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RESEARCH

Integration of Transport, Survival, and Sampling Efficiency in a Model of South Delta Entrainment

William E. Smith[1]

ABSTRACT

A Bayesian hierarchical model that integrated information about state and observation processes was used to estimate the number of adult Delta Smelt entrained into the southern Sacramento–San Joaquin Delta during water export operations by the California State Water Project and the Central Valley Project. The model hierarchy accounted for dynamic processes of transport, survival, sampling efficiency, and observation. Water export, mark–recapture, and fish facility count data informed each process. Model diagnostics and simulation testing indicated a good fit of the model, and that parameters were jointly estimable in the Bayesian hierarchical model framework. The model was limited, however, by sparse data to estimate survival and State Water Project sampling efficiency. Total December to March entrainment of adult Delta Smelt ranged from an estimated 142,488 fish in 2000 to 53 fish in 2014, and the efficiency of louvers used to divert entrained fish to fish facilities appeared to decline at high and low primary intake channel velocities. Though applied to Delta Smelt, the hierarchical modeling framework was sufficiently flexible to estimate the entrainment of other pelagic species.

KEY WORDS

Bayesian hierarchical model, Sacramento–San Joaquin Delta, Delta Smelt, entrainment, sampling efficiency, State Water Project, Central Valley Project, Tracy Fish Facility, Skinner Fish Facility, pre-screen loss

INTRODUCTION

The process of entrainment is broadly defined as the geographic redistribution of a population via hydrodynamic advection. Southern Sacramento–San Joaquin Delta (South Delta) (Figure 1) entrainment, or advection of fishes into the South Delta, occurs during the process of water extraction and is a primary management concern, particularly for those species with threatened or endangered status (USFWS 2008; NMFS 2009). The abundance of fish lost to entrainment has at times been considered a threat to population viability, and many entrainment mitigation actions have occurred at the expense of water exports and foregone agricultural production (Yoon 2014). Assessing the risk imposed by entrainment on population viability depends on the number entrained, the size of the population,

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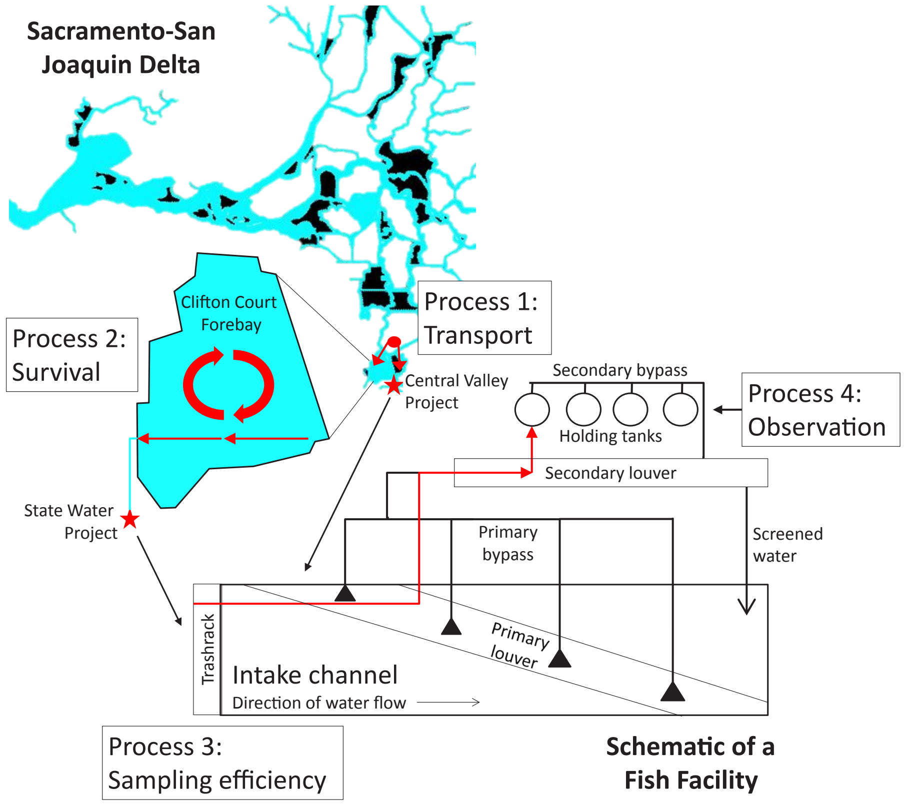

Figure 1 Diagram of the conceptual model of adult Delta Smelt entrainment. The diagram shows the pathway entrained fish follow to the State Water Project through Clifton Court Forebay in *red*. There is no forebay at the Central Valley Project, and fish are only transported through an intake channel.

and the population's productivity or resilience to additional mortality. Understanding the magnitude of entrainment is thus critical for both conservation and management of natural resources. Estimation of the number entrained and evaluation of population effects requires an accounting of a sequence of transport, survival, and sampling processes.

For fish entrained into the South Delta, the conceptual model of the sequence of events from entrainment to observation is that fish move into the southern portion of the Delta and are then transported to the State Water Project (SWP) and Central Valley Project (CVP) through a combination of volitional movement and hydrodynamics (Kimmerer 2008). The most spatially reduced definition of entrainment includes transport to the SWP's Clifton Court Forebay (CCF) or CVP's intake channel, which may be considered points of no return for Delta Smelt, but more spatially expansive definitions include transport through the Old and Middle River corridor, where entrained fish are exposed to predation before arriving near the SWP and CVP (collectively, "the projects"). After transport to regions near the projects, entrained fish are exposed to a source of elevated mortality (also known as pre-screen loss) before becoming available for sampling by the fish facilities located at both water export facilities. Fish available for fish facility counts are subject to an inefficient sampling process (also known as salvage) by a set of primary and secondary louvers, and entrained fish sampled by the louvers are further sub-sampled at a known rate. While these processes are only sparsely informed by data for many species, it is possible to develop a flexible modeling framework that can incorporate better, future data while still taking advantage of the data currently available.

Models to estimate the abundance of South Delta entrained fish have varied, but none have employed hierarchical modeling, resulting in ambiguity in what aspects of uncertainty are represented in the entrainment estimates and the associated errors. The conceptual model of entrainment above outlines three components of a hierarchy of processes that can be described mathematically by conditional probabilities of transport, survival, and sampling (sampling efficiency). Kimmerer (2008, 2011) was the first to estimate adult Delta Smelt (*Hypomesus transpacificus*) entrainment using a single, static expansion factor with a measure of error, but components of the expansion factor, transport, survival, and sampling efficiency vary dynamically with hydrodynamic and other environmental conditions. Another study estimated juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) entrainment rates directly using tagging data (Zeug and Cavallo 2014), but once again, static rates of survival and sampling efficiency were assumed. Accounting for variation in the sequence of events that leads to the observation of entrained fish, through integrated modeling, should lead to a more complete description of process and observation errors and more accurate estimates of entrainment.

The proliferation of Bayesian modeling tools, such as programs WinBUGS and JAGS, has facilitated a more nuanced treatment of uncertainty in models of animal populations (Link et al. 2002). Bayesian hierarchical modeling presents opportunities to integrate diverse sources of information and account for the compounding error associated with a sequence of events or processes (Cressie et al 2009; Kery and Schaub 2011). A prior Bayesian hierarchical model of post-larval Delta Smelt entrainment relied on transport data from a coupled hydrodynamic particle-tracking model (Smith et al., forthcoming). Not surprisingly, simulation testing indicated that entrainment estimates were only accurate to the extent that transport data were accurate, and transport data accuracy declined with later life stages. Additional limitations were a lack of direct information to estimate CCF survival, and the assumption that no mortality occurred at the CVP; however, both of these limitations can be addressed in a model of adult Delta Smelt entrainment.

The Bayesian hierarchical model presented here estimates latent states of abundance, defined as adult Delta Smelt entrainment, and four coupled dynamic processes: transport, survival, sampling efficiency, and observation. The adult model addresses deficiencies identified for post-larvae by taking advantage of adult mark–recapture data to inform survival between entrainment and observation (i.e., pre-screen loss), but since adult transport is an unknown function of behavior and hydrodynamics, modeled transport is limited in spatial extent to the region adjacent to the SWP and CVP. The spatial limitation results in lower estimates of entrainment than if transport and predation in the Old and Middle rivers are accounted for.

