranteed to work best for another.

Simulated annealing is an ad hoc search procedure that gives good results although we lack a mathematical understanding of its success in finding optimal solutions. Such heuristic algorithms do not guarantee finding a globally optimal solution and have no way of measuring the distance of individual solutions from the global optimum. However, these algorithms have at least two ad-

vantages over optimization methods that have mathematical guarantees: (1) they are feasible for large problems, and (2) they are completely general and can be used with any (ecological) simulation model. This frees the ecological model to describe relationships between organisms, their environment, and potential management policies with whatever degree of complexity is needed. Because the ecological model is separate from the optimization, the model does not have to be simplified or otherwise tailored to meet the assumptions of a particular optimization method.

Simulated annealing has three possible disadvantages. First, SA is not the best choice for optimization problems with a structure that is suitable for nonheuristic methods, such as linear programming. Simulated annealing would not take full advantage of such a problem's structure and would therefore be slower to reach a solution. Second, SA is inherently a sequential algorithm that does not lend itself to parallelization, although finding hybrid parallel algorithms is an active area of research. Third, SA is very slow compared with other heuristic methods.

Metropolis et al. (1953) first introduced SA after observing an optimizing process in physical systems whereby thermodynamic systems minimize free energy during cooling (e.g., annealing of metals). At high temperatures, molecules of a liquid move freely. If the liquid cools slowly, its atoms are able to line themselves up to form a pure crystal. If the liquid is cooled too quickly (quenched), it solidifies in a higher energy state and does not reach the crystal state that has the lowest free energy. In terms of a mathematical optimization problem, the crystal is the global optimum, and the quenched solution is one of many locally optimal solutions. The ability of SA to find global optima derives from its ability to avoid becoming trapped in local minima by permitting "uphill" movements.

We used the SIMANN program developed by Goffe et al. (1994) to optimize each of our two objectives under the ORCM model. As initial conditions, we constructed a flow regime, Q, by setting the daily flows for each period to 4.248 m^3/s. We ensured reasonably large initial step sizes. During the SA search, SIMANN used ORCM to evaluate its objective function (i.e., calculate the number of recruits or the variation in spawning times for each new trial flow regime). As the search progressed, changes in flow depended on V, a vector of step sizes having a value for each of the 20 periods. Step sizes were adjusted as the search

progressed to ensure acceptance of roughly half the trial flow vectors evaluated. In each subsequent step of the search, a new vector of seasonal flows $\mathbf{Q}'$ was chosen by varying the average daily flow during one 2-week period, i. If we let q_i represent the ith element of vector $\mathbf{Q}$, then the updated flow at the next step was

$$q_i' = q_i + (U \cdot v_i), \tag{7}$$

where U represents a uniformly distributed random number between -1 and 1, and v_i is the ith element of $\mathbf{V}$. The updated flow vector was provided to the ORCM model, which then calculated the new value of the objective function, Z'. If Z' was greater than Z, flow regime $\mathbf{Q}'$ was always accepted as a new starting point for the search. If Z' was less than Z, acceptance became less likely as the size of the difference and the duration of the search increased.

In optimizations constrained by the amount of flow available, we constructed an initial flow regime by dividing total annual flow evenly across the 20 periods. We imposed constraints by rejecting solutions if the sum of the 2-week flows and summer flows exceeded the specified upper limit on annual flow.

Model predictions.—We first present the optimal flow regimes for the maximize-recruitment objective for five total annual flow scenarios (four scenarios with different constraints on total annual flow and one scenario with no limit on annual flow). We also compare these SA-derived optimal flow regimes with historical flows. Next, we present the number of ORCM-simulated recruits produced by each of the annual flow scenarios. To understand how increasing the limit on annual flow influenced differences in recruitment among scenarios, we then present average egg-to-fry and fry-to-smolt mortality rates and the duration of successful spawning for each scenario. To explain the differences in mortality rates among annual-flow scenarios, we show river temperatures at two locations in the river for the scenario with no limit and the scenario with annual flows of 122 hm³ or less.

We present the optimization results designed to maximize variation in spawning times and compare these with results from optimizations designed to maximize recruitment for two annual flow scenarios (no limit and ≤489 hm³). We compare predictions for the two objectives, including the optimal flow regimes, the predicted number of recruits, the mean and standard deviation of

spawning times of successful recruits, and the contribution of the late-fall run.

Finally, we present average results for historical flow regimes for water years 1980–1989. These values were predicted by ORCM by assuming 5,000 spawners for each year and historical daily flows and temperatures. Comparisons of results under optimal flow regimes with results under historical flows and temperatures measure how much improvement would have been realized by following an optimal flow regime.

