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Journal

San Francisco Estuary and Watershed Science, 22(4)

Authors

Wang, Xiaochun

Perry, Russell W.

Pope, Adam C.

et al.

Publication Date

2024

DOI

10.15447/sfews.2024v22iss4art4

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RESEARCH

Individual-Based Ecological Particle-Tracking Model (ECO-PTM) for Simulating Juvenile Chinook Salmon Migration and Survival Through the Sacramento-San Joaquin Delta

Xiaochun Wang^{*1}, Russell W. Perry², Adam C. Pope², Doug Jackson³, and Dalton Hance²

DATA ACCESSIBILITY

Data and resources for this study are available from <https://data.cnra.ca.gov/dataset/eco-ptm-paper>. Appendix A (Behavioral Parameter Estimation and Goodness-of-fit) and Appendix B (Estimating Parameters of the XT Model) contain the descriptions of the likelihood function used to fit ECO-PTM models and the XT model implemented in ECO-PTM.

ABSTRACT

Recovery of endangered salmon species in the Central Valley of California amidst prolonged drought and climate change necessitates innovative water-management actions that balance species recovery and California's water demands. We describe an individual-based ecological particle-tracking model (ECO-PTM)

that can be used to assess the efficacy of proposed actions. Based on a "random walk" theory, the model tracks the travel time, routing, and survival of individual particles in a flow field simulated by the Delta Simulation Model 2 hydrodynamic module (DSM2 HYDRO). The random walk particles are parameterized to have fish-like swimming behaviors, including upstream and downstream swimming, probabilistic holding behaviors, and stochastic swimming velocities. Particle routing at key junctions is based on well-established statistical models, and route-specific survival is calculated using the XT mean free-path length model. Behavioral parameters were estimated by fitting several competing models to a multi-year dataset of travel times from acoustic-tagged juvenile salmon. The model's baseline simulations under historical flow conditions from 1991 to 2016 successfully replicated essential relationships between salmon outmigration survival and hydrodynamic conditions, consistent with previous studies and the STARS (Survival Travel Time and Routing Simulation) statistical simulation model. Simulation results for management scenarios revealed multi-faceted influences on fish survival, including Delta flow, flow at key junctions, route alterations, seasons, and water-availability characteristics. Importantly, these results highlight ECO-PTM's potential to predict improvements in fish survival from proposed actions, serving as a foundation

SFEWS Volume 22 | Issue 4 | Article 4

<https://doi.org/10.15447/sfew.2024v22iss4art4>

* Corresponding author: xiaochun.wang@water.ca.gov

1 California Department of Water Resources
Sacramento, CA 95814 USA

2 US Geological Survey
Western Fisheries Research Center
Cook, WA 98605 USA

3 QEDA Consulting, LLC
Seattle, WA 98105 USA

for informed future research, decision-making, and effective management strategies to enhance the survival prospects of outmigrating salmonids within the Sacramento–San Joaquin Delta ecosystem.

KEY WORDS

DSM2, ecological modeling, Particle Tracking Model, individual-based model, Chinook Salmon, Sacramento River, Sacramento–San Joaquin Delta, hydrodynamic model, emigration, flow, salmon survival, travel time, routing simulation, STARS.

INTRODUCTION

The Central Valley of California, USA, harbors the southernmost native Chinook Salmon (*Oncorhynchus tshawytscha*) populations in the world. Several of these populations have been federally listed as threatened and endangered as a result of climate change, habitat degradation, fishing, introduction of invasive species, and diversion of water for domestic and agricultural use (Yoshiyama 1998; Williams 2006; Johnson and Lindley 2016). Of particular concern is how Chinook Salmon are affected by the Central Valley Project (CVP) and State Water Project (SWP), which form one of the world's largest water-delivery systems that supplies water to over 25 million people and supports the nation's largest agricultural economy (Healey et al. 2016). Thus, restoring endangered salmon populations in the Central Valley presents a formidable challenge that requires careful consideration of both species recovery efforts and California's water demands.

Given these circumstances, resource managers are exploring and evaluating various scenarios to modify the operation and infrastructure of CVP and SWP in the Sacramento–San Joaquin River Delta (hereafter, the Delta). The Delta, sitting squarely at the center of California's water-delivery system, is a complex network of natural and man-made channels that receives Sacramento River water from the north and San Joaquin River water from the south, and which empties into San Francisco Bay to the west (Figure 1). The CVP and SWP use the Delta as a conduit to deliver

water from the Sacramento River in the north, to pumping stations in the south, where the CVP and SWP divert water into canals for distribution to central and southern California.

During their migration to the ocean, juvenile salmon from both the Sacramento and San Joaquin rivers must negotiate the complex channel network of the Delta. Over the past 2 decades, much has been learned about how juvenile salmon migrate through the Delta (Perry et al. 2016). As juvenile salmon migrate downstream, they distribute among the Delta's complex channel network, and their survival differs among migration routes, as a result of each route's unique biotic and abiotic characteristics such as water temperature, food availability, and predator populations. For example, Perry et al. (2010) found that fish diverted from the Sacramento River into Georgiana Slough and the southern Delta survived at significantly lower probabilities than all other migration routes. This finding has been confirmed for multiple populations of Sacramento River Chinook Salmon (Perry et al. 2018; Hance et al. 2022). Because of survival differences among migration routes, the proportion of the population using each route is a significant factor that determines the overall outmigration survival through the Delta. As such, a number of studies have focused on how river flow, tidal forcing, and water diversion-gate operations influence the routing of juvenile salmon at key river junctions in the Delta (Perry et al. 2015; Hance et al. 2020; Romine et al. 2021). Research has also been conducted to determine the effectiveness of a non-physical barrier or a floating fish-guidance structure to influence the routing of outmigrating juvenile salmon (CDWR 2015, 2016). Other research has investigated Delta-wide relationships between river flow and the travel-time, routing, and survival of migrating juvenile salmon (Perry et al. 2018; Hance et al. 2022).

The statistical models applied in analyses of field studies have limitations in addressing management actions aimed at altering flows to protect and restore salmon populations. Even though statistical models may be used for

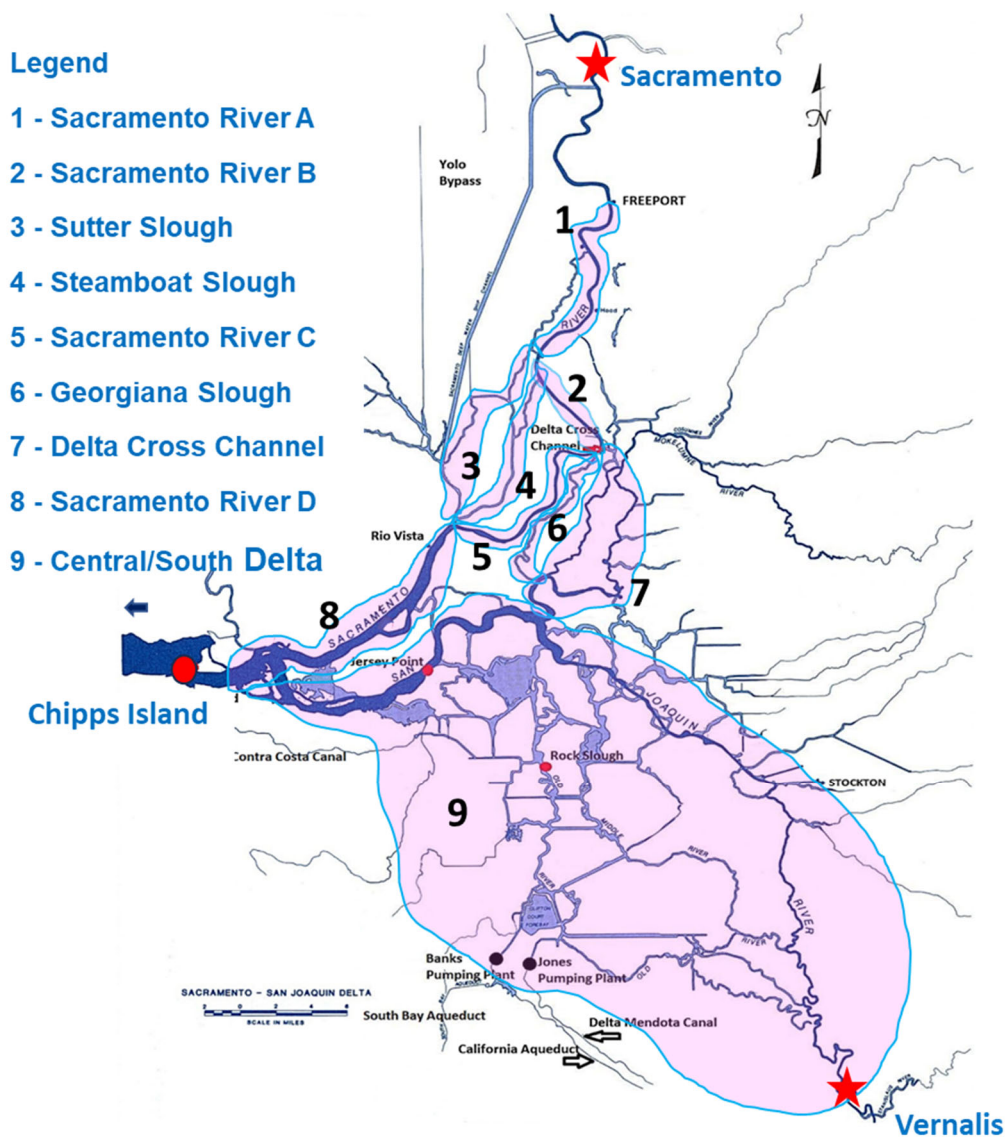


Figure 1 Map of the Sacramento–San Joaquin River Delta showing the location of nine calibration/validation/survival calculation reaches. The start and end points of the reaches coincide with the locations of acoustic telemetry stations: regions 1 and 2 represent riverine channel groups, regions 8 and 9 are tidal channel groups, and regions 3 through 7 are transitional channel groups. The red stars at the cities of Sacramento and Vernalis represent the northern and southern boundaries of the Delta, respectively. The red circle at Chipps Island denotes the Delta exit.