METHODS

Study System

Water is extracted from the South Delta to supply over 25 million people with drinking water (CDWR 2011) and to supply a $50 billion agricultural industry in California (CDFA 2017). Water extraction is often sufficient to reverse the net flows in the Old and Middle rivers, resulting in the South Delta entrainment of many native and non-native aquatic species (Grimaldo et al. 2009). Some entrained species are threatened or endangered, such as the small osmerid, Delta Smelt (Bennett 2005; CDFW 2018). The fate of entrained adult Delta Smelt is mortality via direct export from the Delta (Castillo et al. 2012), predation (Clark et al. 2009), thermally induced mortality (Swanson et al. 1998), or reproductive isolation. Fish facilities are designed to screen fish from exported water so that they may be moved by truck and released elsewhere in the Delta. The regional term for this screening and trucking process is “salvage”; however, Delta Smelt survival of the process may be low. Predation (Aasen 2013), injury (Morinaka 2013), and stress (Afentoulis et al. 2013) are potential sources of mortality after screening, and additional mortality from each source is likely after transport and release. Since survival of the screening and trucking process is likely to be

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low, "salvaged" fish are treated as a component of entrainment losses.

Conceptual Model

The conceptual model of adult entrainment comprised four coupled dynamic processes. See Figure 1 for a model diagram that shows the location of each process. For the current model, entrainment was defined as all fish arriving at either the entrance to the SWP's CCF or the CVP intake channel.

1. **Transport.** The proportion of total entrainment attributed to the SWP or CVP was a function of the proportion of total exports going to each. Transport was defined by attribution to either SWP or CVP. Fish in the vicinity of the Projects that did not enter the CCF or CVP intake channel were not considered entrained. This assumption resulted in lower estimates of entrainment, compared to an assumption that transport and mortality began at a point further away from the SWP and CVP.

2. **Survival.** Fish transported to the SWP had to survive CCF and intake channel predation before becoming available for SWP fish facility counts, and fish transported to the CVP had to survive intake channel predation before becoming available for CVP fish facility counts.

3. **Sampling efficiency.** After transport and survival, fish became available for fish facility counts by a set of primary and secondary louvers that acted like a net to divert fish to holding tanks. Predation within diversion (bypass) channels and holding tanks was one aspect of sampling efficiency, though variation in this component has not been quantified. Prior studies of louver efficiency documented variation due to water velocity in the primary intake channel. Preliminary analysis of mark–recapture data indicated that CVP sampling efficiency was maximized at moderate velocities, and declined at both high and low velocities.

4. **Sub-sampling and observation.** Fish diverted by the louvers into holding tanks were sub-sampled at a known rate that was treated as a fixed quantity in the model. Counts of fish in sub-samples were a stochastic process, or random with some expected value.

Delta Smelt Data

Fish Facility Data

Sampling of fishes entrained by the SWP and CVP has been conducted since 1979 at the California Department of Water Resources's Skinner Fish Facility and at the US Bureau of Reclamation's Tracy Fish Facility. Entrained fish that reach the SWP and CVP intake channels are diverted by louvers to holding tanks, where they are sub-sampled and enumerated (Appendix A). Some fish pass through the louvers and become unavailable for observation, and only up to 25% of diverted water and fish are sub-sampled during an approximately 30-minute interval every 2 hours (Karp et al. 1997). Data collected during the months of December–March and years 1993–2016 were used to estimate adult Delta Smelt entrainment. Counts from fish facilities were aggregated by month to avoid severe 0-inflation in later years when Delta Smelt were less abundant.

Mark–Recapture Data

Mark–recapture data yielded direct information about the sampling efficiency of fish facilities and survival of transport to the fish facilities. Four tagging experiments were conducted by subcutaneously injecting adult Delta Smelt of hatchery origin with a dye, and releasing tagged fish at critical junctions in the entrainment and sampling process. Delta Smelt tagging experiments at the Skinner Fish Facility, which samples fish at the SWP, were reported by Castillo et al. (2012). They conducted two experiments. In the first experiment, six independent groups of 100 adult Delta Smelt were tagged and released in the intake channel of Banks Pumping Plant; a fraction were recovered by the Skinner Fish Facility, some were predated in the intake channel, and the remainder passed through the louvers and were exported. The proportion of tagged fish recovered from the intake channel releases can be used to estimate the sampling efficiency of the Skinner Fish Facility, including losses from predation in intake channels. In the second experiment, six independent groups of tagged fish (mean number per group = 1,426) were released in eastern CCF and recovered by the louvers after being exposed to predation in the CCF and the intake channel. The CCF releases provide a combined estimate of pre-screen loss in the CCF and sampling efficiency. The difference between recapture rates of intake and CCF releases was used to estimate the pre-screen loss in the CCF.

Two experiments, paralleling those at the SWP were also conducted at the CVP. Sutphin and Svoboda (2016) reported on Delta Smelt tagging experiments at the Tracy Fish Facility, which samples fish at the CVP. In the first experiment, 67 independent groups of adult Delta Smelt (mean number per group = 110) were tagged and released in the intake channel of Jones Pumping Plant, and a fraction were recovered by the Tracy Fish Facility. Tagged fish in the first experiment were exposed to predation from the piscivore community that resides in the CVP intake channels before being sampled by the louvers. Like the SWP experiments, the first CVP experiment provided information about the sampling efficiency of the Tracy Fish Facility, including losses from intake channel predation. In the second experiment, piscivorous fish were removed from the intake channel using gill nets (Bark et al. 2013). Six independent groups of tagged fish (mean number per group = 25) were released in the CVP intake channel immediately after predator removal, and these fish were exposed to fish facility sampling assuming no predation. The difference between recapture rates of the first and second CVP experiments provided information to estimate intake channel predation. Full census of all fish diverted to holding tanks was completed for all mark–recapture studies.

My use of tagged fish to model Delta Smelt sampling efficiency and survival relied primarily on five assumptions:

1. All tagged fish retained their tag.
2. All tagged fish were recognized at recapture.
3. Tagged fish were representative of untagged adult Delta Smelt.
4. Groups of tagged fish released after CVP predator removals were assumed to experience no predation, and variation in recapture rates after CVP predator removals was attributed to sampling efficiency.
5. Recaptures of fish released in intake channels occurred in less than 24 hours.

I further assumed that sampling efficiency—measured at the daily scale from tagged fish—represented sampling efficiency for entrained fish counted at fish facilities, which were summarized at the monthly scale.

Water Operations Data

Mean monthly water export rate for the CVP's Jones Pumping Plants and CCF inflow, as a proxy for SWP export rate, were published online in the Dayflow database (*https://www.water.ca.gov*). Castillo et al. (2012), Sutphin and Svoboda (2016), and Bark et al. (2013) included channel velocities measured during CVP mark–recapture experiments, but all other primary channel velocities were calculated by dividing volumetric flow by channel depth, published online by the California Department of Fish and Wildlife (*ftp://ftp.dfg.ca.gov/*), and channel width. CVP channel width was 25.6 m (Reyes et al. 2018), and SWP channel width was calculated by multiplying number of intake bays operating by bay width of 7 m, measured from satellite imagery (GoogleEarth). Export ratios were then standardized by subtracting 0.5 and dividing by the standard deviation of export ratios, and velocities were standardized to have facility-specific mean 0 and standard deviation 1.

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Mathematical Model

The model hierarchy began with an unobserved latent state of abundance of entrained fish $\delta_{y,m}$ in month m and year y (Table 1), which represented Delta Smelt arriving at either the entrance to the SWP's CCF or the CVP intake channel.

Table 1 Definitions of all indices, data, and parameters used to model adult Delta Smelt entrainment

Symbol	Description
Indices	
i	mark–recapture trial number
m	month
y	year, where December is included with the subsequent calendar year
FF	fish facility
Data	
$n_{\mathrm{SWP,Forebay,i}}$	number tagged in SWP CCF tagging experiment
$r_{\mathrm{SWP,Forebay,i}}$	number of recaptures in SWP CCF tagging experiment
$n_{\mathrm{CVP,predator\ removal,i}}$	number tagged in CVP predator-removal tagging experiment
$r_{\mathrm{CVP,predator\ removal,i}}$	number of recaptures in CVP predator-removal tagging experiment
$n_{\mathrm{FF,intake,i}}$	number tagged in intake channel tagging experiment
$r_{\mathrm{FF,intake,i}}$	number of recaptures in intake channel tagging experiment
$obs_{\mathrm{FF,y,m}}$	number observed at fish facilities
$export.ratio_{\mathrm{m,y}}$	ratio of SWP exports to total exports
$velocity_{\mathrm{FF,y,m}}$	primary channel velocity
$\rho_{\mathrm{FF,y,m}}$	sub-sampling rate
Parameters	
$\delta_{\mathrm{y,m}}$	latent state of the total number of entrained adult Delta Smelt
α	logistic regression parameter of transport model
β_{Forebay}	logistic regression parameter of CCF survival model
β_{intake}	logistic regression parameter of intake channel survival model
γ	logistic regression parameter of sampling efficiency model
$\sigma_{transport}$	transport error
$\sigma_{sample,\mathrm{FF}}$	sampling error
$p_{transport,\mathrm{y,m}}$	probability of transport to SWP
$p_{survive,\mathrm{Forebay}}$	survival probability of CCF
$p_{survive,\mathrm{intake}}$	survival probability of intake channel
$p_{sample,FF,\mathrm{y,m}}$	sampling probability

Transport

Entrained fish were then transported to either the SWP or the CVP with year–month specific logit-normal transport rate $p_{transport,\mathrm{y,m}}$ for transport to the SWP. The quantity $1-p_{transport}$ represented transport to the CVP. Transport was informed by the proportion of exports going to the SWP *export.ratio*. A logit-normal model of $p_{transport}$ was developed that used *export.ratio* as a covariate and allowed to vary by month m and year y with standard deviation $\sigma_{transport}$.

$$\mathrm{logit}(p_{transport,\mathrm{y,m}}) \sim \mathrm{Normal}\left(\alpha_1 * \left(export.ratio_{\mathrm{y,m}} - \alpha_2\right), \sigma_{transport}\right), \tag{1}$$

where α were logistic regression parameters and α_2 was fixed at 0. The model structure represented the assumption that $p_{transport}=0.5$ when $export.ratio=0.5$. If α_2 was *export.ratio* at 50% transport and standardized $export.ratio=0$ when export volumes were equal between SWP and CVP, the model was forced to split δ equally between the two facilities when exports were the same.