Results

Seasonal Flows that Maximize Recruitment

The SA search reached our stopping criteria after very long periods of computation (on the order of months). Progress for several of the maximize recruitment optimizations was marked by long periods with no improvement, punctuated by intermittent bursts of improvement (Figure 2).

The predicted optimal pattern for allocating seasonal flows among the 20 periods changed as the total amount of annual flow increased (Figure 3A–E). When we simulated dry hydrologic conditions (i.e., a low limit on total annual flow), the optimal flow regime allocated water more evenly across months, but it allocated more water in winter than in fall or spring (Figure 3A). This was the only scenario that did not provide elevated spring flows. As total annual flow increased (Figure 3B–E), the amount of flow allocated during spring months increased dramatically. We observed that high spring flows remained optimal in all hydrologic-year types, except for the very driest. As total annual flow increased, flows provided during winter months did not increase very much (Figure 3A–E). When we simulated an unlimited supply of water, the optimal flow regime allocated high flows during fall months, in addition to the high flows during spring (Figure 3E). As annual flow constraints tightened, we found that elevated fall flows were the first to disappear (Figure 3D) and elevated spring flows were the last to disappear (Figure 3D, A). These results suggest that providing a minimum level of winter flow is critical but that values above this minimum level are not particularly beneficial for maximizing fall chinook salmon recruitment.

Once winter needs are met, additional flows during spring are more beneficial to recruitment. Recruitment increased sharply for total annual flows up to 489 hm³ (Figure 4). Increasing annual flow beyond 489 hm³ led to progressively smaller in-
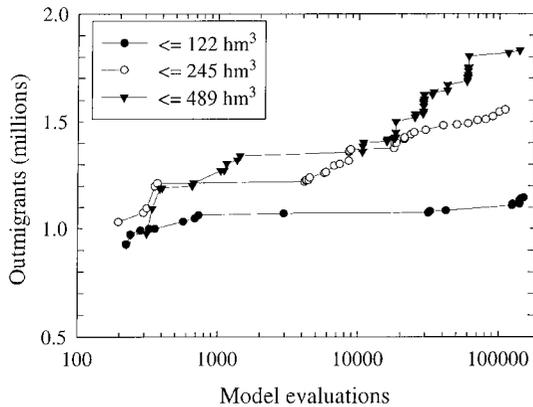
FIGURE 2.—Progress during the course of a simulated annealing search. The maximum value of the objective (i.e., the number of out-migrants) increases with the number of model evaluations of trial flow regimes. Results are shown for three optimizations with different constraints on total annual flow ($\leq$122, $\leq$245, and $\leq$489 hm^3, where 1 hm^3 = $10^6 \cdot$ m^3/year).

creases in the numbers of recruits. This relationship suggests that, even when water is released in an optimal manner for salmon, a trade-off exists in drier years between allocating water to instream flow or diverting water for other purposes.

Overall, as the annual flow increased, egg-to-fry mortality increased and fry-to-smolt mortality decreased (Figure 5A). Temperature was a main factor controlling this apparent tradeoff between egg-to-fry and fry-to-smolt mortality (Figure 5B). The decrease in fry-to-smolt mortality with increasing annual flow was caused by elevated flow during the spring. The flow regimes optimized with higher annual flows provided higher flow during spring. These elevated spring flows carried the cooler water released from the dam farther downstream before it reached equilibrium with the air temperature. As a result, juveniles in simulations with optimal flow regimes with higher annual flows were not exposed to lethal (high) spring temperatures. Forty km below the dam, water temperatures were higher under optimal flow regimes with lower annual flow (e.g., the 40-km, $\leq$122-hm^3 line in Figure 5B) than under optimal flow regimes with higher annual flow (e.g., the 40-km, no-limit line in Figure 5B). Consequently, juvenile mortality was lower in simulations with higher annual flow.

The pattern of increasing egg-to-fry mortality with increasing annual flow was due to elevated flow effects on temperature during the fall. Simulations of optimal flow regimes with higher an-

nual flows were characterized by higher egg-to-fry mortality because higher fall flows produced more extreme downstream temperatures. Egg survival during incubation is optimal at 8°C (Figure 5B); warmer and colder temperatures are stressful (Murray and McPhail 1988). In fall, water released from upstream storage reservoirs is typically warmer than the air (Petts 1984), which exposes redds concentrated below the dam to higher temperatures (e.g., the 16-km, no-limit line in Figure 5B) than those farther downstream (e.g., the 40-km, no-limit line in Figure 5B). In years having elevated fall flows, redds farther downstream experience elevated temperatures because faster-moving water travels farther before reaching equilibrium with colder air temperatures.