prediction, the inferences from these regression-based models are largely restricted to the range of covariates and historical observations used to fit the regression model. These models are generally not individual-based and operate on relatively large temporal and spatial scales, thus providing only limited insights into fine-scale hydrodynamics, fish migration, and survival in the Delta. In contrast, mechanistic individual-based models that link individual responses to

environmental stimuli may enable more robust inferences to novel structural or environmental conditions. Such mechanistic biological models are typically based on a physical model (e.g., a hydrodynamic model), which simulates these environmental stimuli using well-established physical processes and principles. For example, statistical models that relate survival to river discharge will be inaccurate under future climate because sea level rise will modify the relationship

between river discharge and tidal dynamics that affect water velocity in the Delta. In contrast, a mechanistic model in which swimming behavior interacts with water velocity will mechanistically capture the effects of sea level rise on fish migration and survival as a result of the modeled effects of sea level rise on water velocity.

To complement these statistical models and provide water-resources managers with a more detailed quantitative assessment tool to explore and evaluate management actions, we have developed an individual-based ecological particle tracking model (ECO-PTM), which includes a juvenile salmon module. To evaluate the likely effects of different management actions on the travel time, routing, and survival of juvenile salmon, the salmon module tracks the random walks of individual particles parameterized to have fish-like swimming behaviors through a simulated flow-field. It is an integral part of Delta Simulation Model 2 (DSM2), which consists of three models: HYDRO, a hydrodynamics model; QUAL, a water-quality model; and ECO-PTM, a particle-tracking model. By utilizing detailed hydrodynamic information from HYDRO, ECO-PTM is able to track the movement of three types of particles: (1) neutrally buoyant particles, (2) position-oriented particles (commonly used to evaluate the effects on Longfin Smelt *Spirinchus thaleichthys* larvae), and (3) juvenile salmon. This paper specifically focuses on the ECO-PTM's juvenile salmon module, detailing its behavior parameter calibration and validation, its routing and survival model implementations, and its applications in evaluating water-resources management actions.

MATERIALS AND METHODS

Study Area and Model Grid

The study area for the ECO-PTM model includes the entire Delta. In the model, the complex network of channels, sloughs, islands, and wetlands of the Delta is represented by the DSM2 computational grid, which captures the interactions between the Delta hydrodynamics and particle movement. The model grid extends from the Sacramento River at the city

of Sacramento in the north to the San Joaquin River near Vernalis in the south (Figures 1 and 2). The model also includes the tributaries of the Sacramento River on the east side, such as the Mokelumne and Cosumnes rivers. The tidal boundary that denotes the downstream end of the DSM2 grid is at the Benicia–Martinez Bridge on the Carquinez Strait. In addition to its spatial coverage, the DSM2 grid accounts for diversions from the Delta system for agricultural, urban, and environmental uses, as well as reservoirs, pumping plants, and other water-storage and operational facilities of CVP and SWP.

Original Particle-Tracking Model

The ECO-PTM juvenile salmon module is based on the original particle-tracking model (PTM) released in 1998 (Smith 1998) and later modified by Miller (2002, 2003), who added a position-oriented particle enhancement that restricts particles to a user-defined layer in the water column, preventing vertical movement beyond that layer.

The original PTM tracks only neutrally buoyant particles. The particle's random walk movement in water bodies is described by the stochastic differential equation of Brownian motion:

$$\dot{X} = \underbrace{f(X)}_{\text{drift, advection term}} + \underbrace{\sqrt{2D} \xi(t)}_{\text{random noise, diffusion term}} \quad \text{Eq 1}$$

Where X is distance of a particle movement; \dot{X} is the particle velocity; $f(X)$ represents the advective or drift component; D is the diffusion coefficient; and $\xi(t)$ represents Gaussian white noise, or the diffusion component of the particle movement that describes the strength of turbulent diffusion in space. Using the Euler Scheme, the numeric form of the Equation 1 update-rule can be written:

$$\hat{X}_{t+\Delta t} = \hat{X}_t + f(\hat{X}_t)\Delta t + \sqrt{2D\Delta t}N_t \quad \text{Eq 2}$$

Where \hat{X}_t and $\hat{X}_{t+\Delta t}$ is the numeric form of the distance at the time t and Δt , respectively. N_t is a random number drawn from a normal distribution $N_t \sim N(0,1)$.

The hydrodynamic information the particle tracking model requires is an output from DSM2 HYDRO. The hydrodynamic model represents the Delta waterways as a series of channels connected by nodes (Figure 2), and it simulates a streamwise one-dimensional (1-D) flow field in the Delta with a user-defined time-step (typically set to 15 minutes). To track particles in a three-dimensional (3-D) space (streamwise, cross-stream, and vertical), the PTM constructs a quasi-3-D flow field using the simulated 1-D flow field

and incorporating two velocity profiles: $F_2(\hat{x}_2)$ and $F_3(\hat{x}_3)$. The cross-stream profile $F_2(\hat{x}_2)$ is described by a quartic function; the vertical velocity profile $F_3(\hat{x}_3)$ is approximated using a von Kármán logarithmic function. More detailed descriptions of the construction of the quasi-3-D flow field can be found in the literature that describes the original PTM (Bogle 1997; Smith 1998; Wilbur 2000; Miller 2002). The estimation of cross-stream and vertical diffusion coefficients (D_2 , D_3) follows the methodology outlined by Fischer et al. (1979).

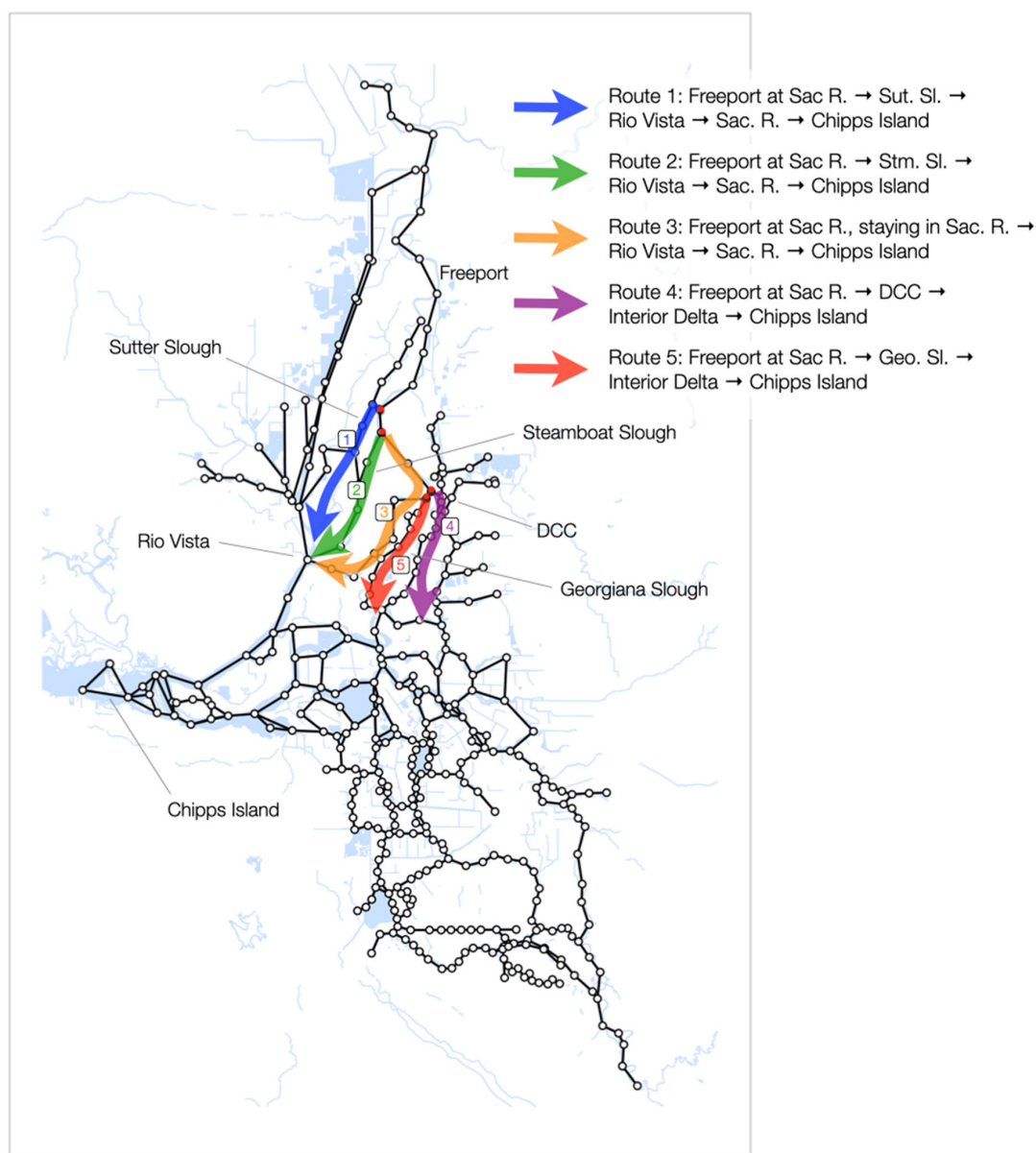


Figure 2 DSM2 computational grid and juvenile salmonid migration routes from Freeport to Chipps Island. Sac R. = Sacramento River, Sut. Sl. = Sutter Slough, Stm. Sl. = Steamboat Slough, Geo. Sl. = Georgiana Slough, DCC = Delta Cross Channel.

