ENHANCED PARTICLE TRACKING MODEL (ePTM) FINAL STUDY PLAN FOR FLOW SURVIVAL RELATIONSHIP

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1. Introduction

The Winter-run Chinook salmon lifecycle model (WRLCM) (Hendrix et al 2014; 2017; 2019) is currently undergoing development by The Regents of the University of California, Santa Cruz, and QEDA Consulting as part of a Cooperative Agreement with the Department of the Interior, Bureau of Reclamation. The goal of this agreement is to develop simulation models to quantify the potential cumulative effects of water operations and proposed habitat restoration on the population dynamics of federally endangered Sacramento River Winter-run Chinook salmon. A specific goal of the agreement is the continuing development of the National Marine Fisheries Service's (NMFS) Enhanced Particle Tracking Model (ePTM) to incorporate multiple water management components (exports, gate operations, etc.) to generate results of simulated fish movements and survival and to provide visualizations that illustrate how predictions change under various management scenarios (Agreement, Objective Six).

Significant effort has been expended over the past decade to both acquire acoustic telemetry data on juvenile salmon movement through the Sacramento-San Joaquin Delta (hereafter, the Delta) (Perry et al. 2010; SJRGA 2013; Buchanan et al. 2018; Notch et al. 2020), as well as to build models of fish migration through the system (Zeug et al. 2012; Goodwin et al. 2014; Sridharan et al. 2016; Beer et al. 2017; Science Integration Team 2018; Perry et al. 2018). However, there is still a need for a process-based understanding of how fish migration and survival occurs through this system in response to the tidal flows (sub-daily changes in the volume of water and direction of flow through the system), hydrologic cycles (seasonal changes to the volume and flow of water through the system), changes in the water management operations (alterations to the operations of hydraulic structures and consequent modifications to the geographical flow patterns) and hydrodynamics (variability in the water velocity and mixing rates of water parcels within the water column, strength of the tides relative to the freshwater flow and the local, regional and system-wide effects of South Delta pumps). *Process-based understanding is helpful in habitat and water management: such understanding can help shed light on* (i) the reasons behind past events,

(ii) what data gaps there are and how to improve real-time monitoring of the system, and (iii) actionable management for the future, particularly for novel, out-of-sample conditions that have not been encountered earlier.

Process-based understanding of fish movement allows decision makers to gain insight into what biological and physical processes are occurring at different scales of motion (Figure 1). For example, animals in the wild are known to assimilate information about their local environment over some time span to allow them to make behavioral decisions and also use their own past experiences about their behaviors to inform what they are going to subsequently do (Gurarie et al. 2009). While fish experience their environment at the scale of a few body lengths; their movements might be dictated by past behavior and by the local flow and water quality environment, resource availability and threats they face. At this local scale, the movements of the fish might not be directly influenced by macro-systemic drivers (such as exports, flow diversions and other management actions). However, as the instantaneous local environment is heavily dependent upon these larger processes, the overall movement patterns (travel time, distribution throughout the system, and survival) might very well be an outcome of these macro-systemic drivers. Using process-based models will allow managers to apply a bottom-up approach that can aid in both understanding what macro-systemic drivers cause observed migration patterns, and as importantly, what macro-systemic drivers have limited or no effect. This will allow decision makers both the ability to handle out-of-sample scenarios, as well as focus on identifying potential management actions that will have a high likelihood of success.