Successful spawning occurred over a longer period under flow regimes with higher annual flow (Figure 6). The earliest successful redds were built in early October for all hydrologic years, but the last successful redds (those that produced offspring that survived to emigrate as smolts) were constructed in mid-November in simulations with low annual flow and as late as mid-February in simulations with high annual flow.

Seasonal Flows That Maximize Spawning Time Variation

The flow regime that maximized the variation in run times (MV) differed from the flow regime that maximized recruitment (MR) for both the unlimited annual flow and the flow of 489 hm^3 or less. Under unlimited annual flow, the MV flow regime was characterized by higher flows than the MR flow regime during first 2-week period in October and then for an extended period in spring between February 4 and May 26 (Figure 7A). One interesting feature of the MV flow regime is the large pulse of high flow between February 4 and 17, just before the March 1 peak in spawning for the late-fall run (Figure 7A). The two management objectives also produced different optimal flow regimes when annual flows were constrained to 489 hm^3 or less. Between October 1 and the end of December, except for 2 weeks between October 29 and November 11, the MV flow regime provided higher flows than the MR flow regime. The MV flow regime provided higher flows than the MR flow regime in April, but lower flows in the surrounding months of March and May.

The parents of recruits spawned later and over a longer period when incubated and reared under MV flow regimes than they did under MR flow regimes (Table 3). For annual flows of 489 hm^3 or
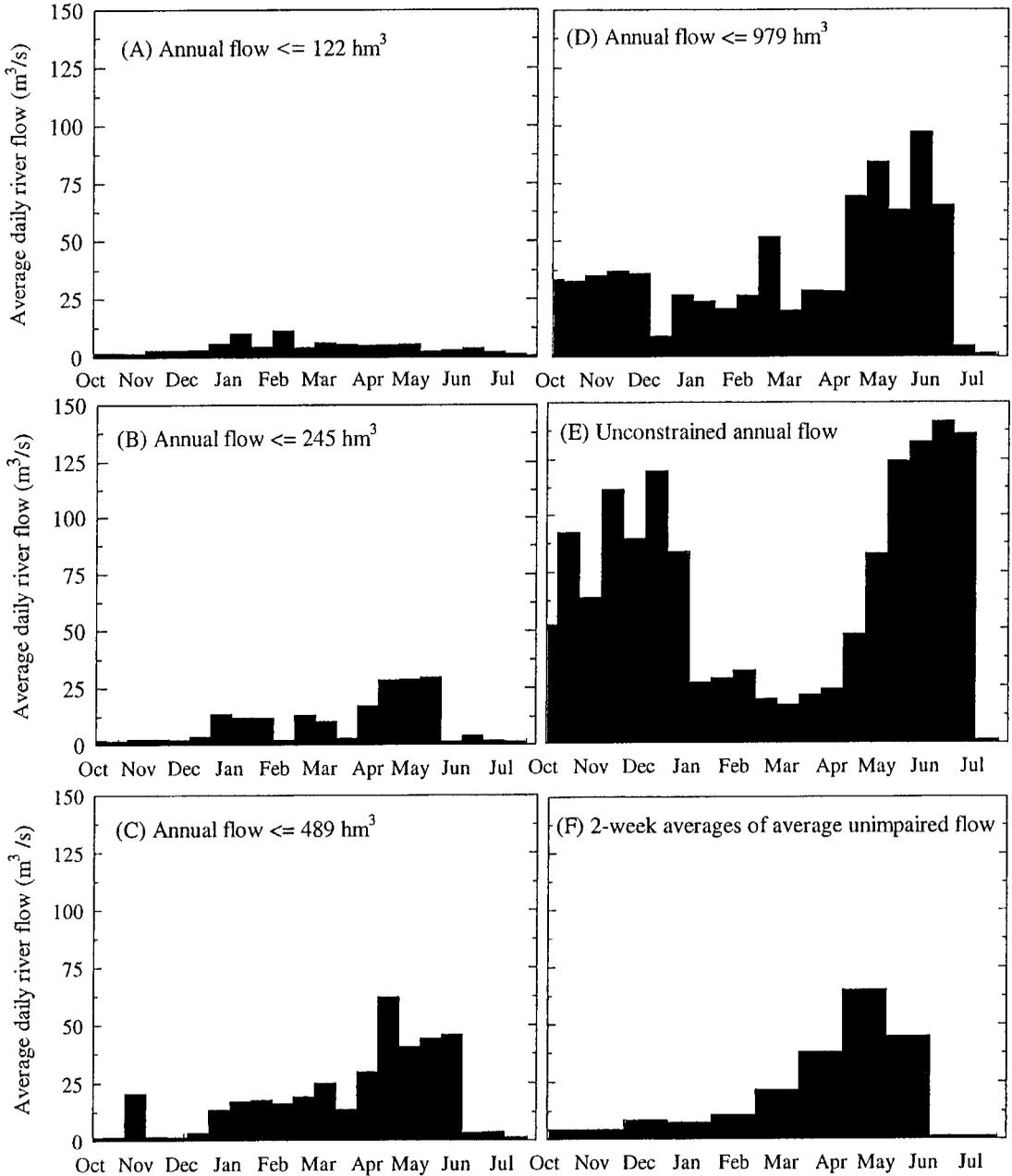
FIGURE 3.—Optimal flow regimes that maximize the simulated recruitment of chinook salmon smolt out-migrants for five scenarios representing a range of constraints on annual river flow: (**A**) ≤ 122 hm^3 (1 hm$^3 = 10^6 \cdot$ m^3/year), (**B**) ≤ 245 hm^3, (**C**) ≤ 489 hm^3, (**D**) ≤ 979 hm^3, and (**E**) an unconstrained scenario. These can be compared with (**F**) the 2-week averages of natural flows above the Don Pedro and LaGrange dams between 1919 and 1992.