Survival and Sampling Efficiency

Mark–recapture experiments in CCF provided data to estimate forebay survival probability $p_{survive,\mathrm{Forebay}}$, and intake channel survival probability $p_{survive,\mathrm{intake}}$ was informed by the difference between recapture rates before and after CVP intake channel predator removal. $p_{survive}$ were minimally informed by only six mark–recapture samples at each facility, so process variation ($\sigma_{survival}$) was not modeled to avoid overfitting. $p_{survive}$ were modeled with logistic regression parameters β_{Forebay} and β_{intake},

$$\mathrm{logit}(p_{survive,\mathrm{Forebay}}) = \beta_{\mathrm{Forebay}} \text{ and } \mathrm{logit}\left(p_{survive,\mathrm{intake}}\right) = \beta_{\mathrm{intake}}. \tag{2}$$

Mark–recapture experiments in the intake channels of the SWP and CVP provided data to estimate fish facility *FF*-specific sampling efficiencies $p_{sample,\mathrm{FF,y,m}}$. The p_{sample} probabilities were found to vary by primary channel velocity and reach an asymptotic value at moderate velocities (Castillo et al. 2012; Sutphin and Svoboda 2016; Smith et al., forthcoming); hence, p_{sample} were stochastically modeled as a second-order polynomial function of *velocity*, regression parameters γ, and standard deviation σ_{sample}.

$$\mathrm{logit}(p_{sample,\mathrm{FF,y,m}}) \sim \mathrm{Normal}\left(\left(\begin{array}{c}\gamma_0 + \gamma_1 * velocity_{\mathrm{FF,y,m}} + \\ \gamma_2 * velocity^2_{\mathrm{FF,y,m}}\end{array}\right), \sigma_{sample}\right). \tag{3}$$

Preliminary data analysis indicated that sampling efficiency parameters could not be estimated independently for SWP and CVP, because of the low number of mark–recapture trials at the SWP. σ_{sample} and the linear and quadratic regression terms were therefore assumed to be equal between the two fish facilities. Based on results from post-larval entrainment modeling, potential variation in sampling efficiency from variation in fish length was assumed negligible. Length-based selectivity of fish facility louvers does not vary at lengths greater than 45 mm FL (Kimmerer 2008; Smith et al., forthcoming), so the effect of length on sampling efficiency could be ignored for adults, which are generally larger than 45 mm FL by December when adult salvage is typically first observed.

Recovery probabilities of CCF-released fish were the product of CCF survival, intake channel survival, and sampling efficiency; recovery probabilities of SWP intake channel releases were the product of intake channel survival and sampling efficiency. Experiments to estimate SWP intake channel survival, paralleling those after predator removals at the CVP, have not been conducted, so $p_{survive,\mathrm{intake}}$ was assumed equal at the two fish facilities.

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Recoveries r_{FF} from mark–recapture trial i were binomially distributed,

$$r_{\text{SWP,Forebay,i}} \sim \text{Binomial}\left(p_{survive,\text{Forebay}} * \begin{matrix} n_{\text{SWP,Forebay,i}}, \\ p_{survive,\text{intake}} \end{matrix} * p_{sample,\text{SWP,i}}\right). \quad (4)$$

$$r_{\text{SWP,intake,i}} \sim \text{Binomial}\left(n_{\text{SWP,intake,i}},\ p_{survive,\text{intake}} * p_{sample,\text{SWP,i}}\right) \quad (5)$$

CVP intake channel recovery rates were the product of survival and sampling efficiency. Recovery probabilities from experiments after predator removals from the CVP intake channel were assumed to be equal to sampling efficiencies alone, thus assuming no predation on this group of tagged fish,

$$r_{\text{CVP,intake,i}} \sim \text{Binomial}\left(n_{\text{CVP,intake,i}}, p_{survive,\text{intake}} * p_{sample,\text{CVP,i}}\right) \quad (6)$$

$$r_{\text{CVP,predator removal,i}} \sim \text{Binomial}\left(n_{\text{CVP,predator removal,i}},\ p_{sample,\text{CVP,i}}\right). \quad (7)$$

Sub-Sampling and Observation

The number of fish expected in fish facility counts was the product of the abundance of entrained fish $\delta_{y,m}$, transport, survival, sampling efficiency and sub-sampling rates. Sub-sampling probability $\rho_{\text{FF,y,m}}$ was calculated as sample time divided by export time, and was treated as a fixed value in the model. Fish facility counts $obs_{\text{FF,y,m}}$ were Poisson-distributed. Other options for modeling count data, given an estimate of abundance and probability of observation, include the binomial and negative binomial distributions.

$$obs_{\text{FF,y,m}} \sim \text{Poisson}\left(\left\{\begin{matrix} \begin{matrix}\delta_{\text{y,m}} * p_{transport,\text{y,m}} * p_{survive,\text{Forebay}} * \\ p_{survive,\text{intake}} * p_{sample,\text{SWP,y,m}} * \rho_{\text{SWP,y,m}}\end{matrix} & \text{for SWP} \\ \begin{matrix}\delta_{\text{y,m}} * \left(1 - p_{transport,\text{y,m}}\right) * \\ p_{survive,\text{intake}} * p_{sample,\text{CVP,y,m}} * \rho_{\text{CVP,y,m}}\end{matrix} & \text{for CVP}\end{matrix}\right\}\right) \quad (8)$$

Simulated Data

The model described above was uniquely specified, and the joint estimability of many parameters was questionable; thus, the model was tested using new data sets simulated from known parameter values. Assuming the operating model described above, 200 sets of true parameter values (α, β, γ, and δ) were drawn from the prior distributions used in model fitting. From known parameter values, new mark–recapture and fish facility count data were simulated (Equations 4–8). We evaluated the estimability of each parameter using three metrics that compared estimated to true values: 95% credible interval coverage of the true value; z-scores that indicated deviations between true simulated and estimated values;

$$z_{\text{y,m}} = \left(\text{mean}\left(\delta_{estimated,\text{y,m}}\right) - \text{mean}\left(\delta_{true,\text{y,m}}\right)\right) / \text{sd}\left(\delta_{estimated,\text{y,m}}\right), \quad (9)$$

and shrinkage that indicated the change in error between posterior and prior distributions

$$shrinkage_{\text{y,m}} = 1 - \text{sd}\left(\delta_{posterior,\text{y,m}}\right) / \text{sd}\left(\delta_{prior,\text{y,m}}\right). \quad (10)$$

Shrinkage values near 1 indicated smaller standard deviations of posteriors compared to standard deviations of priors, and shrinkage values near 0 indicated that standard deviations of posteriors did not change from priors. Z-scores should be randomly distributed with median 0. Z-scores of parameters with normally distributed posteriors (e.g. regression coefficients) should take values between −2 and 2, but parameters with skewed posterior distributions (e.g., δ) were expected to produced skewed z-scores. Relationships between z-scores and shrinkage indicated model misspecification.

Model Fitting and Diagnostics

A uniform prior distribution was derived for the natural log of $\delta_{y,m}$ with a range of approximately log(1) to log($2e^7$). Total population abundance may have ranged as high as $2e^6$ during the time-period modeled (Polansky et al. 2019), and use of a prior with support up to an order of magnitude greater than abundance over the entire range of the population was considered uninformative. All logistic regression priors α, β, and γ were drawn from $\text{Normal}\left(\mathbf{0}, \sqrt{\pi^2/3k}\right)$) distributions, where k denoted the number of parameters in the specific logistic model. A $\text{Normal}\left(\mathbf{0}, \sqrt{\pi^2/3k}\right)$ distribution induced the desired uninformative Uniform(0,1) probability distribution on inverse logistic transformation (Newman 2003). Penalized complexity prior distributions Exponential(3.07) were assigned to sampling standard error σ_{sample}, assuming a prior probability of 0.01 that σ exceeded a value of 1.5 (Simpson et al. 2017). As preliminary data analysis revealed greater potential for bias in transport error $\sigma_{transport}$, a weakly informative Gamma(2,3) prior was applied to transport error, assuming that transport error was greater than 0 and less than 2.