Since the dominant hydrodynamic process in the channels is advection in the streamwise direction, we can simplify Equation 2 by neglecting the diffusion component in the streamwise direction, and the advection components in the cross-stream and vertical directions. By considering the particle streamwise drift term $f_1(\hat{X}_t)$ as a function of the cross-sectional averaged velocity $u_t(\hat{x}_{1,t})$, cross-stream velocity profile $F_2(\hat{x}_{2,t})$, and vertical velocity profile $F_3(\hat{x}_{3,t})$, we can rewrite Equation 2 for the streamwise, cross-stream and vertical directions:

$$\begin{aligned}\hat{x}_{1,t+\Delta t} &= \hat{x}_{1,t} + f_1(u_t(\hat{x}_{1,t}), F_2(\hat{x}_{2,t}), F_3(\hat{x}_{3,t}))\Delta t \\ \hat{x}_{2,t+\Delta t} &= \hat{x}_{2,t} + \sqrt{2D_{2,t}\Delta t}N_t \\ \hat{x}_{3,t+\Delta t} &= \hat{x}_{3,t} + \sqrt{2D_{3,t}\Delta t}N_t\end{aligned}\quad \text{Eq 3}$$

Where $\hat{x}_{1,t}$, $\hat{x}_{2,t}$, and $\hat{x}_{3,t}$ represent distances in the streamwise, cross-stream, and vertical directions, respectively.

Using Equation 3 and a flow-split routing model, the original PTM effectively tracks neutrally buoyant particle movement in the Delta with reasonable accuracy. However, the PTM is not suitable for tracking active swimmers, such as juvenile salmon. To accurately track juvenile salmon particles, swimming behaviors need to be attached to the neutrally buoyant particles.

ECO-PTM Juvenile Salmon Module

Swimming Behaviors

To investigate how Delta flows affect juvenile salmon movements, the juvenile salmon module allows user-specified input parameters that impart swimming behaviors on the PTM's neutrally buoyant particles. The module implements upstream or downstream swimming, probabilistic holding behaviors, and stochastic swimming velocity for each simulated particle at each 15-minute time-step. Since particle movement in the Delta is primarily dominated by drafting in the streamwise direction, the behavioral parameters that affect particle movement in the module are applied to the particle streamwise drift term $f_1(\hat{X}_t)$ (as described in Equation 3) and defined as follows:

μ_v : mean streamwise swimming velocity among all particles,

σ_p : standard deviation of streamwise swimming velocity among all particles,

σ_t : standard deviation of time-step-specific streamwise velocity for each particle,

p_{diel} : proportion of particles that exhibit diel holding by maintaining position during the day between sunrise and sunset,

f_{ST} : streamwise velocity threshold below which particles maintain position to simulate selective tidal stream transport, a holding behavior during a flood tidal phase,

p_{assess} : the probability that a particle will assess its swimming direction at each time-step, and

p_{dir} : the probability that swimming direction will be landward (away from the ocean), given that a particle assesses swimming direction in a time-step.

To simulate juvenile salmon movement, the juvenile salmon module allows the user to specify different values of the swimming-behavior parameters in groups of channels that comprise distinct regions of the Delta. Given these parameter values, an individual particle's movement is simulated as follows. As each individual enters a channel group, a single draw from a normal distribution with mean μ_v and variance σ_p^2 is used to determine the individual's average swimming speed throughout the channel group. Next, at each time-step, the realized swimming velocity for each individual particle is drawn from a normal distribution using this individual average swimming speed and a second variance parameter σ_t^2 . For holding behaviors, at each time-step a determination is made whether the individual will move or hold. All particles move at night, but during the day individuals are randomly assigned to hold at each time-step with probability p_{diel} , which is also allowed to vary among channel groups. Night and day

are delineated through user-specified sunrise and sunset time. For the purpose of ECO-PTM calibration, we used time of civil twilight near the city of Sacramento. Additionally, all particles hold when the water velocity at their location is less than f_{ST} . Holding particles remain stationary until the next time-step.

Particles that move are next assigned a swimming direction (i.e., with or against seaward flow as defined by the DSM2 grid). At each 15-minute time-step, we perform a Bernoulli draw with probability p_{assess} to determine whether to draw a new swimming direction. We set $p_{assess} = 0.01$ so that the expected time between swimming direction assessments was on average 25 hours, or approximately two tidal cycles. If swimming direction is assessed, we then perform a Bernoulli draw with probability p_{dir} to determine if swimming direction is seaward (0) or landward (1). The swimming direction parameter p_{dir} is determined by the logistic function:

$$p_{dir} = \frac{ae^{br+c}}{1 + e^{br+c}}$$

where a , b , and c are parameters that govern the shape of the logistic curve and r represents the log of the velocity signal-to-noise ratio:

$$r = \log\left(\frac{\mu_q}{\sigma_q}\right)$$

where μ_q is tidally averaged flow, and σ_q is tidal strength, defined as the standard deviation from the averaged flow over the preceding two tidal cycles in the simulated particle's immediate location. Individuals then move in the prescribed direction for the duration of that time-step with a net velocity equal to the sum of the local water velocity and the realized swimming velocity. Both the maximum (a) and slope (b) of the logistic function used to calculate swimming direction were fixed, allowing only the intercept (c) to be estimated. We set $a=1$ and $b=-0.55$ so that the probability of swimming direction flipping was constrained between 0 and 1 and could gradually decrease over the range of observed log ratio of tidally averaged flow to tidal strength in the Delta.

We assigned each channel in the DSM2 grid to one of three groups to align with the prevailing tidal regime at that channel's location: (1) riverine channels are located in regions of the Delta where flows are nearly always uni-directional (seaward), (2) tidal channels are located in regions of the Delta where tidal cycles nearly always cause upstream reversals of river flows, and (3) transitional channels are located in regions where the varying strength of freshwater inputs result in river flows that sometimes reverse with flood tides and other times are uni-directional. Channel group boundaries coincided with the locations of acoustic telemetry stations that were used to collect the travel time data to which the model was calibrated (Figure 1). Additionally, we allowed the μ_v and p_{diel} parameters to vary with the tidal region so that each had three distinct values. All other parameters were constrained to a single Delta-wide value.

To estimate swimming-behavior parameters, we fit four competing models to a multi-year dataset of acoustic-tagged juvenile salmonid travel times. The travel time data originates from 2,170 hatchery-raised late-fall Chinook Salmon tagged and released from December 2006 to January 2011 and is identical to the dataset in Perry et al. (2018). The four models fit represent all possible combinations of the selective tidal stream transport and direction assessment behaviors set to either active (i.e., "turned on") or inactive ("turned off"). Each model was fit using simulated maximum likelihood, which allows observed and simulated data to be compared through a likelihood-based framework (Hajivassiliou and Ruud 1994). We chose a joint likelihood with multinomial components for binned travel times, route selection at key river junctions, and a binomial component for whether fish arrived during daytime or nighttime (See Appendix A for details).

We used a particle-swarm optimization routine to identify the optimal set of ECO-PTM behavioral-input parameter values so that simulated particle travel times can closely align with the observed travel times of acoustic-tagged juvenile salmon. Particle-swarm optimization is an optimization

algorithm particularly well-suited to stochastic objective functions (Pedersen and Chipperfield 2010), which simultaneously evaluates multiple solutions, with each solution's gradient affected by other solutions (the “swarm”; Kennedy and Eberhart 1995). Here, we present only the best fitting model, which had active direction assessment and inactive selective tidal stream transport. Thus, in the finalized ECO-PTM juvenile salmon module, the f_{ST} parameter is fixed at a large negative value so that particles do not hold under any tidal conditions. (See “Data Accessibility” for a brief description and link to Appendix A and Figure A1.) The calibrated swimming behavior parameters are shown in Table 1.

Table 1 ECO-PTM behavioral parameter estimates for the best-fit model. All swimming velocity parameters are in ft s^{-1} , diel holding is on a probability scale, and the logistic intercept c is unitless. Negative values indicate swimming velocities directed in the perceived upstream direction.