less, the mean spawning date for the parents of recruits shifted from October 27 under the MR flow regime to November 8 under the MV flow regime. No progeny of the late-fall run were predicted to survive to recruitment. For unlimited an-

nual flows, the mean spawning date shifted from October 31 under MR flow regime to November 7 under the MV flow regime. For unlimited annual flows, this shift toward later spawning under the MV flow regime corresponded to increased sur-
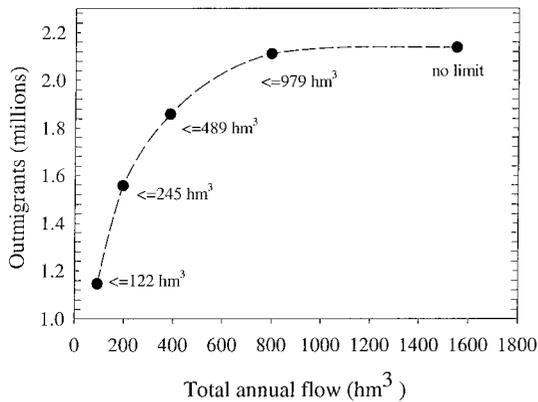
FIGURE 4.—Simulated recruitment of chinook salmon smolt out-migrants under flows designed to maximize recruitment of smolt out-migrants for each of five annual limits on flow.

vival of late-fall progeny (Table 3). Not surprisingly, variation in successful spawning time, as measured by the standard deviation of spawning dates, was greater under the MV flow regimes than under the MR flow regimes for both annual flow scenarios. For annual flows of 489 hm^3 or less, the SD of spawning times of offspring surviving to the recruit stage increased from 11 d under the MR flow regime to 21 d under the MV flow regime. Under unlimited annual flow, the SD of spawning dates increased from 15 d under the MR flow regime to 19 d under the MV flow regime. The same pattern of later mean spawning time and higher standard deviations under MV flow regime was also observed when survival to the fry stage was considered (Table 3).

The number of late-fall-run recruits was highest for the optimal flow regime designed for the MV objective under unlimited annual flows. However, the total number of recruits was substantially smaller in MV flow regimes than in MR flow regimes. For annual flows of 489 hm^3 or less, total recruitment decreased from 1,780,889 under the MR flow regime to 664,300 under the MV flow regime and neither the MR or MV flow regime produced any late-fall-run emigrants. For unlimited annual flow, total recruitment decreased from 1,960,200 under the MR flow regime to 1,369,200 under the MV flow regime. For unlimited annual flow, the MR flow regime produced 3,900 late-fall-run recruits, but the MV flow regime produced 12,500 late-fall-run recruits.

Optimal versus Historical Flow Regimes

According to ORCM predictions, fewer recruits were produced under historical flows (av-

erage = 647,800, SD = 218,095) than under the MR flow regime for annual flows of 489 hm^3 or less (1,780,889) or for unlimited annual flows (1,960,200). The variation in spawning times produced under historical flows (average = 15.0 d, SD = 5.0 d) was also less than the variation in spawning times produced under the MV flow regime for annual flows of 489 hm^3 or less (21.2 d) and the MV flow regime for unlimited annual flow (18.9 d).