The model was fit using R package R2jags (Su and Yajima 2015) and Bayesian statistical software JAGS (Plummer 2003). R code to run the model can be found in Appendix B. A burn-in period of 50,000 was followed by 100,000 samples of posterior distributions. Posterior samples were thinned by 25 to address autocorrelation within Markov chain Monte Carlo (MCMC) chains. Model convergence was assessed by comparing the trace plots of six chains of each model parameter and using Gelman and Rubin's diagnostic (Gelman and Rubin 1992). Model convergence was reached if trace plots showed that all chains were sampling stationary parameter distributions that did not shift with additional samples, and if Gelman and Rubin's statistic was less than 1.05 for all parameters. Correlation between parameters was assessed by calculating coefficients of determination (R^2) for all pairwise combinations of parameter posteriors. Fish facility count residual plots were used to evaluate model fit and bias.

A graphical posterior predictive check was performed and Bayesian P-values calculated for fish facility count data. Posterior predictive checks and Bayesian P-values are based on the premise that a model which sufficiently describes the process that generates observations should be able to replicate observations and their variation. New data, corresponding to each observation, were simulated from joint posterior samples of model parameters. Simulated and observed data were compared using the Freeman–Tukey goodness of fit statistic FT

$$FT_{observed} = \sum\left(\sqrt{observed} - \sqrt{expected}\right)^2 \text{ and}$$

$$FT_{replicated} = \sum\left(\sqrt{replicated} - \sqrt{expected}\right)^2;$$

(Cressie and Read 1984), calculated for each simulated and observed data point. In a well defined model with sufficient fit, approximately half of joint posterior samples of $FT_{replicated}$ are greater than $FT_{observed}$, and Bayesian P-values are approximately equal to 0.5. P-values near 1 or 0 indicate a very low probability that the fitted model can reproduce the observed data, or insufficient fit.

Posterior distributions of δ were compared to estimates of entrainment from a prior model to estimate the number of adult Delta Smelt entrained (Kimmerer 2008; 2011). Kimmerer (2011) reported a salvage expansion factor Θ, that

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when multiplied by the number salvaged, and divided by sub-sampling rate, yielded an estimate of adult Delta Smelt entrainment. Although the distribution of Θ reported by Kimmerer could not be replicated exactly, a lognormal distribution with median = 22-$\sigma^2/2$ and standard deviation $\sigma = 0.22$ approximated the posterior distribution of Kimmerer's (2011) Θ, and these values were used to simulate distributions of entrainment using the Kimmerer model

$$\delta_{Kimmerer,\mathrm{y,m}} = \Theta * \Sigma_{i=1}^{2} obs_{\mathrm{i,y,m}} / \rho_{\mathrm{i,y,m}}, \text{ where} \quad (11)$$

$$\Theta = \mathrm{Lognormal}\left(\log\left(22\right) - 0.22^2/2, 0.22\right). \quad (12)$$

Bayesian hierarchical model estimates of entrainment and associated errors were compared to entrainment estimates derived from the Kimmerer (2011) model using z-scores and Kimmerer-simulated shrinkage. Z-scores for the comparison were calculated from Equations 9, where $\delta_{Kimmerer}$ replaced δ_{true}, and values near 0 indicated similarity between mean posterior dsitributions. Kimmerer-simulated shrinkage was calculated from Equation 10, where sd($\delta_{Kimmerer}$) replaced sd(δ_{prior}), and values near 0 indicated similarity between the posterior error of the Bayesian hierarchical model and Kimmerer estimates of entrainment.

RESULTS

Simulation exercises demonstrated that most model parameters were estimable. 95% interval coverage of true parameter values was at least 94%, and bias in the objective parameter δ (number entrained) was negligible (Table 2; Figure 2). The standard deviations of most posterior distributions shrank from their prior distributions (posterior shrinkage > 0) (Figure 3), indicating that the data were sufficient to inform parameters. Z-scores for all parameters were centered on 0, and the 95% interval of z-scores among all simulations were between -2 and 2 for most parameters. Note that z-scores for the number entrained δ were expected to be skewed, producing more negative z-scores, because of the lognormal prior distribution

Table 2 Results of simulation experiment, showing 95% credible interval coverage of the true simulated value and z-scores of all model parameters, among 200 simulated sets of true values and observations

Process	Parameter	95% coverage	95% interval of z-scores
Transport	α_1	0.97	−1.71, 1.85
	$\sigma_{\mathrm{transport}}$	0.94	−2.07, 1.71
Survival	β_{Forebay}	0.98	−2.00, 1.53
	β_{intake}	0.99	−1.49, 1.11
Sampling	γ_0	0.97	−1.48, 1.74
	γ_1	0.97	−1.93, 1.77
	γ_2	0.97	−1.80, 1.78
	σ_{sample}	0.97	−1.28, 1.78
Abundance	δ	0.98	−2.17, 1.18

that was used. Transport error was associated with a greater fraction of z-scores outside of the range -2 to 2, indicating potential for bias in this parameter. There did not appear to be any relationship between error (z-score) and posterior variance (shrinkage) for any parameter. Compared to other parameters, transport errors $\sigma_{transport}$, appeared to be the least estimable by the Bayesian hierarchical model, with the lowest 95% interval coverage and greatest range of z-scores. Furthermore, inclusion of $\sigma_{transport}$ in the model fit to Delta Smelt resulted in very little change between prior and posterior, indicating that transport error was not informed by the model or available Delta Smelt data. $\sigma_{transport}$ was therefore dropped from the Delta Smelt model, and Equation 1 was modified to $\mathrm{logit}(p_{transport,\mathrm{m,y}}) = \alpha_1 * (export.ratio_{\mathrm{m,y}} - \alpha_2)$.

For modeled years 1993–2016, total December to March entrainment of adult Delta Smelt ranged from a mean posterior distribution of 142,488 fish in 2000 to 53 fish in 2014 (Table 3), and coefficients of variation (standard deviation/ entrainment estimate) were relatively high, ranging from 0.54 to 1.39. For convenience, December estimates are included with the subsequent calendar year; for example, December 1992 estimates are listed with January–March 1993 estimates. The abundance of entrained adult fish appeared to be lower in the late-1990s,