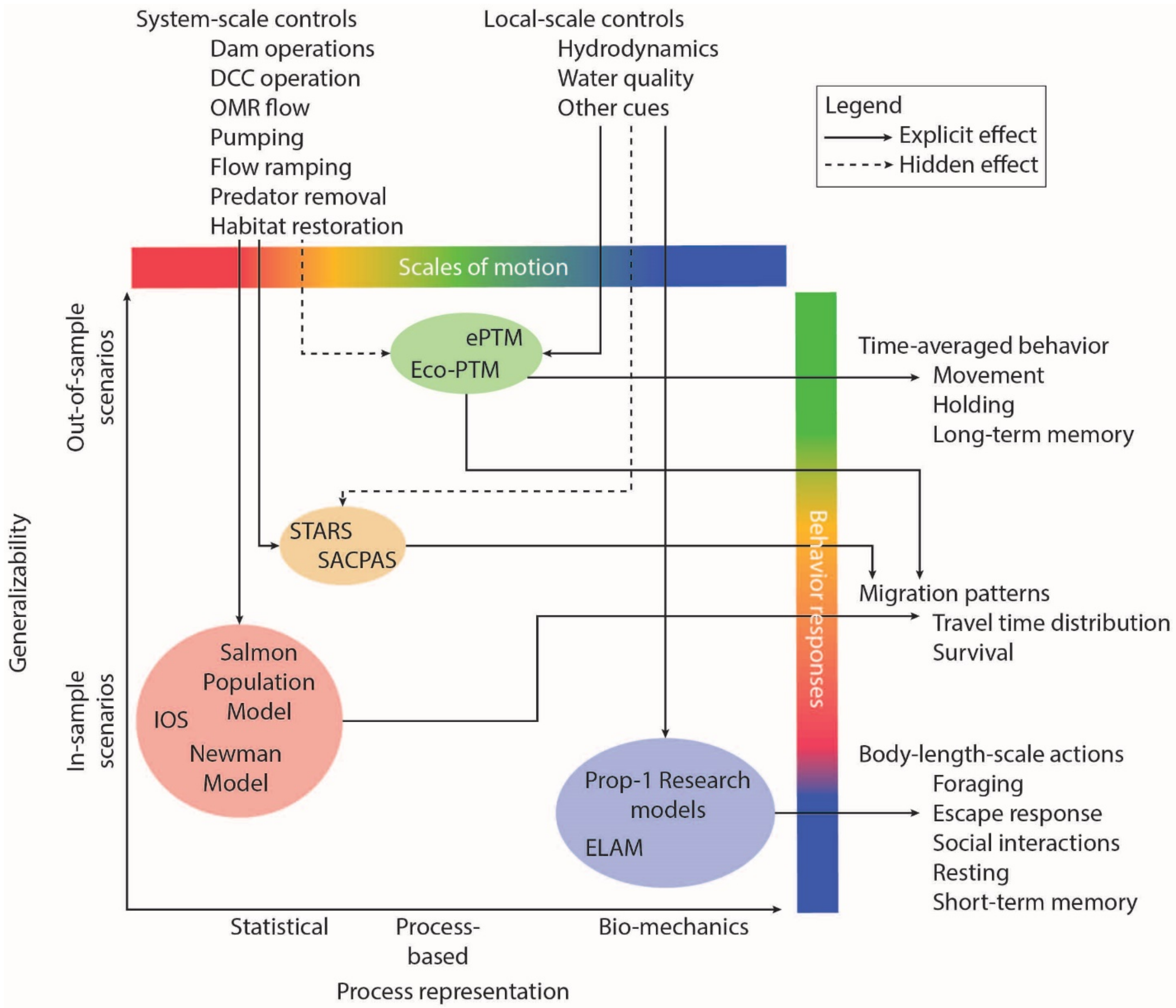

Figure 1. Spectrum of models of salmon migration and their relevance as decision support tools. The x-axis represents physical processes of increasing complexity from left to right and corresponds to increasingly finer scales of motion. The y-axis represents increasing model generalizability from bottom to top with behavior responses averaged over generally increasing time windows. Statistical models represent causal relationships between macro-systemic drivers operating at large scales of motion and overall migration patterns but are only useful within their calibration range. On the other hand, biomechanics models encode highly detailed behavior responses to local sensory cues based on biological first-principles but are not easily generalizable as decision support tools. Process-based models such as the ePTM bridge these scales and may be more widely applicable in out-of-sample scenarios. Models such as STARS, SACPAS, ECO-PTM and ePTM are able to both explicitly represent some local cue-based behaviors as well as macro-systemic effects through hidden correlations.

2. Study approach

Our objective is to develop a data-driven process-based model of juvenile salmon migration through the Delta that is a useful decision support tool in (i) representing structural and non-structural changes to the system, (ii) being able to rapidly test hypotheses about salmon behavior as new science on salmon biology becomes available, and (iii) having self-consistent hydrodynamics and behavior ecology across various spatial and temporal scales so that managers can be confident about the model predictions. To build such a model, we have relied on domain expertise and extensive literature searches.

Until late September 2017, the development of the California Department of Water Resources' (CDWR) ECO-PTM and the NMFS' ePTM proceeded along similar trajectories. We will refer to this older version of NMFS' ePTM as ePTM Version I. When we initially began developing ePTM Version I in 2013, salmon behavior ecology in tidal systems was less well understood. Under these circumstances, the more phenomenological approach adopted in Version I represented the best available science at the time.

We have since adopted a *Lagrangian* approach in the ePTM, which has resulted in ePTM Version II. In the Lagrangian approach, fish make behavioral decisions based on local environmental cues. This departure has been motivated by three recent developments: (i) the crucial importance of understanding routing at channel junctions was discovered through recent work on critical streakline or bifurcating streamline theory that was published in a series of technical documents between 2014 and 2018 (Perry et al. 2014; Sridharan et al. 2017), (ii) information has become available about the importance of cross-channel variability in fish groupings and its influence on routing through channel junctions (Steel et al. 2013; Perry et al. 2014; Hance et al. 2020), and (iii) additional knowledge about responses by fish to their local environment in the scientific literature and through concerns voiced by stakeholders during Version I of the ePTM development.

We are also concurrently studying the fundamental biophysics of juvenile salmonid migration using both the one-dimensional and two-dimensional acoustic telemetry experiments conducted in various locations within the Delta and will incorporate these findings into ePTM Version III. In ePTM Version III, we will also extend the calibration of the model to the South Delta. While ePTM Version III is outside the scope of our current agreement with USBR, we wanted to briefly describe it here. Currently, the ePTM Version II behavior modules are being calibrated using late-Fall-run Chinook salmon tagging data which is restricted to the North Delta. The model structure is such that simulated fish behavior will change depending on where they are physically within the system. The behaviors of modeled fish in the South Delta are currently being represented using the calibrated values of behavior parameters corresponding to locations in the North Delta that are hydrodynamically similar to the location of the fish in the South Delta. In Version III, we will use telemetry data for Fall-run Chinook salmon originating in South Delta hatcheries available for six years to calibrate the South Delta behavior parameters. Although this is a different run than the Winter-run Chinook salmon, for which the ePTM is being currently calibrated, it may still be worthwhile to use this data to calibrate the behavior parameters in ePTM Version II specifically for the South Delta because both runs belong to the same species.

3. Issues in ePTM Version I

ePTM Version I had several issues that needed to be resolved. There were six main issues that were identified by various domain experts in hydrodynamics, biology and salmon ecology through stakeholder outreach in September 2017, and review by the Independent Review Panel for the 2015 Long-Term Operations Biological Opinions in 2015 (Anderson et al. 2015).

(i) Unrealistic routing through channel junctions: Routing is of critical importance to predicting overall survival in the Delta. The routing model used in the DSM2-PTM randomizes the position of individual simulated fish within the water column and routes a fraction of the simulated fish through a specific downstream channel proportional to the flow entering that channel. This routing method was adopted in all the junctions in ePTM Version I. This routing mechanism is satisfactory only for inert, neutrally buoyant particles that are essentially equivalent to infinitesimal parcels of water with the ambient properties of the water column, in a straight, uniform, rectangular, channel, averaged over multiple tidal cycles. But this is an oversimplification, and the overall conclusion is that the inert, neutrally buoyant particle is not a good model of fish routing.

(ii) Problems with simulated fish swimming orientation: In ePTM Version I, the orientation of simulated fish within a channel was determined based on a quantity called the Signal to Noise Ratio (SNR). Here, signal indicates the flow through a channel averaged over two tidal cycles (about 25 hours), and noise indicates the variability of flow about this value. If the estimated SNR value in a given channel was high (i.e., variability in the magnitude of the flow was low) over a 25-hour period, then simulated fish entering this channel would more likely orient themselves with the flow. If the SNR value was low (i.e., variability in the magnitude of the flow was high), then simulated fish would more likely make a random selection about the direction they swim in. The basis for this formulation was that fish would more likely swim with the flow in reaches of the Delta where the flow is largely riverine (i.e., does not reverse with the tide-phase) and that fish would more likely swim in a randomly selected direction in the tidal reaches of the Delta where the flow regularly reverses with the tide-phase. Two problems with this formulation were identified: (i) first, the SNR can be very high for highly variable unidirectional flow, associated with rainfall, storm events, dam releases, and power peaking, thereby rendering the actual behavior of the simulated fish inconsistent with the intended behavior, and (ii) second, biologists were concerned about the prescience of the simulated fish, i.e., in reality, a fish would not have knowledge of the conditions over the past 25 hours in a channel in which it has not yet arrived.

(iii) Problems with swimming speed assignment: In ePTM Version I simulated fish were assigned a swimming speed drawn from a normal distribution. This swimming speed would be added to the local hydrodynamic flow velocity observed by the simulated fish to produce a net migration rate at which the fish moves. A random draw from the normal distribution can also result in negative swimming speeds, and as the choice of orientation direction described previously could also be opposite to the flow, these two parameters could confound each other and produce emergent behaviors that cannot be logically explained. Indeed, biologically unrealistic swimming speeds were being produced in the calibration, which indicated that there was systematic misrepresentation occurring within the model.