Discussion

Seasonal Flows That Maximize Recruitment

The seasonal flow patterns that maximized predicted recruitment changed with the total amount of water available annually. This suggests that management of flows to recover salmon stocks requires different regimes in dry hydrologic years than in wet hydrologic years. Fall flows increased in scenarios exceeding 900 hm^3; a relatively low minimum winter flow was always optimal, and spring flows increased as the availability of water increased. These patterns suggest the following priorities for flow management aimed at increasing recruitment of fall chinook salmon: (1) provide a winter minimum flow in all hydrologic years, (2) obtain additional flows to provide high spring flows in all but the driest years, and (3) provide fall attraction flows in very wet years.

The importance of the high fall and spring flows that characterized optimal seasonal flow regimes developed with unlimited annual flow depends on the management objectives for the river. A flow regime with lower fall flows and more moderate spring flows (e.g., Figure 3C) did almost as well in maximizing overall recruitment as the unlimited optimal flow, which maximized recruitment by supplying much more water (Figure 3E). Although the flow regimes using more water produced more recruits, the incremental benefits of higher annual flows decreased as annual flow increased. The importance of the extra water should be evaluated in terms of whether the increment in recruitment is needed to sustain the population.

An extended period of successful spawning and survival of the late-fall run contributed to higher recruitment in wetter years. Only the two optimal flow regimes designed for the wettest conditions (Figures 3D and 3E) successfully reared late-fall-run smolts (Figure 6). The latest date that an individual out-migrant was spawned shifted by 3 months as constraints on annual flow were relaxed, probably because of the extended block of high
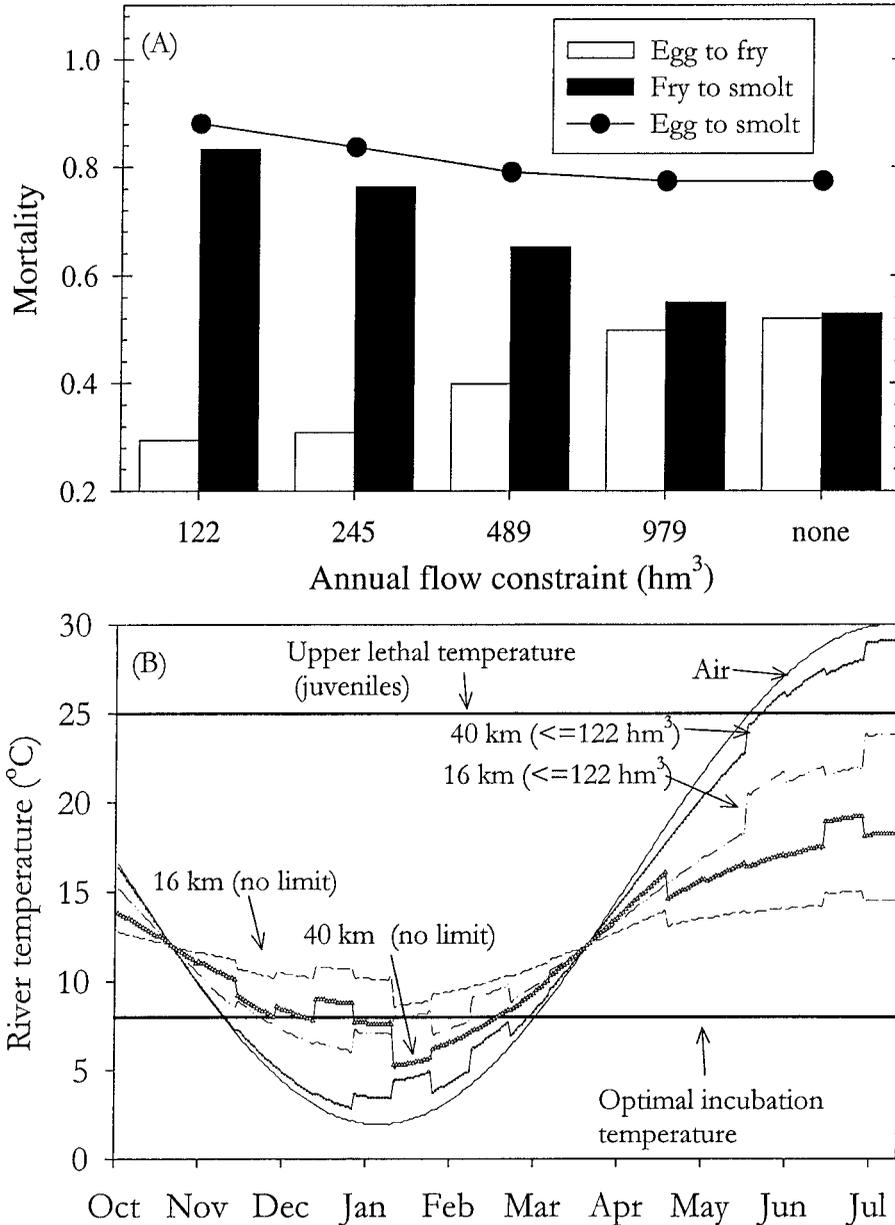
FIGURE 5.—**(A)** Simulated proportion of chinook salmon eggs killed before reaching the fry stage (egg-to-fry mortality) and the proportion of simulated fry killed before migrating as smolts (fry-to-smolt mortality); the line summarizes the total fraction of eggs killed (egg-to-smolt mortality). **(B)** Seasonal changes in river temperatures at two distances below the dam and under two optimal flow regimes: annual flow constrained to be ≤122 hm³ (1 hm³ = 10⁶ · m³/year) and no limit on annual flow. Simulated air temperature, upper lethal temperature for juvenile chinook salmon, and optimal temperature for eggs are shown for reference.