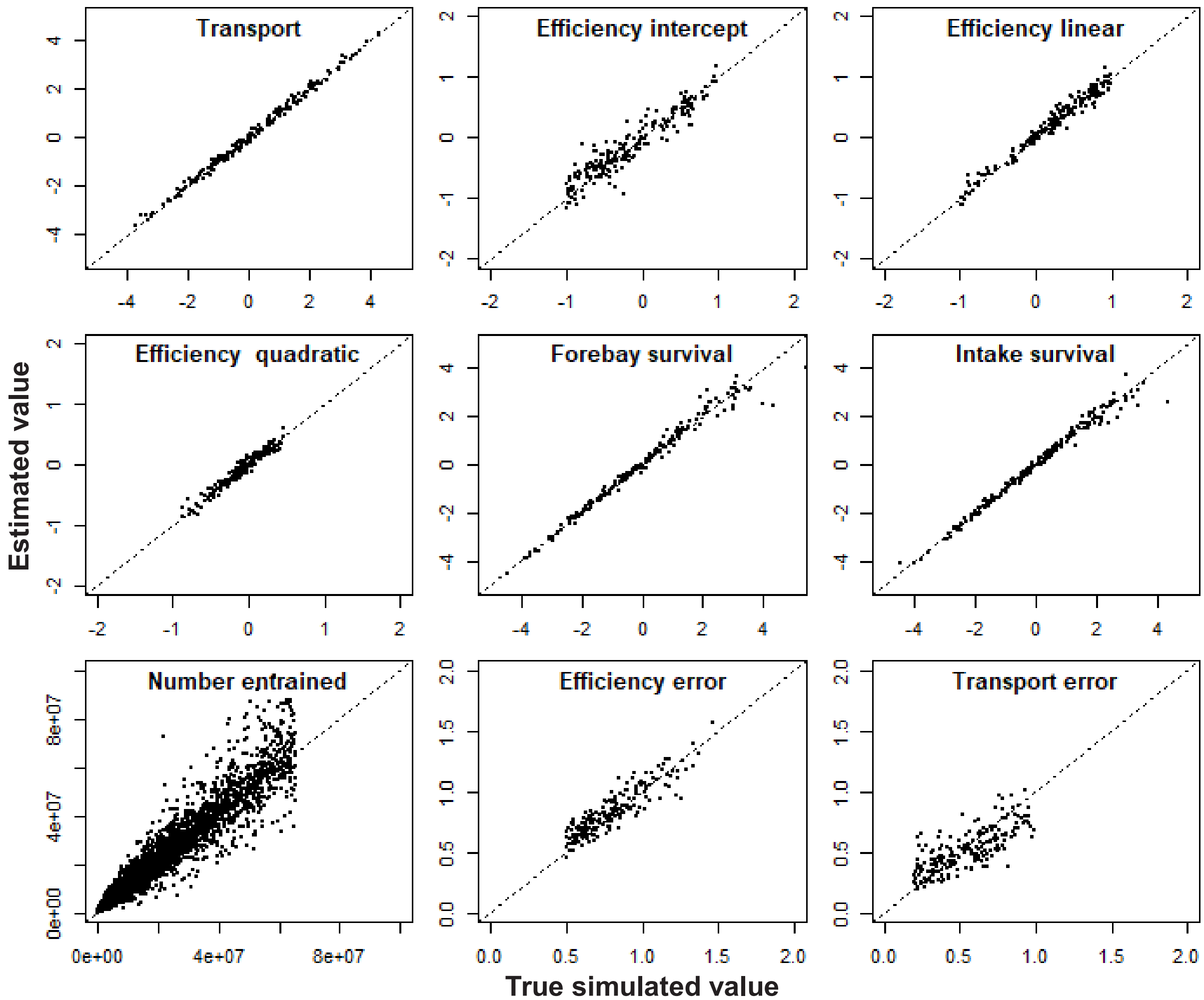

Figure 2 True simulated versus estimated (posterior mean) values for all model parameters, among 200 sets of simulated parameters and observations. The dashed line indicates a 1-to-1 relationship.

before reaching high levels in the early 2000s and declining again by 2007 (Figure 4). Summaries of the posterior distributions of all transport, survival, and sampling efficiency parameters can be found in Table 4. Mean posterior CCF survival was 0.39 (95% credible interval = [0.29, 0.55]), and the intake channel survival estimate was 0.93 (95% credible interval = [0.80, 0.99]). Sampling efficiency model estimates indicated that efficiency was maximized at moderate primary channel velocities and declined at very low and very high channel velocities (Figure 5).

All diagnostics indicated adequate model fit. Bayesian P-values were 0.35 and 0.45 for SWP and CVP fish facility count data, respectively; the estimated model was sufficient to reproduce the observed data. Standardized residuals ranged −1.4 to 1.1 (Figure 6). Inflated error at low predicted values was produced when low values of expected salvage were divided by low values of the joint probability of transport, survival, and sampling. The largest salvage events were the best fit by the model and corresponded to the largest entrainment estimates. All residual posterior distributions contained 0, because cases of poor fit were accounted for by poor precision in estimates. All posterior distributions of errors and regression parameters appeared to shift and contract from their prior distributions (Figure 7), indicating that each was informed by the available data for adult Delta Smelt. Modest posterior correlations ($R^2 = 0.43$) were evident

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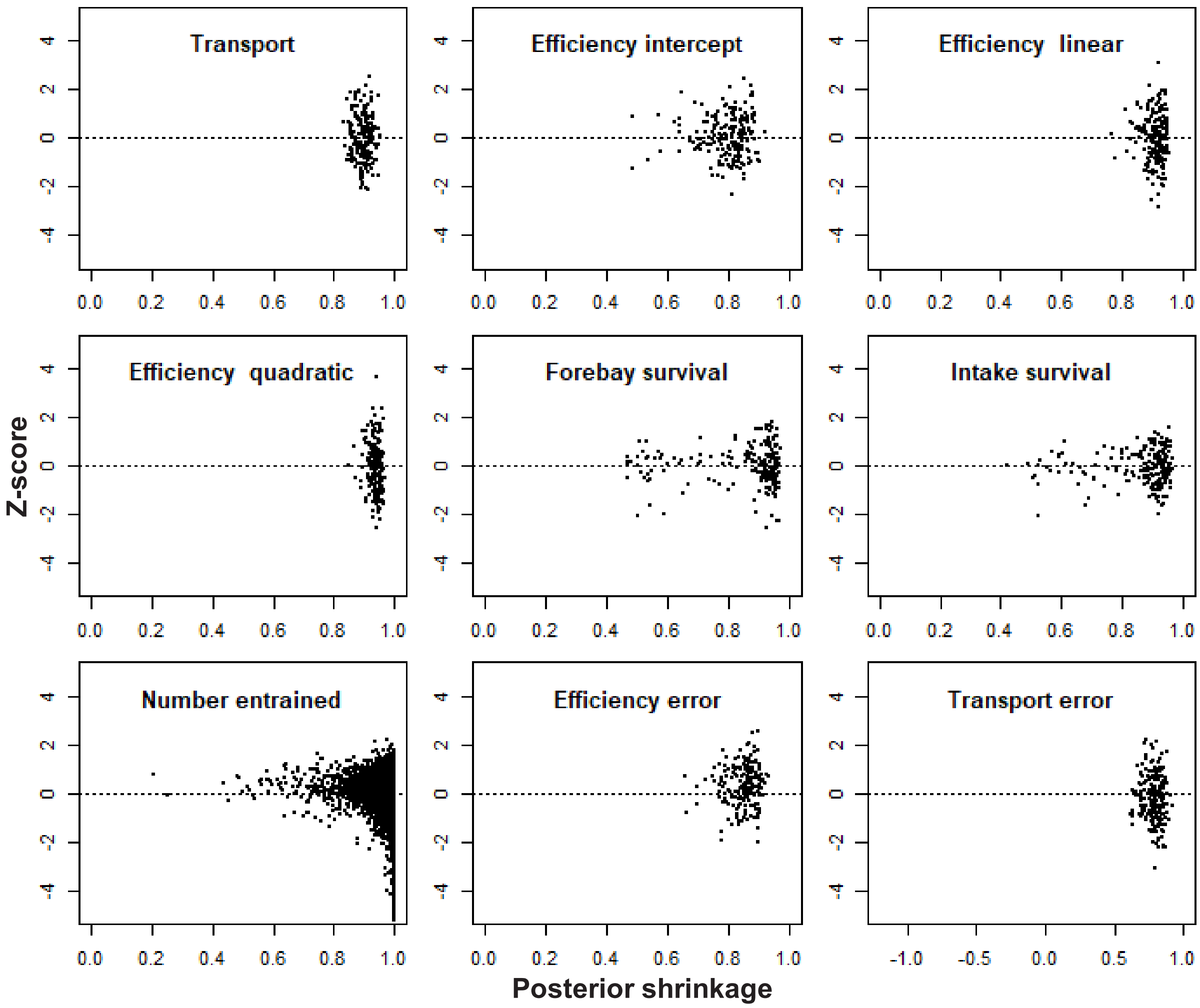

Figure 3 Z-scores versus posterior shrinkage for all model parameters, among 200 sets of simulated parameters and observations. Z-scores represent deviations in estimated values (posterior means) from true simulated values, and higher values of posterior shrinkage represent greater change in posterior variances from prior variances.

between the linear and quadratic parameters of the louver efficiency model but not among other model parameters ($R^2 < 0.1$).

Compared to a previous model to estimate the entrainment of adult Delta Smelt (Kimmerer 2008; 2011), Bayesian hierarchical model estimates were of similar magnitude but generally lower and associated with greater error (Figure 8). Z-scores were negative for all year–month combinations, demonstrating lower hierarchical model estimates. Values of Kimmerer-replicated shrinkage were less than 0.5 or negative, demonstrating greater error associated with most hierarchical estimates of entrainment. Periods with the greatest discrepancies between hierarchical and Kimmerer model estimates (lowest z-scores) had similar error estimates (shrinkage near 0), while periods with lower discrepancies between hierarchical and Kimmerer model estimates (z-scores near 0) were associated with greater error (shrinkage > 0).

DISCUSSION

The Bayesian hierarchical model presented here was a representation of the conceptual model of entrainment as a sequence of events beginning with transport to the SWP and CVP fish facilities and culminating in counts from sub-samples at fish facilities. Though similar to a past model of adult Delta Smelt entrainment (Kimmerer 2008; 2011), the model presented here improved upon

Table 3 Estimates of adult Delta Smelt entrainment. The month of December is included with estimates from January–March of the subsequent calendar year.