Tidal region	μ_v	σ_p	σ_t	p_{diel}	c
Riverine	-0.135	0.530	0.034	0.503	1.04
Transitional	-0.276	0.530	0.034	0.725	1.04
Tidal	-0.608	0.530	0.034	0.601	1.04

Migration Routing

At river junctions where a main channel divides into two or more tributary channels, the default setting of the PTM is to route particles directly proportional to flow that enters each channel. However, numerous studies have shown that migrating juvenile salmon may not enter river channels in direct proportion to flow (Perry et al. 2014, 2015; Cavallo et al. 2015; Hance et al. 2020; Romine et al. 2021;). In particular, detailed studies have been conducted where the Delta Cross Channel (DCC), Sutter Slough, Steamboat Slough, and Georgiana Slough diverge from the Sacramento River, and we used relationships developed in these studies to parameterize routing at key channel junctions (Figure 1). Reducing entrainment of migrating juvenile salmon into the interior and southern Delta can occur through closure of the Delta

Cross Channel gate, fish-exclusion devices at Georgiana Slough, or routing into Sutter and Steamboat sloughs. Routing at these locations is particularly important to salmon survival because entrainment into the DCC and Georgiana Slough diverts fish toward the southern Delta and pumping stations, where survival is lower than the Sacramento River and Sutter and Steamboat slough routes (Perry et al. 2010, 2018).

Although several studies estimate routing at daily to weekly time-scales, we relied on findings from analyses that estimate how routing varies in response to tidally varying flows at the 15-minute time-scale, which matches the DSM2's time-step. For Sutter and Steamboat sloughs, we used the model of Romine et al. (2021), which fit multinomial regression models to acoustic telemetry data of juvenile salmon to estimate how channel-specific flow, rate of change in flow, and proportion of flow affected the probability of fish entering each channel. Thus, we used the parameter estimates for each variable, as reported in Romine et al. (2021), to predict the probability of a particle entering each channel, given the flow conditions at the time the particle entered the junction.

Similar to the approach taken at Sutter and Steamboat sloughs, we used two models to simulate routing at the junctions of the Sacramento River, the DCC, and Georgiana Slough under differing flow conditions. First, Perry et al. (2015) fit a three-route multinomial model to telemetry data under tidally reversing flows at total inflows $< 14,000 \text{ ft}^3 \text{ s}^{-1}$. This model uses flow into each channel, the rate of change in flow, and an indicator variable for upstream flow to predict the probability of fish entering each channel. However, because this model was developed using data collected during low, tidally reversing flows, we also used the model of Hance et al. (2020), which was fit to telemetry data of juvenile salmon collected during higher non-reversing flows. This model used 2-D telemetry data in a statistical model based on the critical streakline entrainment zone hypothesis (see Box 3 in Perry et al. 2016) to explore the effects of such factors as fish distribution across the

channel, streakline location, and fish positions relative to the streakline. The statistical model of Hance et al. (2020) consists of two parts: (1) a beta regression model to characterize the cross-stream distribution of fish, and (2) a logistic regression model to determine the routing probability based on the position of fish relative to the streakline.

Given these models to calculate the probability of fish particles entering each channel, we performed multiple Bernoulli draws to randomly select which channel the particle entered. For all other junctions in DSM2 where acoustic-tag data were unavailable to parameterize junction-specific models, we calculated routing probabilities using the default routing probability calculation in the original PTM.

Survival

To simulate juvenile salmonid survival along the migration routes that pass Chipps Island, we implemented a predator-prey model known as the XT model (Anderson et al. 2005). The XT model expresses survival of migrating juvenile salmon as a function of both distance traveled and travel time:

$$S_{i,m} = \exp\left(-\frac{1}{\lambda_m} \sqrt{x_m^2 + \omega_r^2 t_{i,m}^2}\right)$$

where $S_{i,m}$ is the probability of individual i surviving through reach m , x_m is the mean distance (km) between predator and prey encounters in reach m , x_m is the length of each reach (km; not to be confused with x in Equation 3), ω_r is defined as the random encounter velocity (km day⁻¹) for Delta region r , and $t_{i,m}$ is the travel time (day) of individual i through reach m . The inverse of λ_m is the instantaneous mortality rate with respect to net distance traveled and travel time, and the random encounter velocity (ω) can be thought of as the sum of the variances of the predator and prey's random component of directed swimming velocity (Anderson et al. 2005).

To estimate the parameters of the XT model, we implemented the Bayesian multi-state mark-recapture model of Perry et al. (2018), which was

applied to telemetry data from juvenile late-fall-run Chinook Salmon that migrated through the Delta during the winters of 2007 through 2011. However, we replaced the logit link function used by Perry et al. (2018) with the XT model described above. In addition, whereas Perry et al. (2018) combined Sutter and Steamboat sloughs into one reach, we divided Sutter Slough and Steamboat Slough into separate reaches. We then re-fit the multi-state model to the same dataset as used in Perry et al. (2018), estimated XT model parameters for nine different reaches of the Delta, and used these estimates to parameterize ECO-PTM. (See “Data Accessibility” for a brief description and link to Appendix B.)

To implement the XT model within ECO-PTM, the XT model parameters are applied according to the reach where an individual particle is located. The PTM calculates the particle travel time and uses it to calculate the individual fish survival probability at the end of each reach. Particles that do not arrive at the downstream end of a reach by the end of the simulation are censored from further analysis and are not included in survival calculations. We then perform a Bernoulli draw with $S_{i,m}$ probability to determine if the particle has survived. The population survival probability for each reach is calculated according to the percentage of surviving particles among those arriving at the end of the reach. Reach-specific survival probabilities are then used to calculate route-specific survival, defined as the total survival between Freeport and Chipps Island for fish that use different migration routes. ECO-PTM tracks survival for five migration routes between Freeport and Chipps Island (Figure 2). The total survival probabilities were calculated by combining survival probabilities from all routes according to the proportion of particles that enter each route.

ECO-PTM Model Testing

As a publicly available, open-source model in the DSM2 suite of models, ECO-PTM is intended to be readily modified and extended by other scientists and developers in the research and resource-management community. As such, we created several black-box tests to facilitate

inspection and verification of the model outputs. Black-box testing focuses on verifying overall model functionality, and complements other methods that test individual components of the software in isolation. This test suite serves two main purposes. First, it was used to verify the particular version of the model described here. Second, the test suite will be provided as part of the official ECO-PTM release by the California Department of Water Resources (CDWR). The test suite provides a set of automatic tests that can be easily run whenever the ECO-PTM is modified, to obtain a qualitative and quantitative understanding of how the primary model outputs have changed.

The test suite comprises 14 tests that were designed to assess the routing, travel time, and survival characteristics of the ECO-PTM under low-, high-, and medium-flow hydrologic conditions. A primary purpose of the test suite is to facilitate the comparison of a modified version of the ECO-PTM to the base ECO-PTM. Therefore, the automatic test framework generates two types of visualizations for most tests: plots containing data from the modified model, and plots with data from the modified model superimposed on data generated by the base ECO-PTM.

Tests 1 and 2 are designed to assess the probability of entrainment at key junctions that have a major influence on whether fish enter the low-survival interior Delta: the Sutter Slough, DCC, and Georgiana Slough junctions with the mainstem Sacramento River. Entrainment probabilities are assessed using a combination of spatial heat maps and histograms. Test 3 generates heat maps showing counts of unique particles that visited each channel in the Delta, providing an overview of large-scale migration-route patterns. Tests 4 through 13 generate plots of travel time and survival probabilities for fish released into each of the 10 reaches. Test 14 provides a higher-level assessment of the model by calculating travel times and survival probabilities for five possible through-Delta routes. The survival probabilities are displayed using a map of the routes, color-coded according to the route-specific survival.

In addition to the suite of tests to verify the model, we included tests that facilitate code coverage testing and profiling. Code coverage testing measures how much of the source code is being executed when a program runs. Knowledge of code coverage can help identify code that is not being accessed during testing, and thus may have hidden bugs; reveal obsolete or unnecessary code that cannot be reached; and help flag code that is inadvertently unreachable as a result of logical errors in the program. Code profiling helps identify computationally expensive parts of the codebase and can help target efforts to increase the computational efficiency of the model.

As black-box tests, these tests only assess model outputs, not the details of the algorithm implementations. Therefore, they are intended as just a single component of a more comprehensive test program that includes other strategies, such as careful code review, unit testing, etc.

Model Simulations

We performed simulations to evaluate the model's performance and the effectiveness of CDWR's water-resources management actions. The scenarios and how we conduct the simulations are described below.

Historical Baseline

To establish a historical baseline, we conducted a series of ECO-PTM simulations that covered the years from 1991 to 2016. These simulations were based on the Delta's historical hydrodynamic conditions simulated by DSM2 HYDRO. In each simulation, we released a cohort of 9,600 fish particles into the Delta over a single day, starting close to Freeport. Subsequently, we let the cohort traverse the Delta from Freeport to Chipps Island over a simulation period that lasted 150 days. Throughout this simulation period, we tracked these particles' movements, and estimated the likelihood of survival when a particle arrived at the end of a particular reach on its journey (Figure 1 shows the start and end of nine such survival reaches). By following the methods discussed earlier, we calculated the route-specific and combined through-Delta survival probabilities at the end of the simulation.

Simulations were performed by “releasing” fish particles every day for the period from October 1 through June 31 for 1991 to 2016. This simulation approach amounted to a total of 6,984 distinct daily simulations that we summarized into daily probabilities of through-Delta survival. Specifically, daily survival probability refers to the total survival of each daily cohort that entered the Delta, integrated over their travel time between Freeport and Chipps Island. We then compared these simulated survival probabilities for daily cohorts of fish that entered the Delta to the survival predictions produced by STARS (Survival Travel Time and Routing Simulation), a statistical simulation model described below.