spring flow. Because late-fall adults are not in the system during fall, one might be tempted to conclude that the high fall flows provided in these two wetter regimes could be reduced without affecting

the late-fall run. However, it is possible that high fall flows reduce fall-run survival of eggs and alevins in redds and thus reduce competition with later-emerging and smaller offspring of late-fall
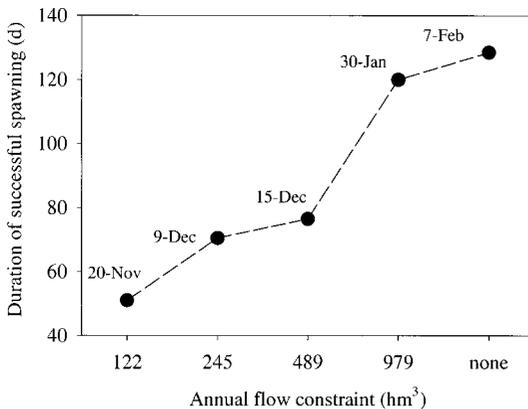
FIGURE 6.—The duration of simulated chinook salmon spawning dates used by parents of successful smolt out-migrants under optimal flow regimes designed to maximize recruitment under different limits on annual flow (1 $hm^3 = 10^6 \cdot m^3$/year). Data labels indicate the final dates of successful spawning.

spawners. The two flow regimes that require the most water may be important to consider if restoring the late-fall run is a management priority.

One approach to designing flow patterns is to assume that we cannot understand all of the complex influences of flow on salmon and that the best policy is, therefore, to mimic the natural flow patterns under which salmon life histories evolved (National Research Council 1996). Our model-based results, like those of Bartholow and Waddle (1995), support the notion that seasonal flows shaped with a peak during spring are best for chinook salmon. The shape of the optimal regime for annual flows of 489 hm^3 or less (Figure 3C) is similar to the shape of the 2-week average natural flow regime (Figure 3F). Natural flows in the San Joaquin basin are dominated by spring snowmelt, with 60% of discharge occurring between April and June (Lettenmaier and Gan 1990). According to Moyle and Yoshiyama (1997), the highest survival of chinook salmon in the San Joaquin River occurs when naturally high flow events coincide with times of smolt emigration.

Seasonal Flows That Maximize Spawning Time Variation

Smith et al. (1995) recommend that conservation efforts focus on genetic differences along the primary axes that permit reproductive isolation and thereby define species and races. In salmon, distinct races are defined by temporal partitioning of spawning times as well as by geographic partitioning (e.g., Utter et al. 1995). In the specific case of the Central Valley, J. L. Nielsen (U.S. Forest Service, personal communication) determined that the two late-fall populations of chinook salmon (Sacramento and San Joaquin) are more similar to each other than to any other spawning run in the basin. However, some stakeholders in the Central Valley question the historical importance of the late-fall run in the San Joaquin and Tuolumne rivers and argue that restoration is not warranted. The results of this study suggest that regulating flows in a manner that would conserve a wider range of run times would produce fewer total recruits than would regulating flows in a manner that maximizes total recruitment.

Optimal versus Historical Flow Regimes

Optimal flow regimes produced considerably more recruits and greater variation in spawning times than did average values during the historical period, especially for the MR objective. The significance of these increases, like all differences predicted here, depends on both the uncertainty of ORCM predictions and the sensitivity of the chinook stocks to flow-related differences in recruitment or variation in spawning time.

Caveats and Future Directions

Designing seasonal flow patterns that provide higher flows when salmon need it most can help to guide conservation and restoration efforts. Three caveats limit the applicability of the results presented here. First, some salmon stocks may be limited by factors other than flow regime. Second, the optimal flow regimes identified here depend on the assumptions about the effects of flow on survival, growth, reproduction, and movement in the ORCM model. There are many possible flow effects that are not explicitly simulated in the model, and predictions about the effects of changes in flow regime should always be verified in the field. Third, the water required by an optimal flow regime might not be available when it is needed.