(iv) Lack of clarity about migration through the Old and Middle River (OMR) corridor: The influence of the swimming speed and probability of confusion together could have serious consequences with respect to what happens when simulated fish are in the OMR corridor, and when the flow is reversed by exports occurring at the State Water Project (SWP) and Central Valley Project (CVP) pumps. These consequences could not be logically explained using the confounding interactions of sub-models within ePTM Version I.

(v) Meaning of parameters in the survival model: The use of Anderson et al. (2005) survival model is problematic in tidal flows, because the distance a particle has traveled is different from the displacement in the original formulation. Therefore, the meaning of the parameters in the ePTM Version I model were unclear.

(vi) Cumbersome calibration-validation method: The calibration-validation methodology in ePTM Version I used a novel Gaussian Process (GP) based emulation approach (Dancik et al. 2010) to overcome computational limitations of directly calibrating the ePTM; however, we identified two issues with the approach. First, although the Gaussian Process calibration methodology promised to propagate all sources of uncertainty, the scale of the calibration problem itself prevented propagation of all sources of uncertainty. Second, because the methodology required building a separate model that emulated the ePTM, the framework proved inflexible and too cumbersome to easily accommodate alternate behavior hypotheses.

4. Developments in ePTM Version II

To develop a defensible and biologically plausible model, we surveyed over 30 peer-reviewed papers on acoustic telemetry of Chinook salmon and salmonids in general in both the Delta and other systems. Additionally, we also analyzed the telemetry data collected between 2006 and 2010. The behaviors implemented in ePTM Version II represent a minimalistic consensus of the observations in the telemetry dataset as well as the literature. We present below the salient findings from a key selection of papers on which our behavior model is based.

4.1. *Migration behavior observed in the data and in the literature*

The following behaviors have been routinely observed in acoustic tagging studies of juveniles of different species of salmon:

(i) There is a strong urge to migrate away from their natal streams (e.g., Sturrock et al., 2015),

(ii) Migrating or moving animals exhibit both a short-term and long-term memory of their past actions (Bracis et al. 2015),

(iii) There is a spatial and temporal distribution of swimming velocities (e.g., Lehman et al., 2017; data),

(iv) Individual fish swim faster towards the ocean when flow oceanward is slower and vice versa (McCormick et al., 1998; data),

(v) Until a salinity threshold somewhere downstream in the estuary, fish swim actively with the direction of flow during the ebb tide, and hold position during the flood tide (McCleave, 1978; Solomon, 1978; Healey, 1980; McCormick et al., 1998; Moore et al., 1998; Hedger et al., 2009). Fish hold position between a threshold upstream velocity, and a maximum upstream velocity, beyond which they cannot hold position anymore, and then they drift (Lacroix and McCurdy, 1996; Miller and Sadro, 2003; Lacroix et al., 2005). This type of behavior is known as Selective Tidal Stream Transport (STST) (Bennett and Burau 2015).

(vi) Beyond a salinity threshold, in the lower estuary, fish mostly swim towards the ocean (Lacroix and McCurdy, 1996; McCormick et al., 1998; Moore et al., 1998; Hedger et al., 2009). In this salinity regime, there is a more uniform day/night migration split, whereas in freshwater fish exhibit a higher propensity to migrate during nighttime hours only (Chapman et al. 2013).

(vii) Fish do not behave like passive particles, but instead exhibit greater control over their downstream routing decision at channel junctions, and this control depends on the position of the critical streakline or bifurcating streamline which splits water mass between the downstream channels (Perry et al. 2014; Sridharan et al. 2017).

4.2. *Behavior model in ePTM Version II*

In the ePTM, fish are assigned behavior attributes that are updated every 15 minutes. These behavior attributes allow us to simulate expected fish movements. For example, different fish swim at different rates relative to the flow, while most fish seem to hold position during the flood phase of the tide. Such behaviors can be captured by assigning randomly chosen swimming velocities to different simulated fish, and constraining a large proportion of the fish to hold position relative to the local flow during the flood phase of the tide.

To incorporate the broad findings described in section 4.1 into a defensible, biologically realistic and parsimonious model, we adopted the following updates to the behavior model. These behavior parameters will adjust themselves during the calibration process to manifest movement outcomes in different parts of the system based on the patterns of movement in the data with which the model is calibrated.

(i) Swimming speed for each fish at each timestep will be drawn from a log-normal distribution.

(ii) Fish either swim during the day with a probability of $\boldsymbol{p_{DS}}$ or hold position.

(iii) We include memory of past actions using a probability of persisting orientation from the previous timestep, $\boldsymbol{p_M}$.

(iv) Fish will hold position with probability, $\boldsymbol{p_{STST}}$ when the average landward water velocity in the cross-section the fish is occupying exceeds a threshold, $\boldsymbol{u_F}$, based on average water velocity.

(v) Probability of orienting with the flow depending on a saturating function of instantaneous water velocity if a Bernoulli draw for memory produces a value higher than $\boldsymbol{p_M}$.

(vi) Fish enter downstream channels depending on their location relative to the bifurcating streamline. This is also known as the critical streakline hypothesis of routing.

4.3. ***Updates based on stakeholder recommendations***

We addressed the six major issues in ePTM Version I during the development of ePTM Version II. We expect that this will result in a model that is rooted well in the fundamental physical processes that govern juvenile salmon migration. Specifically, we have adopted the following approaches to address each issue.

(i) Realistic routing through channel junctions: We have recognized the importance of localized routing to global transport and fate dynamics (Sridharan et al. 2017; Sridharan 2019) and have developed a streamline preserving routing model through all channel junctions. To ensure that simulated fish distributions are non-uniform within the water column, we have also parametrized the velocity profile and turbulent mixing profile within the water column for curved channels from laboratory experiments (Gandhi et al. 2016). This model follows the spirit of the critical streakline approach, while turbulent mixing within the water column can introduce perturbations in the positions of simulated fish, so that some simulated fish on either side of the critical streakline have a probability of entering a downstream channel on the other side of this streakline.

(ii) Biologically plausible swimming orientation: Our simulated fish in ePTM Version II are now truly Lagrangian in their world view, i.e., they have a persistence of memory over time that allows them to remember the direction in which they were swimming for a period of time separated from the ePTM timestep, as well as a probability of responding to the instantaneous flow in their vicinity when outside of their memory window. There is ample evidence in the literature that biological organisms exhibit such short-term memory which diminishes with time (Codling et al. 2008). In this formulation, when fish assess which direction they should swim, they do so using the instantaneous flow cue. By incorporating both a persistence memory as well as a local cue-based orientation mechanism, we will be able to capture both short-term and long-term memory processes. When this flow is at peak ebb, the fish will more likely swim with the flow. When this flow is at slack tide, the fish will more likely randomly select their swimming direction. The biological basis for this behavior is that the fish would be using local visual and tactile cues to determine the strength of the flow.