STARS

To evaluate the performance of ECO-PTM under the historical baseline, we compared ECO-PTM simulations to the Delta STARS model. STARS is a simulation model that predicts real-time daily survival, travel time, and routing of juvenile salmon that migrate through the Delta using daily Sacramento River flows at Freeport and DCC operations (Perry et al. 2019). The model is based on a Bayesian analysis of acoustic-tagged late-fall-run Chinook Salmon data (Perry et al. 2018). Our goal was to assess whether ECO-PTM—when applied to the historical conditions observed in the Delta—matched patterns in predicted survival from a statistical model.

To compare the simulation results with ECO-PTM, we conducted simulations with STARS under the same historical condition for the same time-period as the ECO-PTM historical baseline simulations. STARS used historically observed daily DCC operations and flows at Freeport in the Sacramento River, while ECO-PTM used the 15-minute time-step historical simulation from DSM2 HYDRO. With the observed data, STARS produced survival probabilities from Freeport to Chipps Island for daily cohorts of fish that entered the Delta, which we paired with a corresponding ECO-PTM simulation using particle releases on that particular day. We then compared daily survival probabilities produced by STARS with those simulated by ECO-PTM.

Management Action Scenarios

The CDWR is currently evaluating whether non-physical barriers can be used to either guide fish away from low-survival routes or guide them into high-survival routes. Therefore, we used ECO-PTM to evaluate the potential effectiveness of implementing non-physical barriers such as a Bio-Acoustical Fish Fence (BAFF) on migration routing and survival at two critical river junctions: Georgiana Slough and Steamboat Slough (Figure 1). The BAFF deployed at Georgiana Slough consisted of multiple behavioral stimuli including a bubble curtain, strobe lights, and sound generators. Field experiments have confirmed that a BAFF was able to reduce entrainment in Georgiana Slough and direct fish away from the southern Delta where survival is lower (Perry et al. 2014). Theoretically, further benefits could be gained by implementing a non-physical barrier to guide fish into Steamboat Slough, which has high survival (see Appendix B) and diverts fish from Georgiana Slough at an upstream junction (Figure 1). ECO-PTM provides an effective tool to comprehensively assess the benefits of the non-physical barriers before they are installed.

To simulate the functions of the barrier, which are to increase or reduce the routing probability into a given channel, ECO-PTM was programmed to allow users to input a percentage either to increase or to reduce route probabilities, based on the historical routing-probability calculation. We evaluated three management scenarios to simulate the potential effectiveness of a non-physical barrier:

Scenario 1. Increasing entrainment into Steamboat Slough by 30 percentage points over the flow-dependent routing probability (i.e., adding 0.3 to the routing probability).

Scenario 2. Decreasing entrainment into Georgiana Slough by 50% of the flow-dependent routing probability (i.e., multiplying the routing probability by 0.5).

Scenario 3. Combining Scenarios 1 and 2.

We chose to add a constant proportion in Scenario 1 because the routing probability into Steamboat Slough is very small at low Sacramento River flows (Perry et al. 2018; Romine et al. 2021). If this low calculated routing probability were multiplied by a percentage, the final routing probabilities would still be very small, which would be counter to the goal of increasing the routing probability. In contrast, at Georgiana Slough, both routing probability and the effect of the BAFF decline as flow increases (Perry et al. 2014, 2015), which is consistent with the constant fractional change used in Scenario 2.

It is worth noting that realizing a 30% increase in entrainment to Steamboat Slough in Scenarios 1 and 3 presents engineering challenges, given the flow and channel conditions at the junction. The inclusion of this scenario is motivated by an interest in understanding how sensitive salmonid survival is to entrainment into Steamboat Slough. The key question is whether a substantial increase in entrainment to the slough would indeed enhance overall survival of salmonids through the Delta.

Because the non-physical barriers do not affect Delta hydrodynamics, the same historical hydrodynamic simulation was used for the management action study. This historical hydrodynamic simulation encompassed a wide range of water-year types, including seven Critical, five Dry, four Below Normal, four Above Normal, and eight Wet water years (water-year classifications are obtained from the California Department of Water Resources: <https://cdec.water.ca.gov/reportapp/javareports?name=WSIHIST>). In addition, the 28-year hydrodynamic simulation has a good representation of hourly, daily, fortnightly, and annual tidal cycles that interact with inflows to affect Delta hydrodynamics. Last, daily simulations were conducted from October to June, the outmigration period of Chinook Salmon.

RESULTS

Baseline Survival

Route-specific survival simulated by ECO-PTM showed a pattern similar to Perry et al. (2010;

2013), with fish that took the Georgiana Slough route being considerably less likely to survive than fish that took other routes (Figure 3). Among the other routes, Steamboat Slough exhibited the highest survival rate, followed by the Sacramento River and Sutter Slough, although there was significant overlap in the interquartile ranges around these estimates (Figure 3). Throughout the 26-year study period, the simulated survival of migrating fish was observed to increase in response to increases in Sacramento River inflow rates, similar to findings from field studies of juvenile salmon survival (Perry et al. 2018; Figure 4, “Baseline” panel). Given the high correlation between Sacramento River inflow and through-Delta survival, the model was able to capture the seasonal changes in through-Delta survival. The model results suggest a higher probability of surviving during the rainy season, from December to March (Figure 5), as well as during wet years (Figure 6).

Although our simulation captures the average flow–survival relationship observed by other studies, ECO-PTM results reveal that survival of daily cohorts can vary significantly when Sacramento River inflows are low, ranging from approximately 20% to 60% (Figure 4, “Baseline” panel). This finding indicates that factors other than mean river flow (e.g., tides, spatial flow variation) can influence particle travel times, and, in turn, survival. Moreover, variability in daily survival decreases when Sacramento River inflows are high (e.g., exceeding 50,000 cfs), and the incremental benefits on survival of further increasing river inflow become less pronounced.

Comparison of ECO-PTM with STARS

The simulation results from ECO-PTM agreed well with STARS simulations (Figure 7). Both models displayed similar patterns of seasonal and interannual variation in daily survival. Survival was typically lower in early fall and late spring, coincident with lower inflows during these seasons. Among years, Above Normal and Wet years typically exhibited higher survival rates for a longer period of time compared to Dry and Critical years. Daily survival simulated by ECO-PTM mostly fell within the STARS model’s range

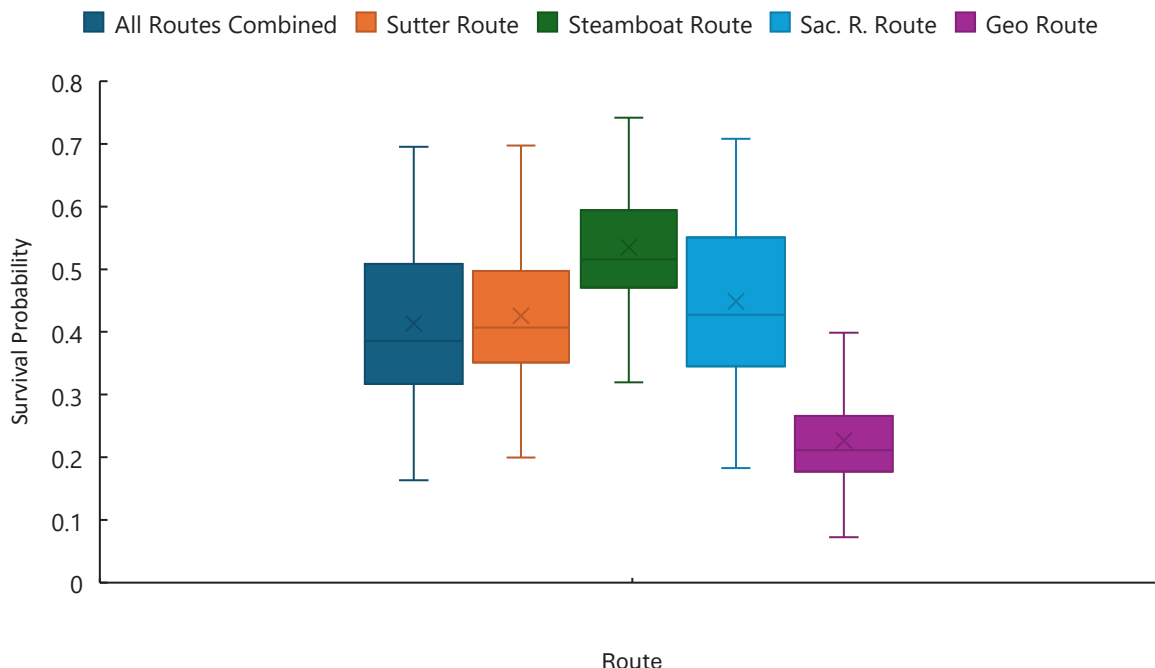


Figure 3 Baseline through-Delta survival probabilities for different routes simulated by ECO-PTM. The *boxes* are drawn between the first and third quartiles from the survival probabilities from all the simulations, with an additional *line* along the second quartile to mark the median. The *whiskers* represent the minimums and maximums outside of the first and third quartiles. Xs are mean marks.