Year	Entrainment estimate (standard error)
1994	4,719 (3,347)
1995	24,499 (15,340)
1996	49,294 (35,993)
1997	11,069 (10,128)
1998	6,342 (4,153)
1999	12,793 (10,338)
2000	142,488 (125,105)
2001	97,853 (92,434)
2002	54,559 (44,486)
2003	116,495 (62,959)
2004	119,356 (105,203)
2005	24,292 (33,751)
2006	3,320 (2,406)
2007	221 (227)
2008	3,495 (2,886)
2009	521 (581)
2010	676 (529)
2011	459 (321)
2012	2,168 (1,275)
2013	2,792 (1,815)
2014	53 (61)
2015	759 (619)
2016	119 (112)

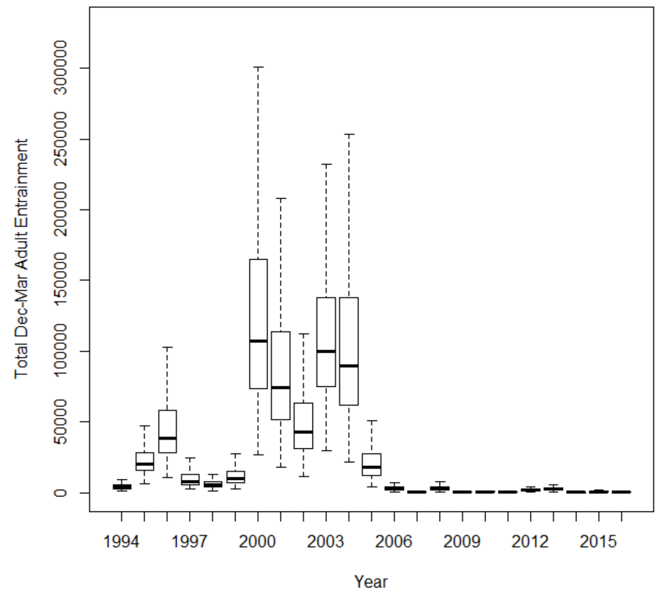

Figure 4 Posterior distributions of adult Delta Smelt entrainment

Table 4 Posterior means and 95% credible intervals (parentheses) of all transport, survival, and sampling efficiency parameters

Process	Parameter	Estimate
Transport	α_1	1.17 (0.77, 1.57)
Survival	$\beta_{Forebay}$	−0.46 (−0.90, 0.19)
	β_{intake}	2.55 (1.39, 4.53)
Sampling	γ_0	−0.92 (−1.34, −0.50)
	γ_1	−0.19 (−0.41, 0.04)
	γ_2	−0.42 (−0.61, −0.23)
	σ_{sample}	1.31 (1.12, 1.54)

the former method by modeling dynamic rather than static transport, survival, and sampling probabilities, and by developing a likelihood that did not necessarily result in estimates of 0 entrained when 0 fish were observed at fish facilities. In general, the hierarchical and Kimmerer models provided similar estimates of the number of Delta Smelt entrained, but hierarchical model estimates of entrainment were lower and associated with greater error compared to the Kimmerer model. Rather than a limitation of the Bayesian hierarchical estimates, the greater entrainment error estimates should be considered evidence of the *advantages* of the hierarchical approach. Entrainment estimates quantify a greater fraction of the uncertainty associated with transport, survival, and sampling efficiency than was previously possible, and the relatively high levels of error were associated with low sample sizes or noise in the data that informed each process. This effect is apparent in the simulation results in the combination of high coverage and range of z-scores for entrainment estimates; though error existed in estimates (non-0 z-scores), the uncertainty in estimates meant that true values were captured in 95% credible intervals.

Kimmerer modeled transport from a more distant location, the lower Old and Middle River, compared to the hierarchical model,

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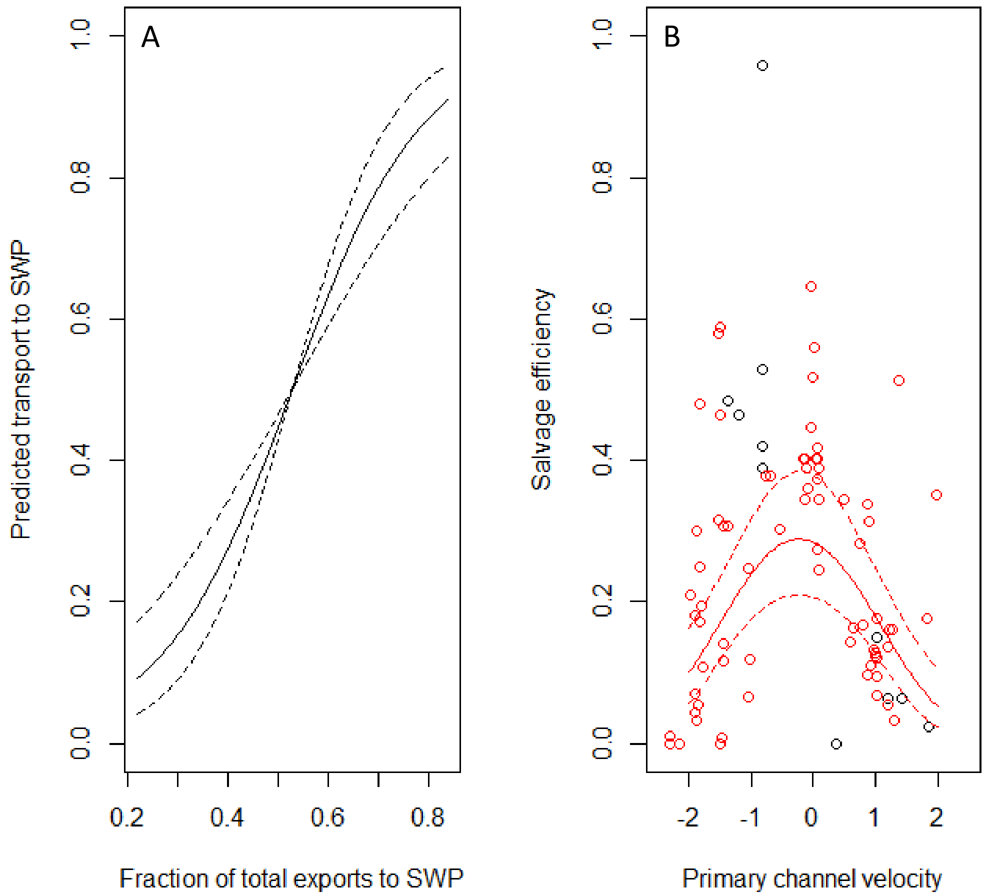

Figure 5 Transport (**A**) and sampling efficiency dynamics (**B**) estimated by the model. Median estimated rates are depicted with *solid lines*, and 95% credible intervals are shown with *dashed lines*. The proportion transported to the State Water Project (SWP) was an unobserved quantity, but the sampling efficiency model was informed by mark–recapture data. Recapture rates, divided by survival rates, are indicated by *black open circles* for SWP data and *red open circles* for Central Valley Project data. Efficiency predictors were standardized to have facility-specific mean 0 and standard deviation 1.

which modeled transport from a region near the Projects. By modeling transport as a function of Old and Middle River flows, Kimmerer accounted for a greater fraction of entrained fish that died before becoming available for observation; however, the Kimmerer transport model introduced unknown biases by assuming that hydrodynamic conditions, represented by Old and Middle River flows, were a proxy for the movement of entrained fish.

The choice to restrict the model of transport to a region near the water export facilities was dictated by data availability rather than biological realism. While the transport of earlier life stages may be modeled like a passive particle in hydrodynamic models, adult behaviors complicate models of their transport. The model presented here is sufficiently flexible to incorporate future information about adult Delta Smelt transport, such as transport rates developed from 3-D particle-tracking and hydrodynamic models that account for environmental cues such as tidal stage and turbidity (Gross et al. 2017; Korman et al. 2018). The Bayesian hierarchical model treated transport probabilities as binomially distributed with two possible outcomes: transport to the SWP or transport to the CVP. A more expansive treatment of the spatial distribution of entrained fish is possible if transport probabilities are multinomially distributed, with some probability of being transported back downstream to relative