Additionally, our orientation model is general enough to incorporate the possible effects of rheotaxic behavior. We have observed in the acoustic tagging data that in the upper Sacramento and San Joaquin Rivers that fish tend to move with a net migration rate that is slower than the flow, and fish in the lower Delta tend to move with a net migration rate that is faster than the flow. This indicates rheotaxic behavior that varies by reach.

(iii) Parsimonious swimming speed assignment: To ensure model parsimony, as well as to ensure that sub-models are not confounded, ePTM Version II draws swimming speeds from a single truncated log-normal distribution at every ePTM timestep. This ensures that only positive values of swimming speed are drawn from a distribution with only two parameters. This speed is then multiplied by the swimming direction and added to the hydrodynamic velocity to produce the net migration rate.

(iv) Simulating complicated scenarios such as migration through the OMR corridor: We have decoupled the swimming speed module from the orientation module, and now simulated fish are Lagrangian. These changes reduce confounding of parameters within the model and ambiguity about what will happen in complicated scenarios. We expect ePTM Version II to more accurately match observations even in complicated flow scenarios such as flow reversals in the OMR corridor due to South Delta pumping.

(v) Meaning of parameters in the survival model: In the XT model, we now use $r = \frac{1}{\lambda}$ as the per-kilometer survival rate (which is easier to understand than mean-free path length). We define $\omega^2 t$ as the "diffusion coefficient" due to (i) correlated fine-scale fish movements at the sub-ePTM time step not captured by the model, (ii) hydrodynamic fluctuations affecting the fish at the sub-ePTM time step, (iii) uncaptured hydrodynamic model physics, and (iv) nature of the predators, viz., actively moving or stationary. A thorough evaluation of the implications of the XT model has allowed us to retain both the distance traveled as well as the time taken to traverse that distance within the survival model. In ePTM Version II, we have defined X in the XT model as the Lagrangian path length, as the sum of the simulated fish's displacements over each time step. This makes the model a more realistic process-based survival model based on mean-field theory.

(vi) Efficient calibration-validation methodology: There will be two types of applications of the ePTM: time-sensitive water operations and management scenario evaluations, and longerterm scientific discovery. Whenever the model is updated, we must have a robust calibration-validation workflow in place to facilitate both these types of applications.

For short-term time-bound calibration-validation of the model, we will adopt a point estimation approach wherein ePTM runs with a large set of parameter values will be setup to simulate multiple replicates of each released fish for different reaches within the system. Within each reach, the survival rate and travel time distributions for each of these replicates will be compared with the observed survival rate and travel time distributions that have been estimated from mark recapture studies. Some measure of this comparison will serve as an empirical likelihood function whose value will be optimized by searching through Gaussian process regression fit. The replicated simulated fish corresponding to each fish will give us estimates of uncertainty and allow us to use the Gaussian process surface to fit the true signal rather than the noise in the relationship between the empirical likelihood function and the ePTM model parameters. The key difference between the Gaussian process regression approach adopted here and the emulator approach adopted to calibrate ePTM Version I is that we will be fitting a unique regression surface to each release and each reach so that parameter point estimates can be obtained quickly and in parallel for each reach. We will also perform an out-of-sample validation to evaluate the performance of the model fit. A drawback of the point estimation approach is that it will not be feasible to get high-quality uncertainty estimates around the optimal parameter values. However, this will allow for point estimates and some estimates of uncertainty with relatively fast computational time.

For the long-term calibration-validation process including more robust uncertainty estimates, we have undertaken a rigorous assessment of the optimal workflow needed to optimize parameter values of a stochastic simulation model using rigorous statistical methods. In this approach, recognizing the stochastic nature of the ePTM, the distribution of observed travel times and survival rates within different reaches of the Delta will be compared with distributions obtained from the ePTM Version II simulations. Multiple parameter values are used to simulate travel times and survival rates and these are compared to the observed data using suitable distance metrics or statistical likelihoods. Over multiple training epochs, an evolutionary algorithm generates parameter value sets and those parameter sets that produce small distances between the observed and simulated distributions are favored. To evaluate the applicability of this approach, we have built a simplified "Toy ePTM" that can rapidly produce datasets, evaluate alternative distance metrics, and compare the ability of the calibration method to estimate known parameter values. Once the method has been evaluated on the Toy ePTM, the same approach will be used to calibrate the full ePTM. Examples of statistical methods exhibiting these properties are Approximate Bayesian Computation (ABC) with Sequential Monte Carlo sampling (SMC; Scranton et al. 2014), Particle Swarm Optimization (PSO), and other machine learning algorithms. The primary advantage of these approaches over the GP based emulator is that we can now estimate parameters directly from ePTM Version II model runs instead of using an emulated model of ePTM results. It is also much more straightforward to propagate the sources of uncertainty in the data through the parameter estimation using these approaches than with the GP based emulator. Additionally, the calibration/validation workflow does not require the infrastructure to be rebuilt whenever the model itself changes. Further, as only distance metrics or likelihoods are evaluated, it allows for multiple model hypotheses to be tested simultaneously.

To calibrate the model, we are using the acoustic telemetry data collected between 2006 and 2010 on late-Fall-run Chinook salmon. This dataset with about 1,500 tagged fish in total has been extensively quality controlled and utilized by the scientific community (e.g. Perry et al. 2010). To use the data for calibration, we only retain the first detections at riverine stations (where the flow does not reverse), and last detections at tidal stations (where the flow reverses). To be consistent with the mark-recapture framework that was used to generate survival probabilities, we define domain reaches identical to the definition in Perry et al. (2010). In the calibration, simulated fish are released in the model according to the observed arrival times at upstream ends of reaches, and behavior parameters are calibrated such that the distributions of travel times and survivals through the reaches most closely match the observations. As part of the development of ePTM Version III, we are investigating the use of other acoustic telemetry data that has been continuously collected since 2012.

4.4. *Stakeholder hypotheses of fish migration mechanisms within the Delta*

Apart from the model updates we undertook based on stakeholder and peer review, we are also collecting and cataloging hypotheses on migration mechanisms. These hypotheses include those supplied by various stakeholders in response to the NMFS solicitation. Stakeholder hypotheses reflect valuable domain expertise of the scientific and management community and highlight the truly participative nature of model development in this region. Such inputs are indicative of a genuine interest by key participants to solving challenging multi-disciplinary problems.

We appreciate the science-based critical thinking that has gone into each hypothesis and the underlying motivation to help the modeling team develop a fruitful product. These hypotheses typically are aimed at explaining migration as a function of various environmental drivers and management actions at various scales of motion. Once the ePTM Version II is calibrated and validated, we will test as many of these hypotheses as is possible using our model. Many of these hypotheses may also serve as valuable examples of model validation cases that have not been identified by us. Stakeholder hypotheses generally fall into five categories:

(i) Those that have been already tested: These include null hypotheses and other simple behaviors that can serve as a useful baseline to compare simulated salmon movement against.