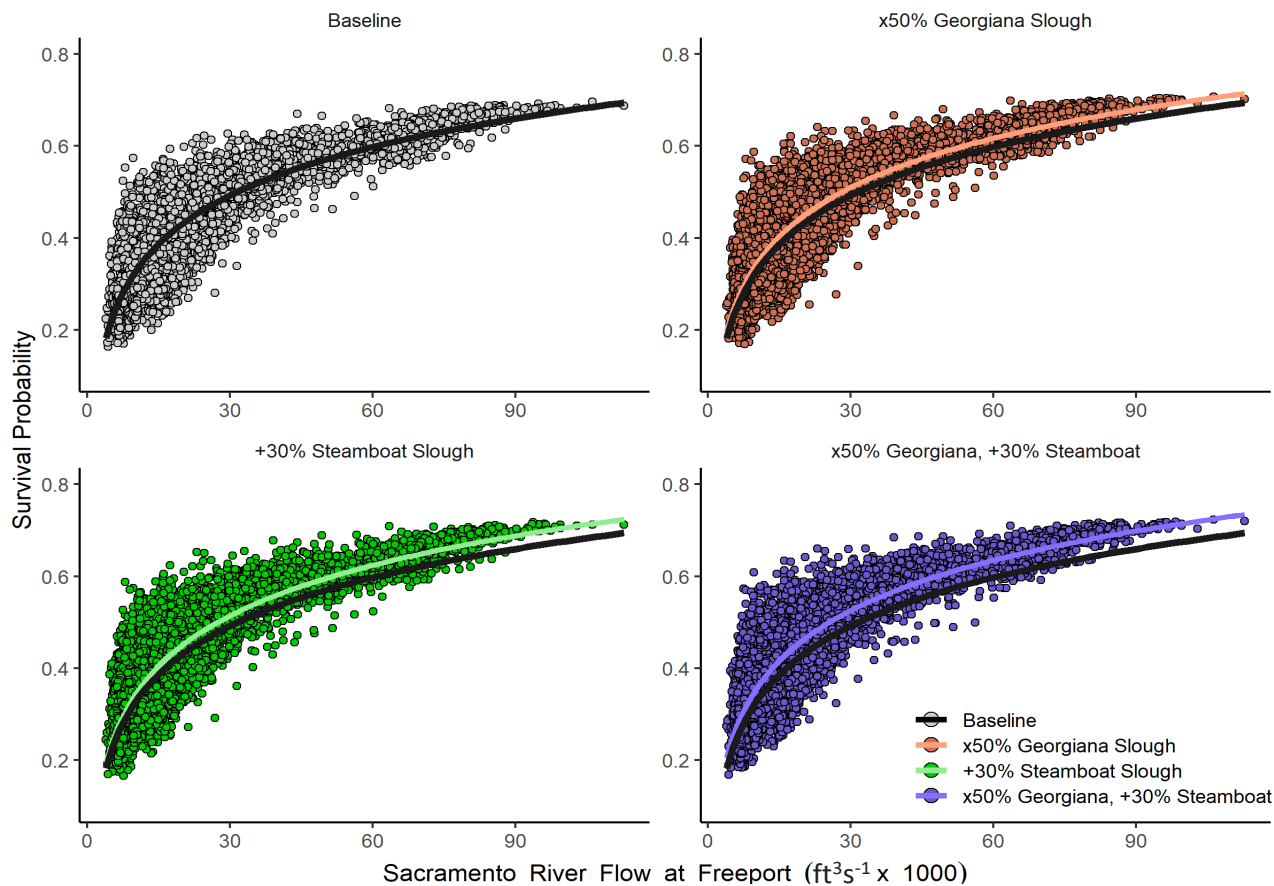


Figure 4 Daily survival probability of salmonids simulated by ECO-PTM vs. flow for all scenarios. The *cloud of dots* are survival probabilities for all simulations, and *each dot* represents the survival probability for each daily simulation. The *lines* represent the logarithmic trendlines of the data. The baseline scenario is shown in each panel for comparison against routing scenarios.

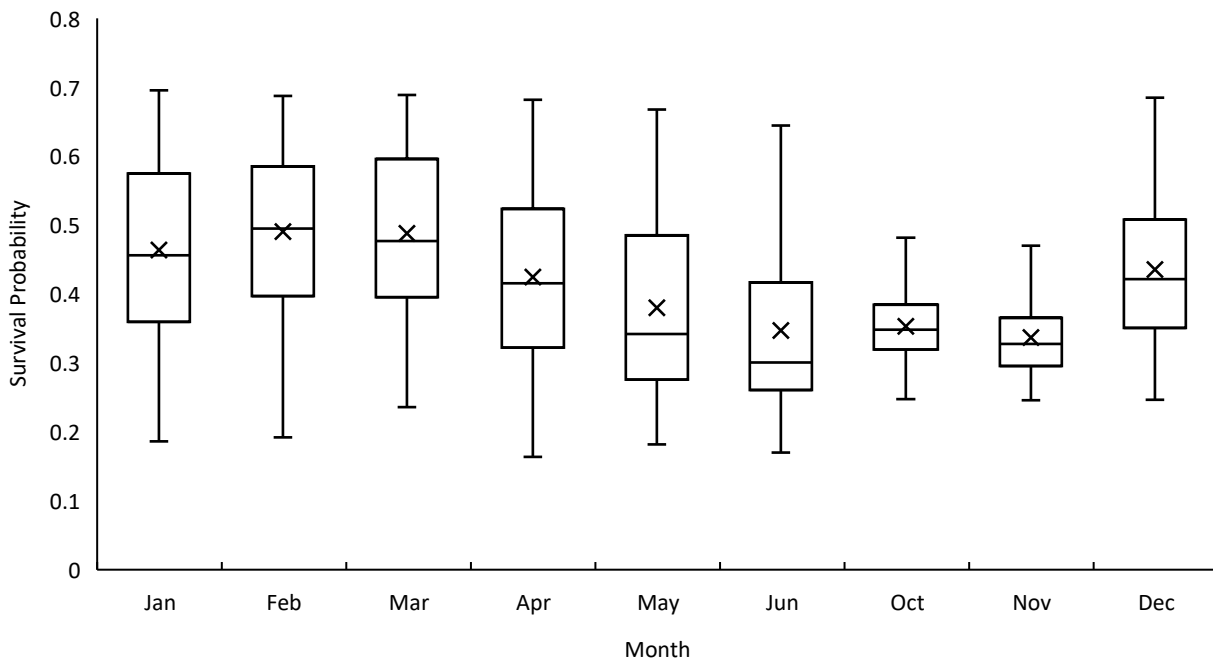


Figure 5 Baseline survival probabilities of salmonids simulated by ECO-PTM for each month. The *boxes* are drawn between the first and third quartiles from the survival probabilities from all the simulations, with an additional *line* along the second quartile to mark the median. The *whiskers* represent the minimums and maximums outside of the first and third quartiles. Xs are mean marks.

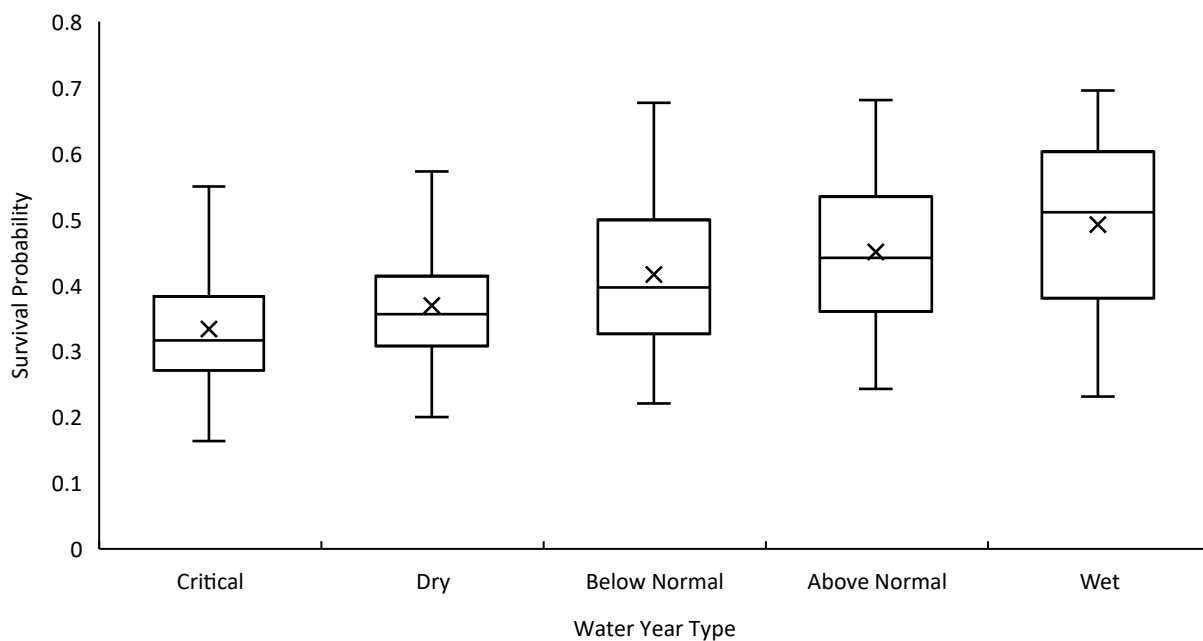


Figure 6 Baseline survival probabilities of salmonids simulated by ECO-PTM for each water-year type. The *boxes* are drawn between the first and third quartiles from the survival probabilities from all the simulations, with an additional *line* along the second quartile to mark the median. The *whiskers* represent the minimums and maximums outside of the first and third quartiles. Xs are mean marks.

of uncertainty (Figure 7). However, ECO-PTM exhibited more day-to-day variability in daily survival than STARS, likely the result of the finer spatio-temporal resolution of flow information that drives ECO-PTM particle movement relative to STARS, which is based solely on mean daily flow at Freeport.