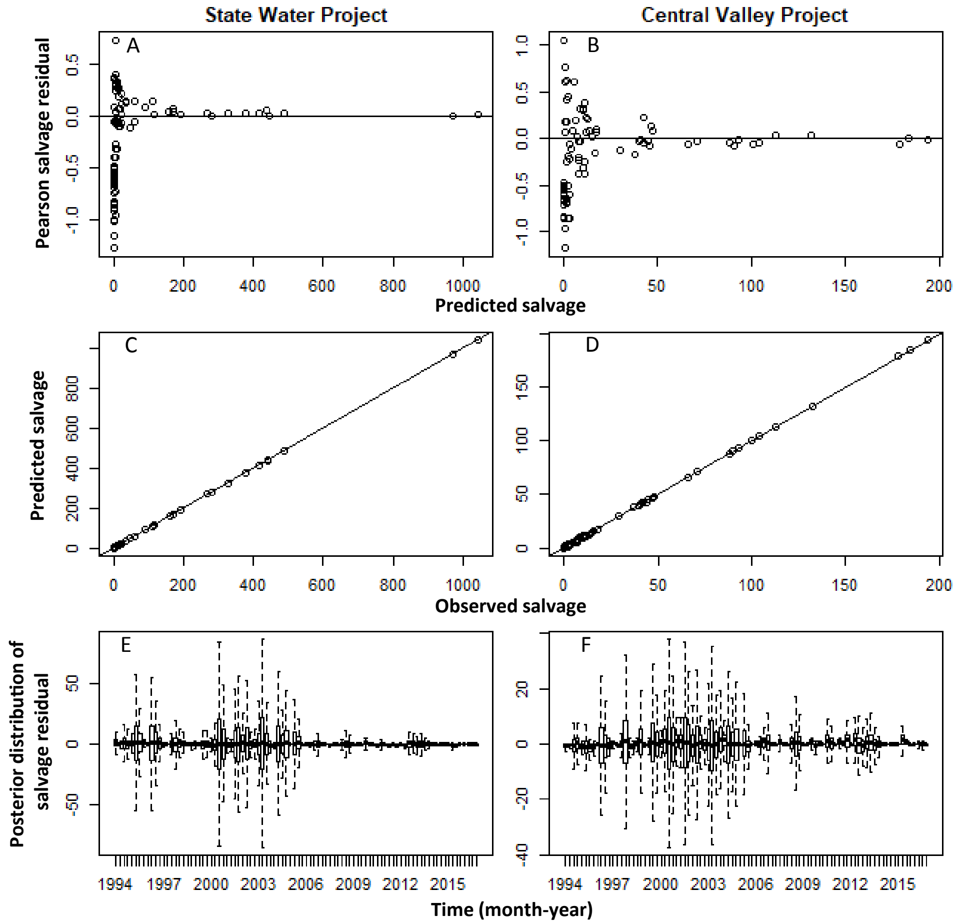

Figure 6 Fish facility count residual plots. *Top panels* (**A** and **B**) show standardized residuals versus predicted fish facility count. Observed versus predicted fish facility count is shown in the *middle panels* (**C** and **D**); the solid line shows a 1-to-1 relationship. The time-series of posterior distributions of Pearson residuals is shown in the *bottom panels* (**E** and **F**).

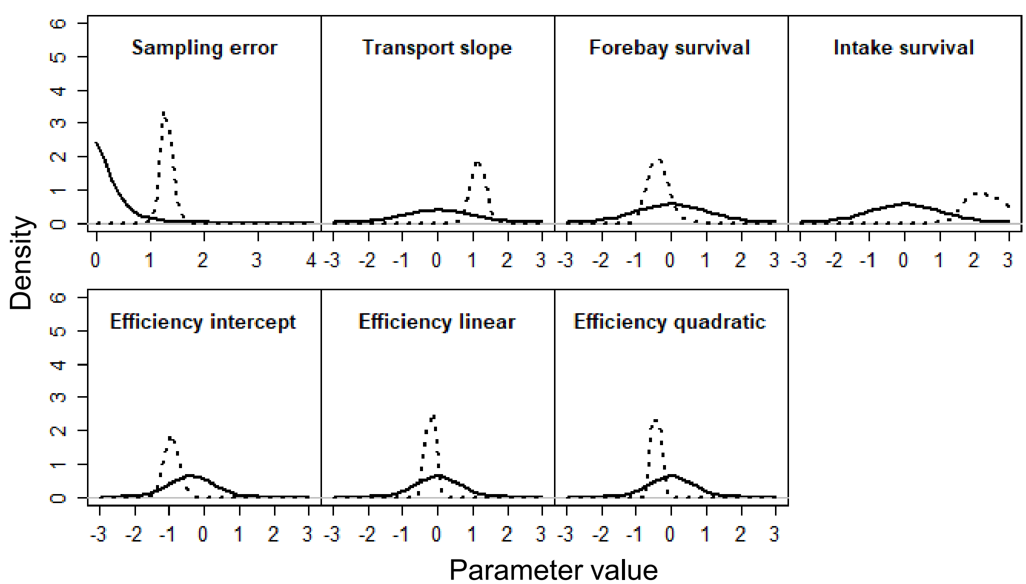

Figure 7 Prior (solid lines) versus posterior (*dashed lines*) distribution densities of all model parameters and error values

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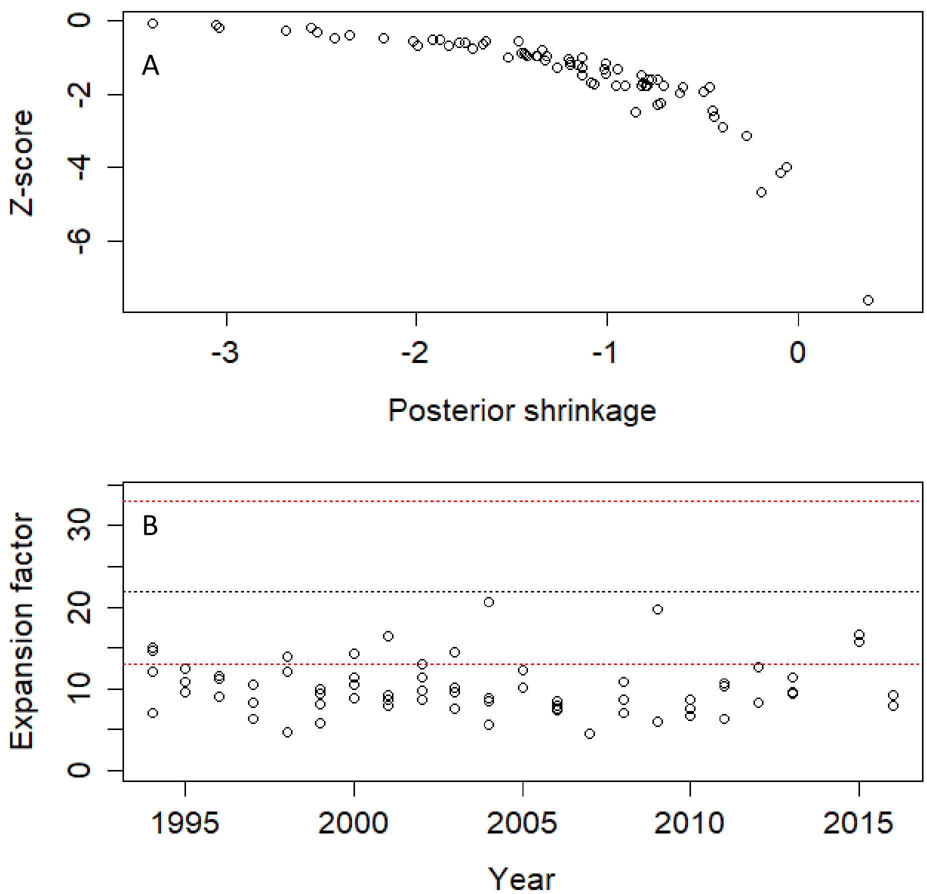

Figure 8 Comparison of Bayesian hierarchical model estimates of adult Delta Smelt entrainment to estimates from an alternative model, presented by Kimmerer (2008, 2011). Z-scores and posterior shrinkage (**A**) represent differences in the mean and standard deviation of entrainment estimated using the two models. Positive z-scores represent cases in which Bayesian hierarchical model estimates were greater than Kimmerer model estimates (posterior means), and greater shrinkage values indicate smaller standard errors for Bayesian hierarchical model estimates compared to Kimmerer model estimates, with shrinkage = 0 representing the case in which both methods produced the same standard error. Expansion factors (**B**) represent in the inverse product of transport, survival, and sampling. Bayesian hierarchical model estimates are shown with *open circles*, and Kimmerer (2008, 2011) estimates (*black*) and 95% credible intervals (*red*) are shown with the *dotted lines.*

safety, arriving at the SWP or CVP, or being distributed elsewhere in the South Delta where they become geographically isolated from the population or perish. Particles encoded with fish behaviors, released at some downstream location (e.g., the mouth of Old and Middle rivers) and transported for a period of time by a hydrodynamic model, may be considered multinomially distributed observations of Delta Smelt transport. This approach leads to a model that accounts for errors in a hydrodynamic model of transport by treating them as observation errors (Smith et al., forthcoming). This approach could be used to account for losses during transport through the Old and Middle rivers, should information to estimate Old and Middle River mortality become available.

An alternative modeling approach, applied by Korman et al. (2018), expands upon the spatial origins and fates of entrained fish. A spatially stratified estimate of Delta Smelt abundance was redistributed based on transport rates from a 3-D particle-tracking model that was coded with assumed behaviors (Gross et al. 2017). While the more spatially expansive approaches are preferred, because they can account for a greater fraction of the number of fish entrained, their application to Delta Smelt is limited by the available science to model behavior and the quality of information to estimate the spatial distribution and abundance of Delta Smelt.