(ii) Those that can be tested directly using the ePTM: These hypotheses propose causal relationships between fish movement and environmental inputs at the scale of motion investigated using the ePTM.

(iii) Those that will require additional work: This category involves hypothesized relationships between system-wide flows and operations and overall migration patterns. These also include hypotheses which will require the use of additional data sources, or additional data collection efforts.

(iv) Those that could form the basis of new studies: This category includes mechanisms that have not been explored before in the literature, but have enough supporting evidence in animal migration studies, and could be considered plausible mechanisms of movement.

(v) Those that cannot be tested using the current formulation of the ePTM: While valuable to consider, there are some hypotheses requiring the use of water chemistry models or other biochemical processes not simulated by the ePTM that cannot be tested directly using this model.

We list both the stakeholder hypotheses as well as our initial assessment of how we might test them in Appendix A.

5. **Details of the ePTM model**

To outline some salient differences between ePTM Version II and other approaches, we compare the ePTM Version II with the ECO-PTM and the STARS models, as we believe these models to most realistically represent decision support alternatives in the Delta. Both ePTM Version II and ECO-PTM are largely similar process-based models. The differences lie primarily in the treatment of the survival model, the hydrodynamics and the routing. A fundamental difference between ePTM and the STARS model (Perry et al. 2018) is that the STARS model uses a coarse approximation of the hydrodynamic processes in the Delta, treating the entire Delta as one DSM2 grid cell. This is because Freeport flow is used to drive the model. The STARS model can be considered to be a nine-grid-cell model of the Delta if travel times and survival within each reach defined within the model are driven by the flow through that reach. We list specific comparisons in Table 1.

Table 1. Comparison of ePTM, ECO-PTM and STARS

ePTM Version II	ECO-PTM	STARS
• Windows-based • DSM2 grid defines resolution of model • Instantaneous local hydrodynamics drive behavior at 15-minute timesteps	• Windows- and Linux-based • DSM2 grid defines resolution of model • Instantaneous local hydrodynamics and Eulerian averaged hydrodynamics over multiple tidal cycles drive behavior at 15-minute timesteps	• Platform-independent • Model resolution is over nine sub-domains within the Delta • Tidally averaged flows and gate operations drive daily survival estimates in each model reach
• Redefined parameters in XT model to better describe physical processes in the model under tidally reversing flows	• Using XT model with two main differences relative to the ePTM: using a constant x (reach length) instead of the particles' actual travel distances and obtaining other key parameters (mean free path and random velocity) from previous statistical analyses as opposed to estimating as part of the PTM calibration	• Using XT model with two main differences relative to the ePTM: using a constant x (reach length) instead of the particles' actual travel distances and obtaining other key parameters (mean free path and random velocity)
• Swimming speed drawn from log-normal distribution for each fish at each timestep • Fish's orientation at each timestep is a logistic function of strength of flow around it provided it does not choose to go in the direction it is currently going in. This will result in more realistic and parsimonious representation of fish migration through complex flow regions such	• Swimming speed drawn from normal distribution for each fish at each timestep • Fish's orientation (direction of migration) at each timestep within a DSM2 channel is a logistic function of ratio of mean river flow to standard deviation in flow over past two tidal cycles	• Travel times drawn from a log-normal distribution • Fish orientation not represented

as in tidal channels and near pumping flows		
• Routing through junctions based on streamlines according to Critical Streakline/Bifurcation Streamline theory expected to result in more realistic migration route selection	• Routing in key junctions (Sutter Slough, Steamboat Slough, Delta Cross Channel, and Georgiana Slough) based on statistical models; routing through other junctions is according to flow split	• Routing in key junctions (Sutter Slough, Steamboat Slough, Delta Cross Channel, and Georgiana Slough) based on statistical models
• Direct calibration of ePTM parameters through statistical methods allowing estimation of uncertainty and multiple model comparison (likely ABC-SMC, PSO, or other machine learning approach)	• Travel time-focused calibration using particle swarm optimization	• GLM models are calibrated using MLE or Bayesian methods

6. **Flow-survival relationship within the Delta**

The ePTM is a random fish-track generator in which simulated fish respond to water operations and local hydrodynamics through biological behavior agents. The model can generate many thousands to millions of tracks and ultimate fates (escape to Chipps Island, entrainment at the pumps or mortality by predation) of migratory fish during various scenarios. Within these scenarios, the hydraulics (channel geometry, morphology, network topology), hydrology (flows, flow routing and sea-level rise), water operations (gate and barrier operations and water diversion) and behavior (alternate hypotheses of fish movement rules) can be changed. By averaging or smoothing the model generated fish tracks and performing whatever analysis the decision maker sees fit, they can gain insights on patterns of how real fish will likely respond to management actions. As the behavior models become increasingly realistic with new data and calibration to that data, model confidence can be improved. Even with the relatively simple, yet hydrodynamically and biologically plausible behaviors in the model currently, the model can be used to quantify the uncertainty envelope of the effect of a management action by varying the behavioral parameters about their calibrated values and studying the resulting multiple fish tracks.

The ePTM results can be summarized into monthly survival estimates and uncertainty bounds on those estimates for Sacramento River, Yolo Bypass and Delta-rearing fry that migrate through the Delta as smolts. These estimates are input into the NMFS WRLCM which is used to perform life cycle analysis of the Winter-run Chinook salmon during various operating scenarios which can involve changes to the water management and/or morphology of the delta. The WRLCM and the ePTM also depend on other models such as CALSIM II/III and DSM2 to simulate flows during the various operating scenarios. CALSIM provides boundary conditions which are used to force DSM2. ePTM uses the hydrodynamic flows solved using DSM2 and layers behavior (i.e., fish swimming speed and orientation in response to those flows) and how fish move through the system with a ground velocity that is a combination of the hydrodynamic water velocity and the fish swimming speed.

The ePTM can be used to evaluate migration patterns under alternate management actions, as well as under various alternate operating scenarios. We discuss some specific examples below.