An important caveat to our results is that flow management alone may not be capable of solving the problems that salmon face. Any conservation effort that fails to focus on restoring access to upstream river habitat will probably fail for certain races, such as spring and winter chinook salmon, that historically relied on these areas for spawning (Healey and Prince 1995). For these stocks, flow management should be seen as a second-tier solution following the first-tier solution of providing passage around dams and removal of other barriers to migration. In general, the first step should be
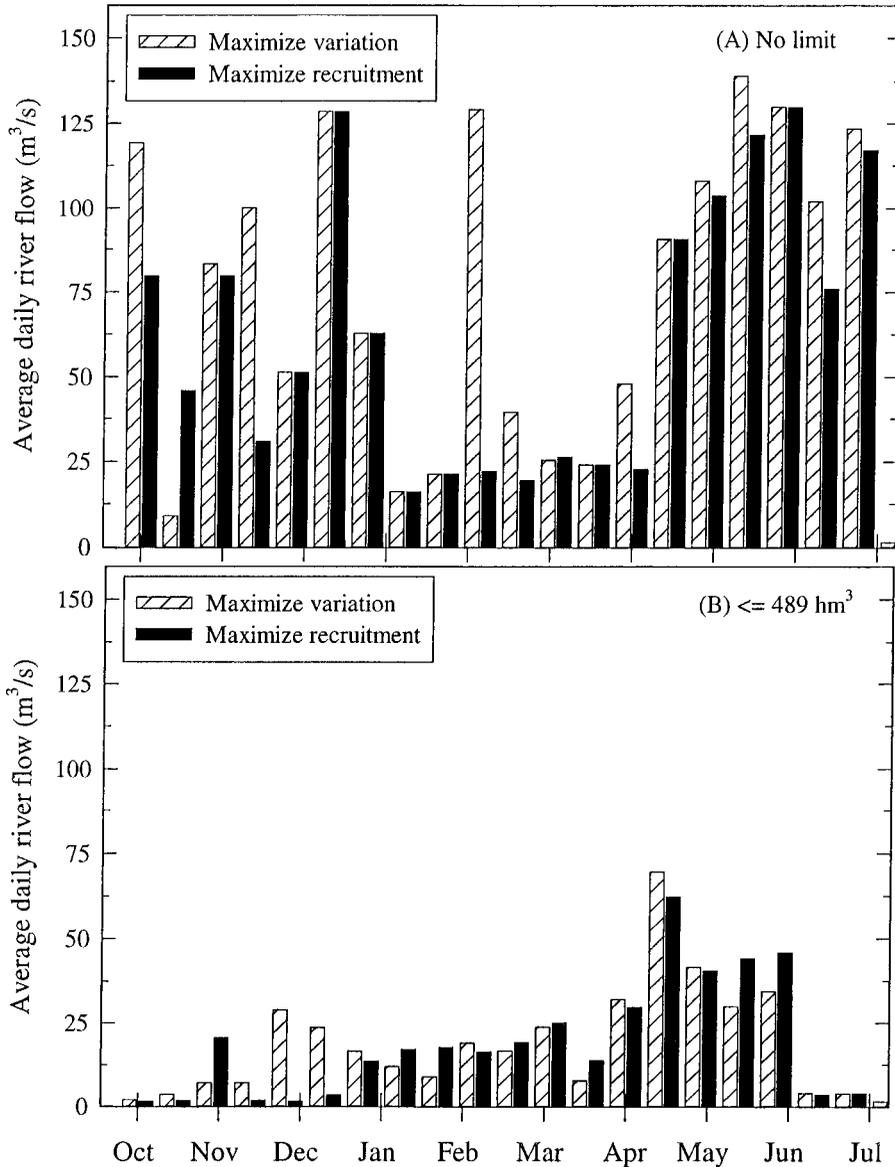
FIGURE 7.—A comparison of optimal flow regimes designed to maximize recruitment (solid bars) and variation in spawning times (hatched bars). Results are shown for **(A)** unlimited annual flow and **(B)** annual flow ≤ 489 hm^3 $(1 \text{ hm}^3 = 10^6 \cdot \text{m}^3/\text{year})$.

to identify improvements that are most likely to effect recovery, which might not always emphasize providing a flow regime that is beneficial for salmon.

Although the ORCM goes farther than other population models for salmon in its attempt to represent mechanistic linkages between salmon biology and flow, it has its limitations. Despite its complexity, ORCM selectively articulates key ecological relationships affected by flow. There are

many numerous indirect effects of flow that ORCM does not represent (e.g., benthic invertebrate production, effects of predation risk on foraging time, debris flow, gravel redistribution).