Management Action Scenarios

Survival probabilities in all three scenarios ranged from 16% to 72% (Figure 4). The difference in survival rates between an alternative scenario and the baseline was calculated by subtracting the daily baseline survival rate from the corresponding daily survival rate of the alternative scenario. Across scenarios, mean survival differences ranged from 2% to 3% (i.e., absolute difference from 0.02 to 0.03), with each alternative scenario predicting slightly higher survival than the baseline scenario. Of the three scenarios, Scenario 3 (Geo×50% STM+30%) yielded the largest absolute survival increase as a result of the combined actions (Figure 8), about 3%. Scenario 1 (STM+30%) and Scenario 2 (Geo×50%), exhibited an approximately 2% absolute survival increase.

Survival differences from the routing management actions varied significantly depending on Delta flow and other conditions, ranging from -4% to 9% compared to the baseline scenario (Figure 8). Among the factors that affect the survival differences, Sacramento River inflows played a significant role. Although the management actions did not alter the fundamental pattern between flow and survival, our simulations indicated that the inflow range of 20,000 to 40,000 cfs provided the most survival benefits, and survival differences were lowest at the lowest flows (Figure 8).

DISCUSSION

The results of these historical simulations demonstrate that ECO-PTM, an individual-based model, produces survival estimates that align closely with STARS, a separate statistical model parameterized from the same acoustic telemetry dataset. This strong

agreement between the two models, despite their distinct modeling frameworks, suggests that both effectively capture the key factors that influence outmigration survival. However, we identified several notable differences between the two models under extreme flow conditions. These differences can be attributed to the fact that STARS focuses solely on daily DCC operations and daily Sacramento River flow at a single location (Freeport), whereas ECO-PTM incorporates the intricate tidal hydrodynamics of the Delta through the utilization of fine-scale hydrodynamics provided by DSM2 HYDRO. Yet even in instances where the models diverge, the survival probabilities simulated by ECO-PTM largely remain within the 80% uncertainty interval of the STARS simulation.

The baseline historical scenario reproduced important relationships between salmon outmigration survival and hydrodynamic conditions. Simulated outmigration survival was strongly related to Sacramento River inflow, consistent with what has been demonstrated by numerous field studies (Perry et al. 2018; Hance et al. 2022; Hassrick et al. 2022). However, we found that daily survival simulated by ECO-PTM varied greatly during low flow conditions. This variability can be attributed to the highly dynamic and intricate nature of the Delta, which is influenced by multiple interacting factors beyond mean daily river inflows, when combined, likely affect the survival of salmonids. Notably, during periods of low Sacramento River inflow, certain additional factors (or their combination) such as tides exert a substantial influence, surpassing the significance of river inflow alone. For example, as river inflow decreases, tidal forcing increases, leading some reaches to transition from uni-directional to bi-directional flow (Perry et al. 2018). Because ECO-PTM integrated the detailed Delta flow field simulated by HYDRO, ECO-PTM effectively accounted for the effects and variability of these additional factors during times of diminished Sacramento River inflows, thus significantly enhancing the model's ability to provide insights into the complex interactions within the Delta ecosystem.

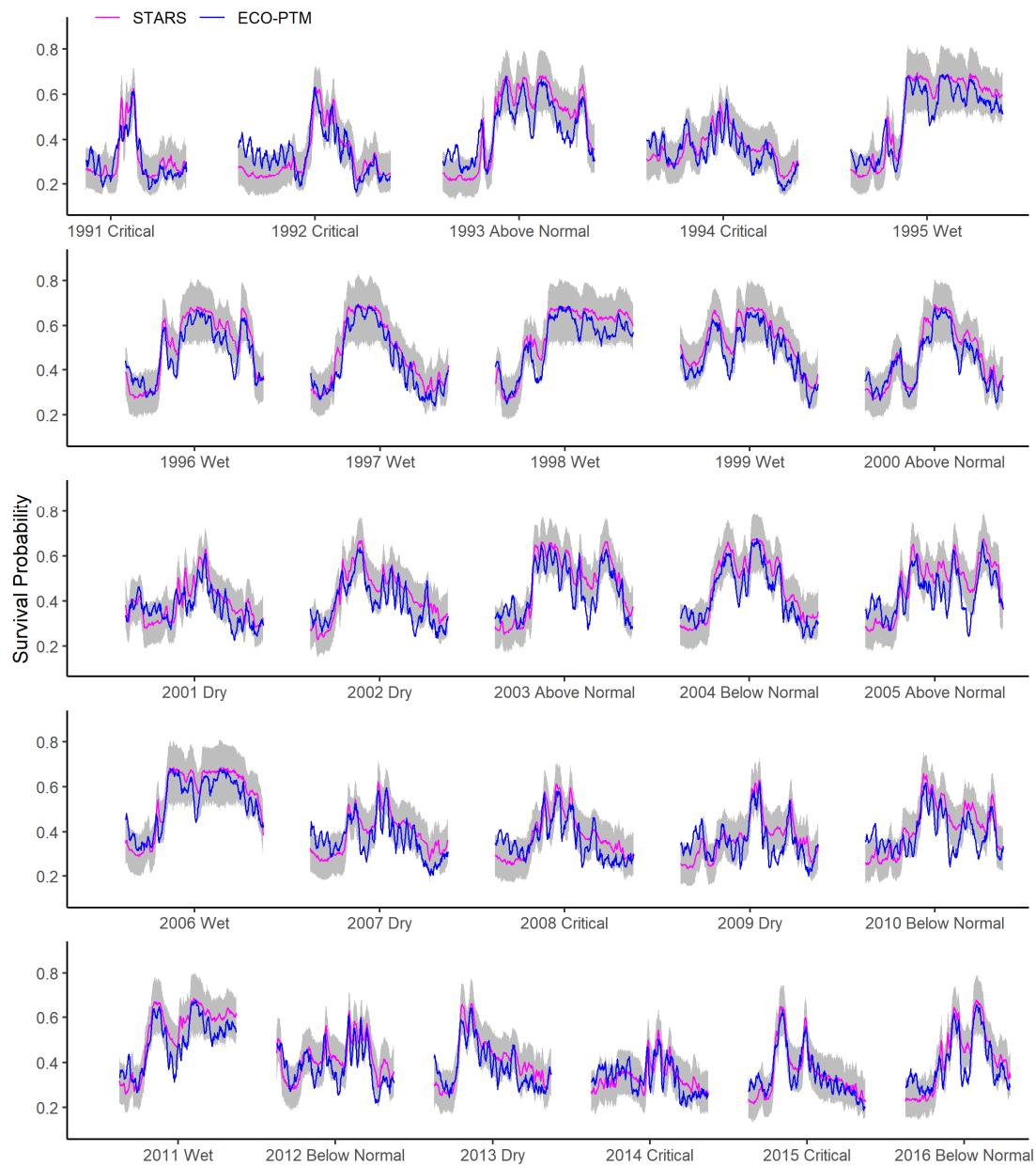


Figure 7 Comparison of simulated survival probability, STARS vs. ECO-PTM 1991–2016. The *gray area* and *pink line* represent the STARS results. The *gray area* indicates 80% credible interval. The *pink line* is median daily survival probability, and the *blue line* is survival probability for each daily simulation by ECO-PTM. Daily survival probabilities are shown for only the salmon migration season of October 1 through June 31.

We also found that the influence of migration route on ECO-PTM survival is consistent with empirical studies of through-Delta survival for some routes, and sheds new light on other routes. First, ECO-PTM simulated lower survival for fish that migrated through the interior Delta via Georgiana Slough (Figure 3), similar

to that reported by Perry et al. (2010, 2013) and Hance et al. (2022). In contrast to other studies, our simulations revealed Steamboat Slough as the highest-survival route, followed by the Sacramento River and Sutter Slough. Previous studies have combined Sutter and Steamboat sloughs into a single route (Perry et al. 2010,