6.1. *Evaluating management actions*

A benefit of developing a model such as the ePTM is that it can be readily used to evaluate water management operations within the Delta. We envision that agencies evaluating the management actions will have the capacity to run the ePTM code with documentation provided by NMFS on a dedicated GitHub site that will become available once the model calibration has been completed and the model has been peer reviewed and published. Consider three examples where the ePTM can be used to evaluate management actions:

1. Estimating entrainment at the CVP and SWP pumps: For various hydrological scenarios developed using CALSIM III, alternative water withdrawal schedules can be prescribed in DSM2, and particles simulating reach-specific fish can be released throughout the Delta and their movement and fate can be tracked. Once the ePTM simulates about three months of fish movements, the ePTM model results can be collected to determine what fraction of fish released in different locations within the Delta were entrained at the pumps. For a typical three month ePTM simulation with 1,000 fish, the runtime is about 10 minutes on a six-core workstation. Using this information, water managers can determine how to optimally withdraw water from the Delta while meeting the ecological objective of minimizing salmon take.
2. OMR flow management to reduce entrainment risk: The natural river flow in the OMR corridor is towards the ocean. However, depending on the freshwater flow in the San Joaquin River, the flood tide may cause flow to be reversed in the OMR corridor. During the flood tide, water can also enter the OMR corridor through Turner and Columbia Cuts and the confluence of Middle River with the San Joaquin River. On longer timescales, pumping operations of the CVP and SWP can reverse flow in the OMR over multiple days. Under these circumstances, pumping freshwater through the Delta Cross Channel might help return the flow in the OMR

towards the ocean. If the pumping levels are very high and the Delta Cross Channel gates are open, water may even be pulled from the Sacramento River into the pumps via the OMR corridor.

The 2019 BiOp (NMFS 2019) proposes several actions to manage exports in such a manner that some running average of OMR flows over 14 days is limited to no more than 2,000, 2,500, 3,500 or 5,000 CFS (depending on applicable criteria, respectively) towards the pumps (NMFS 2019). Such flows are typically considered to be "negative" or away from the natural direction towards the ocean. The trigger for such management action may include monitoring- as well as modeling-based information on turbidity levels in the OMR (for the 2,000 CFS limit), Delta Smelt take (for the 2,000 and 5,000 CFS limits) and annual Winter-run Chinook salmon take thresholds (for the 2,500 and 3,500 CFS limits). The BiOp also requires off-ramps or pumping decreases based on water quality or incidental take cues accumulated or averaged over three days to allow for efficient power-peaking operations at the CVP, and on-ramps or pumping increases once monitoring in the Delta indicates that the migration season for endangered species is over.

The ePTM can be used to evaluate the effectiveness of these actions in near-real time. Multiple DSM2 simulations of two-week to one-month duration with proposed pumping actions can be conducted based on planning simulations current till the trigger events. By applying observed acoustic telemetry-based fish distributions within the Delta as initial release conditions within the ePTM, the DSM2 simulations can be used to drive multiple instances of the ePTM. The estimated take at the pumps can then be evaluated for each model instance to determine the optimal course of action.

3. <u>Evaluating the influence of habitat restoration on migration timing and survival</u>: There are numerous potential direct and indirect impacts of habitat restoration on salmon behavior and biology. For example, by rearing longer in the Sacramento River and its tributaries, by the time fish arrive in the Delta, they will be larger and stronger, and might exhibit faster swimming behavior. However, longer residence times upstream of the Delta will mean that salmon enter the system later in the year during warmer months, when the water temperature is warmer and may lead to thermal tolerance regimes more suitable to predators than to migrating salmon. Additionally, it is likely that improved habitat upstream will result in greater numbers of smolts arriving in the Delta. Furthermore, habitat improvement within the Delta may include

submerged aquatic vegetation and predator removal, which might result in lower predation risk.

The outcomes of these influences can be readily simulated using the ePTM. By modifying the timing of entry and numbers of fish released within the Delta in the model within a given hydrologic scenario and pumping schedule developed using CALSIM III, the upstream habitat benefits can be captured in the ePTM. We note that certain habitat-related analyses cannot be performed currently with the ePTM. For example, the ePTM explicitly does not include size or temperature related behavior or the hydrodynamic and phenotypic effects on submerged aquatic vegetation.

6.2. *Integration with the Life Cycle Model*

The WRLCM is a stage structured population dynamics model in which different life-stages of salmon are modeled using specific statistical and process-based models on a monthly timestep (Hendrix et al. 2014). Within the WRLCM, the ePTM provides monthly survival values for migrating Winter-run Chinook salmon that rear in the Sacramento River, the Yolo Bypass and the Delta (Figure 2) (Hendrix et al. 2017) used to predict population abundances at ocean entry, and subsequent adult escapement, spawning population sizes and Delta entry timing of the next generation of juveniles. In this manner, the ePTM feeds into the larger model over the multi-year or multi-decadal span of the population dynamics simulation. An advantage of the ePTM is that it can be run independently of the WRLCM, and results can be rescaled according to the abundances predicted by the WRLCM in each year of a multi-decadal scenario. This allows the ePTM to be a fully standalone tool. Additionally, within the WRLCM, models such as ECO-PTM or STARS can be interchanged with the ePTM if so desired.

The ePTM also plays a crucial role within the WRLCM as the primary tool to estimate the overall survival during the migration through the Delta on a monthly timescale. Crucial to the accurate estimation of overall survival is the relationship between freshwater flow and survival within the Delta (Perry et al. 2018). This is one of the most stressful passages in the migratory lifestage of Chinook salmon. We had demonstrated in the past that ePTM Version I is able to recover flow-survival relationships over different reaches as well as the whole Delta reasonably well using the XT model coupled with the movement dynamics in the ePTM (Sridharan et al. 2016). Due to its process-based formulation, it is also able to qualitatively recover the impacts of gate operations and South Delta pumping on overall survival. We expect that ePTM Version II will recover this relationship as well.

A salient feature of the WRLCM is its ability to simulate the effect of habitat restoration expressed through area and carrying capacity increases on overall population levels of salmon (Figure 2) (Hendrix et al. 2014). While it is known through beach seine surveys and trawling data that salmon fry rear in the Delta, the exact habitat usage patterns are not yet determined. Habitat restoration upstream of the Delta might result in fewer number of fry that rear within the Delta. On the other hand, habitat improvement within the Delta may result in increased survival of those fry that rear within the Delta. However, the relationship between upstream and in-Delta habitat restoration and the habitat use and survival of fry that rear within the Delta is poorly understood. For this data-scarce problem, the ePTM can be used in two ways to gain insight into habitat use by Delta-rearing fry.

In the past, to simulate the migration and fate of Delta-rearing salmon fry, we had used the ideal free distribution hypothesis (Shepherd and Litvak 2004) to seed simulated salmon fry in the Delta and perform the ePTM simulations subsequently. In the future, we will adopt a two-step approach:

(i) We will evaluate three hypotheses representing a density-independent habitat use model, an involuntary habitat use model, and a density-limited habitat use model. We will simulate the fry distribution either using the ideal free distribution, or by routing passive particles in the ePTM (we consider fry to have poorly developed swimming capabilities compared to smolt) to various locations where they will rear due to a carrying capacity-based stopping criteria (Figure 2). This stopping criteria could be determined by the routing of the fry wherein fry will be routed through the system according to the critical streakline hypothesis and adopt an ideal free distribution between successive routing junction. Alternately, the stopping criteria could also be determined by a greedy habitat allocation algorithm wherein early arriving fry will stop at the first suitable habitable DSM2 node until the carrying capacity of that node has been reached, and later arriving fry will move further downstream in search of suitable habitat.