The ORCM focuses on the scale of daily changes in flow and does not represent the effects of longer- or shorter-term variations in flow. At one extreme, long-term drought cycles require a full life-stage model that incorporates the ocean phase and simulations spanning decades. At the other

TABLE 3.—Model predictions for flow regimes designed to maximize the variation in chinook salmon spawning times and for flow regimes designed to maximize recruitment in the Tuolumne River, California. We report total recruitment, late-fall-run recruitment, and spawning-date statistics (average and SD) for parents of offspring that survived to the fry stage and for those whose offspring survived to leave the river as smolts. The results for optimal flow regimes restricted to an annual flow of ≤ 489 km^3 (1 hm^3 = $10^6 \cdot$m^3/year) and optimal flow regimes with unlimited annual flow are compared.

Model predictions	Annual flow ≤ 489 hm^3		Unlimited annual flow	
	Maximize recruitment	Maximize variation	Maximize recruitment	Maximize variation
Total number of emigrants	1,780,889	664,300	1,960,200	1,369,600
Late-fall-run emigrants	0	0	3,900	12,500
Average parental spawning date for fry	Nov 9	Nov 18	Nov 11	Nov 17
SD of spawning dates (d) for survivors to fry stage	21.0	30.5	25.6	29.3
Average parental spawn date for emigrants	Oct 27	Nov 8	Oct 31	Nov 7
SD of spawning dates (d) for survivors to emigration	11.1	21.2	15.4	18.9

extreme, with its daily time-step and 2-week optimization intervals, ORCM did not represent the effects of within-day variation in flow. Natural variation in flow regimes shape the disturbance regime in rivers in much the same way that fire shapes grassland ecosystems (Reeves et al. 1995; Poff et al. 1997). Unwin (1997) found that flow variability during spring out-migration showed the strongest and most consistent positive relationship with fry-to-adult survival of chinook salmon. Experimental pulse flows in the Stanislaus River, California, stimulated out-migrations in the short-term (2 d) but little additional benefit resulted from prolonged high flows (Cramer 1997). These results suggest that the ability of high flows to speed emigration may be less important than the short-term benefits provided by pulse flows. Pulse flows may serve as a behavioral cue to synchronize downstream movement, allowing smolts to overwhelm potential predators. Increased turbidity associated with pulse flows is also a short-term event (one that may not occur in regulated rivers). Because our study used 2-week periods, our optimal flow regimes are less variable than natural flow regimes. Also, the ORCM does not at present include the fine distinctions between short-term and longer-term benefits of flow. A next step in our analysis would be to introduce processes that operate at different time scales in the ORCM model and to evaluate the effects of including realistic short- and long-term variability in flow without substantially increasing the number of decision variables.

Limitations in flow availability can restrict the ability to manage flows according to an optimal flow regime. Droughts, combined with limits on storage capacity and competing demands for water, can make it difficult to follow a specified regime. Such competing water needs could be incorporated as constraints into an optimization analysis like ours. Likewise, economic considerations could be added in future to address both the benefits to fish and costs to society.

The optimization approach described here could be used to design instream flows for conservation objectives involving different rivers and salmon runs as well as for other species. Applications to chinook salmon that spawn in different rivers would merely require changing values for site-specific model parameters. Applications to different salmon species might require structural changes to ORCM to reflect a more complex life history. For example, chinook salmon show a much wider variation in life history patterns in rivers farther north than in the California river used in our study, including runs that remain in the river much longer and exit as yearlings. Although the specific quantitative results presented here are specific to a particular stock, the qualitative recommendations presented for designing flows that benefit salmon in different hydrologic years and in situations with multiple runs should have wider application.

In this study, we compared the optimal flow regimes designed to independently address two different conservation objectives. It is also possible for optimization to address multiple objectives. With many more optimizations, one could construct a Pareto frontier of flow regimes that assign weights to the two objectives that we considered (maximizing the recruitment and maximizing variation in the spawning times). In our analysis, managing flows to conserve a variety of runs required compromising overall recruitment. This implies that the relative weight assigned to the two objectives should depend on the conservation status of the runs. If the larger runs are stable or increasing, then diversity-enhancing flows may be favored,

whereas a dominant run that is declining may require sacrificing smaller runs. If the temporal metapopulation structure of the runs resembles a core satellite structure, with one dominant run that recolonizes the others by temporal straying, then there is a danger that managing flows for run-time diversity would create temporal sinks, analogous to the spatial sinks described by Pulliam (1988). In contrast, managing for run-time diversity would be important for classic metapopulations that depend on recolonization by temporal strays for persistence.

Acknowledgments

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