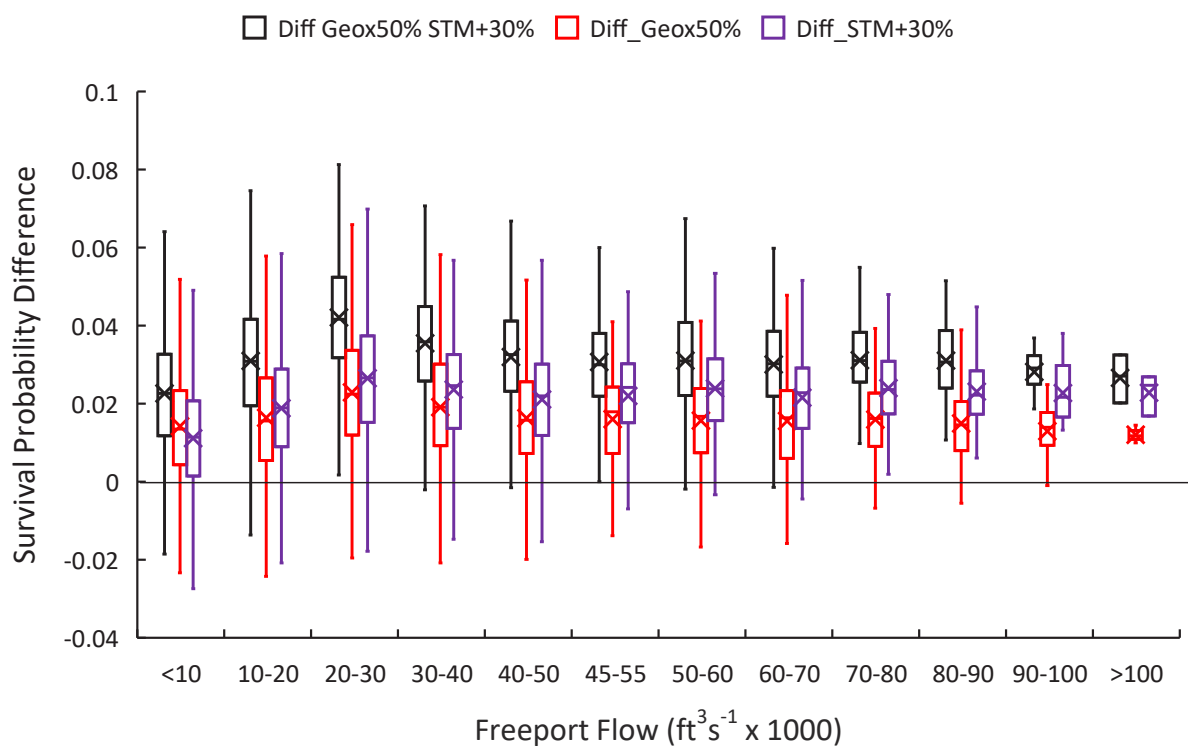


Figure 8 Survival probability difference of each scenario from the baseline vs. flow at Freeport for all ECO-PTM simulation scenarios. The *boxes* are drawn between the first and third quartiles from the survival probabilities from all the simulations, with an additional *line* along the second quartile to mark the median. The *whiskers* represent the minimums and maximums outside of the first and third quartiles. *Xs* are mean marks.

2013, 2018), which tends to average out survival differences between routes. High survival rates for Steamboat Slough were driven, in part, by the parameter estimates from the XT model, which indicated lower mortality rates for Steamboat Slough relative to other reaches (see Appendix B).

The results for all three scenarios demonstrate that many factors can affect how well management actions improve fish survival, such as total Delta flow, flows at key junctions, routing modifications, seasons, and water-year types. It is crucial for managers to consider these factors when making decisions that may have trade-offs for the resources they manage. For example, we found that substantially increasing entrainment into Steamboat Slough at the junction (Scenario 1) did not lead to significant survival benefits at the Delta-wide scale. The relatively small effect of this scenario, even with a substantial increase in entrainment, was unexpected, given that this route had lower mortality rates than alternative routes. There may be multiple reasons for this outcome. First,

most fish that did not enter Steamboat Slough remained in the Sacramento River, which was the second-best route for migrating fish (Figure 3). The difference in survival between the two routes was relatively small, resulting in limited sensitivity to the entrainment increase (Perry et al. 2013). Second, the flow in Steamboat Slough often reverses during low flow periods, which might create difficulties for fish that attempt to enter or remain in Steamboat Slough even when a higher entrainment probability is assigned. We hypothesized that because of these reasons, we did not see significant benefits of the management action.

The application of ECO-PTM to the example management scenarios presented here demonstrates the potential utility of this tool for predicting the effect of proposed management actions. Our application of ECO-PTM also provides valuable groundwork for future research and the development of effective management strategies that improve the survival of outmigrating salmonids through the Delta.

Managers often face the challenge of evaluating novel water-resources management actions (e.g., non-physical barriers) and large-scale structural changes (e.g., temporary rock barriers, levee flooding, and wetland restoration) that fundamentally alter the dynamics of the flow field, as well as fish migration throughout the Delta. Such management actions have typically never been observed in the historical record, making it difficult to anticipate their potential effects based solely on past field studies and statistical models. Hence, managers require tools such as ECO-PTM, which enables novel scenarios to be assessed using a mechanistic, behavior-based model. This approach allows managers to gain insights into the potential effects of these management actions, facilitating informed decision-making about their implementation.

ECO-PTM represents one of a variety of such efforts by the scientific community to apply mechanistic, individual-based models to assess management actions and improve understanding and prediction of the behavior and fates of outmigrating salmonids in the Delta (FISH-PTM: Gross et al. 2021; Eulerian–Lagrangian agent Method (ELAM): Goodwin et al. 2023; ePTM: Sridharan et al. 2023), each with a specific focus and target use case(s). In particular, ECO-PTM is closely related to the ePTM, with which it shares significant conceptual and architectural characteristics. However, the ePTM and ECO-PTM were intended for somewhat different purposes, with ECO-PTM being fully integrated into the official DSM2 release, and the ePTM serving both as a sub-model of the winter-run Chinook Salmon life-cycle model (WRLCM; Hendrix et al. 2019) and a stand-alone modeling tool. These different development trajectories led to two notable differences. First, ECO-PTM applies the XT model at the reach scale using parameters that were independently estimated outside of the model, whereas the ePTM applies the XT model at each 15-minute time-step using parameters that were fit during model calibration. Second, the ePTM uses a bifurcating streamline algorithm for routing at all junctions, in contrast with the statistical models and flow-split routing that the ECO-PTM uses.

ECO-PTM was designed as an open-source model to facilitate further development by modelers in the community. Its source code is readily available online at the GitHub code hosting platform and through the CDWR (2022, 2024a, 2024b). The software architecture allows new features to be incorporated into the existing codebase. For example, modelers can introduce a new routing model by creating a Java class for their unique routing model and then specifying the class name and junction location in the input file. The ECO-PTM then automatically loads the specified class at runtime and calculates routing probabilities based on the custom routing model.

ECO-PTM has limitations and is better suited to some applications than others. First, the model has been calibrated to late-fall-run Chinook Salmon emigrating from the Sacramento River. As such, model users should consider the degree to which inferences drawn from ECO-PTM parameterized with late-fall-run Chinook Salmon apply to their population of interest. Second, although ECO-PTM simulates particles moving through the South Delta, it is better suited to inferences on Sacramento River populations than San Joaquin River populations. However, the CDWR has undertaken a project to parameterize ECO-PTM using telemetry data available for San Joaquin River Chinook Salmon (Buchanan and Skalski 2020). Furthermore, although ECO-PTM includes fine-resolution particle movements, it is calibrated to telemetry data at the reach scale (Figure 1). The results of our calibration to these data show that ECO-PTM simulates realistic juvenile salmonid travel time and survival distributions on the scale of kilometers or tens of kilometers. However, these telemetry data do not include sub-kilometer reaches, and so inferences about movement, routing, or entrainment at fine spatial scales—such as movement and entrainment into the water pumping facilities—may be inaccurate. In these cases, we recommend parameterizing, calibrating, and validating the model with empirical data for a specific case that may be outside the range of data used to develop the existing version of ECO-PTM.

CONCLUSIONS

Given the plight of endangered salmon in the face of prolonged periods of drought and climate change, managers need tools to evaluate novel water management actions that have never been observed in the historical record. While statistical models are valuable for understanding the historical response of salmon populations to environmental variability, their application is limited to the range of historical observations. ECO-PTM offers a more comprehensive approach by integrating a hydrodynamic model with mechanistic models of survival and movement, making its output sensitive to structural changes such as temporary barriers or levee breaches, variability in Delta inflows and tides, and consequences of climate change, such as sea level rise. DSM2 can simulate the simultaneous effect of many water-resources management actions of varying magnitudes, all of which are overlain on a physical template with significant natural hydrodynamic variability. Thus, ECO-PTM is a useful management tool for understanding how the simultaneous interaction of these many factors ultimately affect juvenile salmon survival in a framework that could not be evaluated otherwise.

In conclusion, ECO-PTM, alongside other modeling tools, offers insights into the intricate dynamics of salmon outmigration in the Delta, serving as a tool for predicting the potential effects of management actions. As our understanding of the ecosystem continues to evolve, ongoing research and improvements to such models will play a vital role in formulating effective management strategies aimed at safeguarding and enhancing the survival of outmigrating salmonid populations in the Delta.

ACKNOWLEDGEMENTS

This work was funded by the California Department of Water Resources (CDWR). We extend our deepest gratitude to our CDWR program managers and colleagues, including Ryan Reeves, Bill McLaughlin, Jacob McQuirk, Robert Trang, Mohammed (Shahid) Anwar, Khalid Ameri, Kevin Clark, Kevin Reece, Tara

Smith, and Prabhjot (Nicky) Sandhu. Their encouragement, support, and suggestions were vital to this project's success. Their insights into water-resources management, assistance in management scenario formulation, technical guidance in cloud computing, and various other forms of support were invaluable. Their edits and comments significantly improved the manuscript. Their collective contributions have left an indelible mark on this work, and we are deeply thankful for their involvement. We also express our thanks to Steve Lindley and his NOAA Fisheries team for the collaboration at the early stage of this project, and to Aaron Blake at US Geological Survey for his valuable suggestions. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. Data are not currently publicly available from the National Oceanic and Atmospheric Administration (NOAA). Contact NOAA for more information.

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