(ii) Then, we will simulate the smolt life-stage three months later using the previously determined distribution of simulated fry with the behavior models in ePTM Version II. We expect this two-step "preferential habitat allocation" model to allow us to understand the dynamics of Delta-rearing salmon migration. We will continue to develop the visualization and analytics tools necessary to correctly interpret the model results.

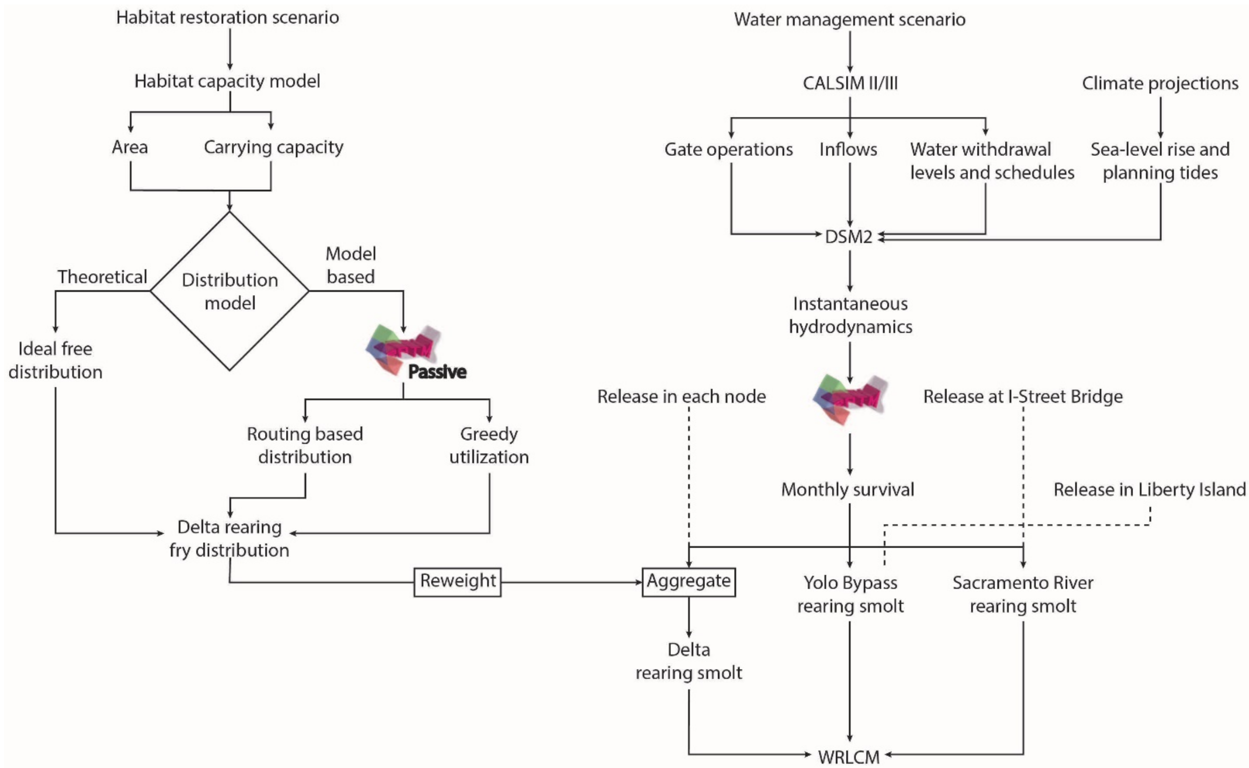

Figure 2. Role of ePTM within the WRLCM. During scenario evaluations, water management alternatives evaluated by CALSIM and climate change projections are used to estimate the instantaneous hydrodynamics in DSM2, which in turn drives the ePTM to predict monthly survival of smolt during their migration through the Delta. In the ePTM, river-rearing, Yolo Bypass-rearing fry and Delta-rearing fry are released respectively at the I-Street Bridge, in Liberty Island and in all the other nodes of the DSM2 grid (dashed lines). Concurrently, habitat restoration alternatives are evaluated using the WRLCM's habitat capacity model to produce area and carrying capacity estimates of different quality habitats at each node of the DSM2 grid. These estimates can be used in conjunction with a distribution model to estimate the distribution of Delta-rearing fry, which will be used to reweight the survivals computed from fry released throughout the Delta.

7. Timeline

Making fundamental changes to the DSM2-PTM code to ensure that the model is self-consistent, i.e., the hydrodynamics and behaviors perform as intended has been time-consuming (Table 1). In particular, incorporating a process-based junction routing model has required substantial changes to the intricacies of the DSM2-PTM code which has been resource intensive (Table 1). While making these changes, we have been careful to ensure that data sources on flow and turbulence profiles from the Delta itself, either through data or 3D model results, can be integrated into the current framework (Table 1). Finally, the initial investment of resources into the new generalized, calibration/validation workflow has been significant (Table 1).

Table 1. Timeline of ePTM development.

Task	Development lead	Duration
Hydrodynamic consistency	UCSC/NMFS	Sep. 2017 – Jul. 2018
Channel bends, mixing and routing	UCSC/NMFS	Aug. 2018 – Nov. 2019
Lagrangian behaviors	UCSC/NMFS/QEDA	Sep. 2017 – Aug. 2019
Code testing	NMFS/QEDA	Jan. 2019 – Mar. 2020
Calibration methodology development	USGS/QEDA	Oct. 2019 – Mar. 2020
Calibration/validation	USGS/QEDA/NMFS	Apr. 2020 – Apr. 2021
Scenario evaluation with WRLCM	NMFS/QEDA	Jan. 2021 – Apr. 2021
Model sensitivity analysis	NMFS	Aug. 2020 – Mar. 2021
Scientific analysis	NMFS	Jan. 2021 – Jun. 2022
Code sharing and documentation	NMFS/QEDA	Jan. 2022 – Jun. 2022
Peer-reviewed publications	NMFS/USGS/QEDA	Jan. 2021 – Jun. 2022
Workshops and usage training	UCSC/NMFS/USGS/QEDA	Sep. 2021 – Jun. 2022

We have engaged with stakeholders through 5 workshops focused on ePTM Version II. The development has involved significant cross-functional collaboration at every stage of the process, resulting in a scientifically rigorous model.

8. **Deliverables**

Once the model calibration and validation are completed, we will produce several reference documents: a model description which will include details about the model assumptions and formulations, a user manual which will describe how to install and run the model, and an application document that will include instructions on how the model should be applied to evaluate management actions. This last document will synthesize the workflow developed at NMFS to evaluate water operations in the California Central Valley using the ePTM within the WRLCM. Along with the source code and salient results, these documents will be made publicly available through the National Marine Fisheries Service biophysical ecology website as well as a dedicated GitHub repository (see our open data commitment below).