Estimated entrainment showed dramatic variation over time, with a minimum several orders of magnitude lower than the peak entrainment estimated during the early 2000s. The reduction in the abundance of entrained adult Delta Smelt may be attributed to changes in hydrodynamic management associated with Delta Smelt and Chinook Salmon (USFWS 2008; NMFS 2009) and with declining population abundance. Though it is tempting to interpret declines in estimated entrainment as evidence of management success, models of population dynamics are required to disentangle the effects of population abundance from per capita rates of entrainment, and to quantitatively link entrainment rates to managed hydrodynamic quantities, such as Old and Middle River flows. Per capita rates of entrainment or proportional entrainment losses, their variation over time, and their links to hydrodynamic covariates are the subject of a subsequent modeling effort, the Delta Smelt Life Cycle Model. Inferences regarding the per capita effects of management changes and environmental variation depend upon accounting for the observational uncertainties described here.

Adult versus Post-Larval Models of Entrainment

Compared to the model of post-larval entrainment (Smith et al., forthcoming), the model of adult entrainment was simpler, and used information that was unavailable for post-larval fish. The adult transport model was simplified to routing to one water export facility or the other, because adult behavior and resulting susceptibility to hydrodynamic transport to the fish facilities were unknown. Transport from the area directly adjacent to the facilities was modeled in the adult entrainment model, while transport from a more expansive spatial unit was modeled for post-larval fish. Data were available to model two sources of adult mortality that occurred between the time of entrainment and sampling, but such data have not been collected for post-larvae. Modeled CCF and intake channel survival accounted for predation mortality, and were estimated from tagging data. These additional data provided a more robust survival estimate, and leveraged additional information about the relationship between channel velocity and sampling efficiency.

Differences in Observed Entrainment at State Water and Central Valley Projects

The salvage of a single fish at the SWP was not equivalent to the salvage of a single fish at the CVP because sampling efficiency and survival are different at the SWP than the CVP. Differences in construction and operation of the two facilities result in different mechanisms that lead to entrainment and eventual observation. Differences manifest in survival probabilities and, possibly, sampling efficiencies, though differences between SWP and CVP efficiencies could not be quantified using available mark–recapture data. The CVP's intake channel is directly connected to the Old River, whereas the State Water Project's intake channel is indirectly connected to the Old River via the CCF. Transit across the CCF exposes fish entrained to the SWP to an additional source of mortality. If a large fraction of fish die in the CCF before becoming available for observation, then CVP catch per unit effort (CPUE; number salvaged/sampling efficiency/volume of water exported/fraction sampled) should be higher than SWP CPUE, because SWP densities are reduced by CCF mortality. Median CPUE at the SWP was 0.05 fish m^{-3}, compared to 0.06 fish m^{-3} at the CVP. Comparing all monthly pairwise CPUEs, the median difference between the SWP and CVP was -0.006 fish m^{-3}. Lower CPUE at the SWP supports the notion that some mortality occurs in the CCF.

Differences in maintenance operations between the SWP and CVP also contribute to different sampling efficiency models. The SWP has multiple compartmentalized intake channel bays that can be independently closed while primary louvers are cleaned (CDWR 1981). The CVP, on the other hand, lacks the ability to independently close primary channel bays during cleaning (Hallock et al. 1968). As louver panels are periodically removed and a fraction of water goes unscreened, some entrained fish may avoid observation and pass the fish facility, reducing overall efficiency.

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Further differences between operations of the SWP and CVP may have resulted in unaccounted-for variation in the transport model. Water movement to each Project is not identical. The radial gates to the SWP's CCF are operated on a tidal schedule, while water is pumped from the CVP intake channel at a more or less continuous rate (Reyes et al. 2018). Differences from tidal operation may be enhanced by the potential for tidally based movements in adult Delta Smelt that make them more vulnerable to advective flows during high tides (Bennett and Burau 2015). Use of particle-tracking data from hydrodynamic models, modeled at a sub-tidal temporal scale, may be a better option to model transport compared to export volumes.

Limitations and Future Directions

Sparse data were a primary limitation for the model. Two types of data were primarily constraining; more robust mark–recapture data would have improved entrainment estimates. Mark–recapture data were limited in several ways. The mark–recapture data to estimate SWP sampling efficiency was constrained by sample size, with only 12 groups of tagged fish released during periods of low variation in primary channel velocities. Low sample sizes and poor coverage of the distribution of channel velocities during the study reduced power to detect differences between SWP and CVP sampling efficiencies if differences exist, and independent SWP sampling efficiency parameters could not be estimated. Only six batches of tagged fish were available to estimate survival at each Project, but future mark–recapture experiments may provide additional data to improve survival estimates. One consequence of the sparse survival data was difficulty in simultaneous estimation of both sampling error and survival process variation. This problem is a common feature of models that attempt to separate observation and process noise (de Valpine and Hilborn 2005). In the model of adult Delta Smelt entrainment, this difficulty was avoided by estimating a single—rather than a dynamic—survival value for all time-periods. The consequence was that survival process variation was ignored, and other process errors may be positively biased (i.e., high sampling efficiency error) to account for unexplained variation in survival. One example that demonstrates the potential misspecification of the survival model was the recovery of 0 fish of 1,402 tagged fish from the final trial of the CCF survival experiment (Appendix A, Table A1), during a period when channel velocities should have optimized efficiency. Given sufficient data, future applications may be able to explain variation in survival using covariates such as residence time, water clarity, or predator abundance. Mark–recapture samples were available to estimate survival in the CCF and in the CVP intake channel, but not in the SWP intake channel. Intake channel survival measured at the CVP was therefore assumed to apply at the SWP; however, it is possible that differences in construction and predator densities lead to different intake channel survival probabilities at the two water export facilities.

In addition to limited data availability, a major deficiency in hierarchical model estimates of adult Delta Smelt entrainment was a minimal understanding of the interaction between fish behavior and hydrodynamic transport. Uncertainties regarding how to model transport over longer distances led to spatial restrictions in the unit of entrainment modeled. The consequence of the reduced spatial unit was that mortality during transport through the Old and Middle River corridor could not be accounted for, and hierarchical model estimates of entrainment were negatively biased to the extent that fish die after they pass some downstream point of no return. A Delta Smelt behavioral model would leverage a more expansive spatial unit of entrainment that accounted for losses in Old and Middle rivers (Korman et al. 2018); however, a recent effort supported by the Delta Smelt Scoping Team to model adult entrainment using particle-tracking data concluded that Delta Smelt movement was a complex interaction between an unknown suite of behaviors and environmental fields (Gross et al. 2017). Although a set of behaviors to explain Delta Smelt distributions was not found, simple behaviors such as passive diffusion, tidal migration, and turbidity-seeking were insufficient; Delta Smelt movement is complicated and requires further study.

A tension between temporal scales exists when using any hydrodynamic quantity, such as export volume or Old and Middle River flows, to fit a model of transport or movement to Delta Smelt observations, because important hydrodynamic variation occurs at finer temporal scales than small populations of Delta Smelt can be measured. At the daily scale or finer, most observations of Delta Smelt are 0, requiring aggregation over monthly scales to avoid severe 0 inflation (e.g., 74% 0s at the daily scale). As a result, the aggregated hydrodynamic quantities used as covariates to fit models of Delta Smelt populations may not represent the true variation in hydrodynamics. It is possible that this necessary temporal mismatch contributed to a lack of convergence and general difficulty in estimating transport error for Delta Smelt; however, the simulation experiment indicated that even with perfect covariates (simulated), transport error was difficult to estimate. Integrating new transport data in the form of observations from particle-tracking models or from tagged fish released between the CVP intake channels and the entrance to the CCF would improve estimates of transport and the variation in this process.

Applications

Mark–recapture data and fish facility counts were the two major data components required to estimate Delta Smelt entrainment. Similar data have been collected for many other species, so the entrainment of a broad suite of species of management concern could be estimated using the hierarchical model. Modeled Delta Smelt transport was limited by our understanding of behavior, but more complex models are possible with more nuanced understanding and different forms of transport data. Although some aggregation was required to avoid severe 0 inflation of Delta Smelt data, the Poisson distribution used to model fish facility counts was suited to observations of 0s, unlike other methods that rely on expanded counts and necessarily result in 0 entrainment when 0 fish are observed at fish facilities. The Poisson distribution could also be applied to abundant species with high counts, and other distributions like the negative binomial could be used to address the high number of 0s at finer temporal scales. Species with existing mark–recapture data to estimate sampling efficiency include juvenile Chinook Salmon, Sacramento Splittail (*Pogonichthys macrolepidotus*) (Sutphin and Bridges 2008), and Pacific Lamprey (*Entosphenus tridentatus*) (Reyes et al. 2017), and fish facility count data for many additional species have been collected for more than 2 decades. Future management of populations experiencing entrainment should be based on robust estimates of numbers entrained and the uncertainties associated with the sequence of events leading to observation.

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