In addition to developing technical documentation for the ePTM, we also expect to develop several scientific papers. In addition to developing ePTM Version II, we have also evaluated various alternatives for representing habitat usage and rearing by Delta-rearing fry. These alternatives allow us to perform ePTM simulations three months after initial entry by fry into the system. This will allow us to use the ePTM to evaluate the effects of habitat restoration alternatives in a quantitative manner. We have already published one manuscript (Sridharan and Hein 2019), a conference proceeding (Sridharan 2020) and one conference poster (Sridharan and Hein 2020) and are currently developing three peer-reviewed manuscripts based on the findings of our ePTM Version III funded research into salmon migration behavior. These manuscripts deal with simplifying migration models, while also gaining a deeper understanding of how fish behave at small timescales from the data. These advances are also allowing us to understand how to seamlessly bridge small-scale behaviors and macro-systemic migration patterns. We will eventually incorporate the findings of this research into ePTM Version III. By using a data-driven scale-bridging approach to represent animal behavior, we will be able to narrow down the behavior hypotheses to the ones that have the best support in the data.

9. **Open data commitment**

We are committed to open access to our data, model and model results. We will make the source code, documentation, model tests, datasets, model results and analyses available on a public GitHub page as soon as the current version of the model is fully calibrated, tested and submitted for publication to a peer-reviewed scientific journal. We will also continue active engagement with stakeholders through regular meetings. In these meetings, we will both discuss the model behavior, as well as provide examples of case studies relevant for decision making. Once the model has been calibrated, we will also share results from simulations through the NMFS Central Valley Salmon Ecology Website.

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Appendix A: Stakeholder hypotheses on Winter-run Chinook salmon migration mechanics

Stakeholder Hypotheses

Here, we list the hypotheses supplied by stakeholders. We also list our interpretation of each hypothesis, the feasibility of testing the hypothesis, and the additional data that may be required to test it.

Legend:
Hypothesis already tested
Can be tested, but confidence will improve with additional data
Can be tested but will require additional work post model calibration
Currently under consideration for a new study
Cannot be tested at this time

S. No.	Hypothesis	Initiator	Development team interpretation	Data requirements	Feasibility
1	Fish have no orientation behavior (essentially neutrally buoyant)	Cramer Fish Sciences	Will do a comparative analysis between the base PTM and the ePTM	Available 1D AT data is sufficient	Hypothesis has been rejected in Sridharan et al. 2017 ASCE paper and other studies.
2	Fish always swim towards the ocean	Cramer Fish Sciences	Can be tested by setting the probability of orienting with the flow as 1 during the ebb-phase and 0 during the flood phase of the tide.	Available 1D AT data is sufficient	No evidence in the literature to show that this is the case
3	Fish swim in the direction of flow during ebb tides, drift upstream during flood tides	Cramer Fish Sciences	Can be tested by setting the probability of orienting with the flow as 1 during the ebb-phase of the tide and 0 during the flood phase.	Available 1D AT data may be sufficient, but also need to look at 2D dataset at Georgiana Slough and need more data and telemetry stations in tidal regions.	Is the subject of two papers being developed for Prop 1 funded scientific research not part of ePTM development
4	Fish swim in the direction of flow during ebb tides, hold otherwise	Cramer Fish Sciences	Implemented in ePTM Version II and can be tested against the available data	Available 1D AT data may be sufficient, but also need to look at 2D dataset at Georgiana Slough and need more data and telemetry stations in tidal regions	Is the subject of two papers being developed for Prop 1 funded scientific research not part of ePTM development
5	Fish swim toward increasing salinity	Cramer Fish Sciences	Currently, one of many hypothesis for oceanward swimming of fish. Is implemented in ePTM as a general knowledge of oceanward orientation.	Require many more telemetry stations downstream and laboratory behavior studies to confirm	Some evidence is available in the literature supporting this claim
6	Fish continue to move in the direction they were going previously (Lagrangian behavior described in ePTM study plan)	Cramer Fish Sciences	Implemented in ePTM Version II and has significant support in the fine-scale animal movement literature	Qualitative testing is possible using 2D fish tracks available at Freeport, HOR and Georgiana Slough	Only simple implementation is possible in ePTM, but is the subject of two papers being developed for Prop 1 funded scientific research not part of ePTM development
7	Neutrally buoyant, surface oriented or	CDFW	Can test this hypothesis once a	Depth stratified pit tag data (may already be available with CDFW	Need recalibration of the model for each orientation

	bottom oriented particles		baseline ePTM has been established through calibration	or USFWS) to study whether fish are selectively using part of the water column to migrate at various locations throughout the Delta; it may be possible to check calibrated ePTM parameter values to obliquely infer feasibility of one strategy over another	
8	Consider factors affecting swimming direction such as size, length, flow, diversion, water quality, food source	CDFW	Size, length data is highly imprecise for AT studies, so it will be difficult to test these factors	Need to analyze 2D datasets more rigorously before implementing ad-hoc hypotheses in ePTM; need precise size and forklength data which is currently unavailable for AT studies	Part of Prop 1 funded scientific research not part of ePTM development and beyond; impact of water quality is subject of upcoming paper as part of Prop 1 funded scientific research not part of ePTM development.
9	Fish migrating out of the a given drainage swim down a gradient of ("away from") chemical cues associated with the drainage they emerged from on ebb tides and *drift upstream* during flood tides	Baykeeper	Requires additional modeling to quantify chemical gradients to drive behavior	Need laboratory studies and field studies at spatial resolution not currently available to confirm	Can be a new study: Jon has agreed to analyze the requirements and feasibility more thoroughly
10	Fish migrating out of the a given drainage swim down a gradient of ("away from") chemical cues associated with the drainage they emerged from on ebb tides and *hold* during flood tides	Baykeeper	Requires additional modeling to quantify chemical gradients to drive behavior	Need laboratory studies and field studies at spatial resolution not currently available to confirm	Can be a new study: Jon has agreed to analyze the requirements and feasibility more thoroughly
11	Fish follow chemical cues associated with Sacramento River water	Cramer Fish Sciences	Requires additional modeling to quantify chemical gradients to drive behavior	Need laboratory studies and field studies at spatial resolution not currently available to confirm	Can be a new study
12	Fish follow the direction of tidally-averaged flow	Cramer Fish Sciences	Need additional knowledge on fish behavior.	Need behavioral studies of fish and many more telemetry stations within the interior Delta	Impossible to confirm with current data
13	Fish swim in the direction of unnatural duration flood tides	Cramer Fish Sciences	Need additional clarification from proposer	Decomposing the tides from riverine flows and pumping flows is difficult with current harmonic analysis methods and available data	Impossible to confirm with current data