Hierarchical modeling of juvenile chinook salmon survival as a function of Sacramento-San Joaquin Delta water exports

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Abstract

A multi-year study in the Sacramento-San Joaquin Delta system was carried out to examine the relationship between the survival of out-migrating Chinook salmon *Oncorhynchus tshawytscha* and the amount of water exported from the system by the two major pumping stations in the southern portion of the Delta. Paired releases of groups of coded-wire-tagged juvenile late-fall run Chinook salmon were made at two locations in the Delta, one in the main stem Sacramento River and one in the interior portion of the Delta where they were more likely to be directly affected by the pumping stations. Shortly after release, fish were recovered downstream by a mid-water trawl, and, over a two to four year period, fish were recovered in samples of ocean fishery catches and from spawning ground surveys. A Bayesian hierarchical model for the recoveries was fit which explicitly accounted for between release variation in survival and capture probabilities as well as sampling variation in the recoveries. Survival of the interior Delta releases was considerably lower than the survival of main steam releases (mean ratio of survival probabilities was 0.35). The ratio of survival probabilities was negatively associated with water export levels, but various model selection criteria gave more, or nearly equal, weight to simpler models which excluded exports. The signal-to-noise ratio, as defined in terms of the export effect relative to environmental variation, however, was very low, and could explain indeterminacy in the results of model selection procedures. Many more years of data would be needed to more precisely estimate the export effect. Whatever the factors are that adversely affect survival through the interior Delta, to determine the overall effect on out-migrating Sacramento river Chinook salmon the fraction of out-migrants that enter the interior Delta needs to be estimated.

1 Introduction

Juvenile Chinook salmon (*Oncorhynchus tshawyschta*) survival experiments have been conducted in the Sacramento-San Joaquin Delta of California since the early 1970s (Kjelson, et al. 1981 and 1982; Kjelson and Brandes 1989; Brandes and McLain 2001). The experiments have involved the release, at multiple locations throughout the Delta, of marked and tagged hatchery-reared juvenile salmon followed by later recovery of these salmon. Survival of juvenile salmon through the Delta is of particular interest because of the Delta's role in water management in California. Two large pumping facilities, the Central Valley Project's C. W. "Bill" Jones Pumping Plant (CVP) and the State Water Project's Harvey Banks Pumping Plant (SWP), are located in the south Delta (Figure 1) and provide water, to over 23 million people, for municipal, agricultural and domestic purposes throughout central and southern California. The Delta is critical for Sacramento-San Joaquin origin salmon survival as all juvenile salmon must migrate through the Delta to reach the Pacific Ocean. There are two races of Central Valley Chinook salmon listed under the Endangered Species Act, winter run as endangered (NMFS 1997) and spring run as threatened, with the other two races, fall and late-fall run, considered species of concern. The role of CVP and SWP exports on juvenile salmon survival through the Delta is of great interest to managers and stake-holders and this interest has been a primary reason for the salmon survival experiments.

Previous analyses of some of these survival experiments, using juvenile fall run Chinook salmon (Kjelson, et al. 1981; Brandes and McLain 2001; Newman and Rice 2002; Newman 2003) which out-migrate through the Delta from March through June (Yoshiyama, et al. 1998), have suggested that survival is negatively associated with water exports. These analyses included data from a very spatially-dispersed set of release locations where many variables other than export levels potentially affected survival.

In this paper we analyze release-recovery data from a more narrowly focused study of export effects, where factors other than exports were to some degree controlled for by temporal pairing of releases. Paired releases of juvenile late-fall run Chinook salmon were made simultaneously in the interior Delta and in the main stem of the Sacramento River downstream of the Delta Cross Channel and Georgiana Slough (Figure 1). The interior Delta is an area of the Delta that out-migrating juvenile salmon can enter from the Sacramento River through either the Delta Cross Channel, when the Delta Cross Channel gates are open, or Georgiana Slough. Fish released directly into the interior Delta are presumably more vulnerable to the influence of the CVP and SWP pumping facilities than fish released in the main stem. In contrast to fall run experiments (Newman and Rice 2002), the temporal pairing of releases controlled for the effects of all factors other than release location and exports on survival. One limitation of the study, however, is that levels of exports cannot be fixed or controlled by researchers due to the precedence of water demands. Another limitation is that the overall effect of exports on out-migrating salmon cannot be determined without knowing the proportion of out-migrating salmon that enter the interior Delta.

Brandes and McLain (2001) analyzed paired release-recovery data that included releases of late-fall run fish and fall run fish. Their analysis procedure was to first calculate freshwater recovery fractions (adjusted for estimates of capture efficiency) and then to regress the fractions against export levels. Based on the data available at the time, they found a statistically significant negative association between the survival of Georgiana Slough releases relative to the survival of Ryde releases and export levels (Figure 1).

One purpose of this paper is to update the analyses of Brandes and McLain (2001) incorporating the since-gathered data but only using late-fall run stock. Late-fall run fish are potential surrogates for winter run salmon (Brandes and McLain 2001), since both runs out-migrate from November through May (Yoshiyama, et al. 1998). A second purpose is to compare results for the Brandes and McLain approach with results based on Bayesian hierarchical models (Carlin and Louis 1996; Gelman, et al. 2004; for a fisheries release-recovery application, Newman 2003). Hierarchical models offer several potential advantages for analyzing multi-release studies. One advantage is parsimony; rather than estimating release-pair specific effects independently, e.g., n independent estimates of relative survival for n release pairs, a single distribution for the effects underlying the results for all release pairs is specified. Another advantage is that such a *random effects* distribution characterizes the environmental variation in survival probabilities, and the hierarchy makes this variation distinct from sampling variation. A third advantage is that a hierarchical model provides a sensible means of combining data from multiple year studies, in this case multiple sets of paired releases with associated recoveries, e.g., giving release-pairs with fewer fish released less weight than those with more fish released.

The paired release-recovery experiment design and the statistical models used for analysis are described in Section 2. Results are given in Section 3. We close with a discussion (Section 4) of the management implications of the results.

2 Methods

2.1 Data

The paired release-recovery data, including numbers released, numbers recovered at various locations, and the water export levels at time of release, are given in Table 1. Fifteen paired groups of juvenile late-fall run Chinook salmon yearlings (mean size $>$ 100 mm), reared at Coleman National Fish Hatchery, were released between 1993 and 2005 during the months of December and January. At the hatchery, each fish had its adipose fin clipped and a coded-wire-tag was inserted into its snout; to read such tags after implantation requires sacrificing the fish. The tag codes were batch-specific, i.e., the same codes were used for thousands of fish, with unique tag codes for each release location. The fish were trucked from the hatchery to the interior Delta (Georgiana Slough) and the main stem Sacramento River (at Ryde or Isleton) (Figure 1), and releases were made at both locations with a day or two.

Within a few weeks of release, recoveries were made in freshwater by a mid-water trawl operating near Chipps Island (Figure 1). The trawl was towed at the surface almost daily for four to six weeks after the fish were released. Typically, ten, twenty minute tows were made each day between roughly 7 AM and noon. Juvenile fish were also recovered at fish facilities located in front of the pumping plants at CVP and SWP. These recovered salmon were transported by truck and released at locations north of the pumps and nearer to the main stem of the Sacramento River upstream of Chipps Island, where they could potentially be caught by the mid-water trawl at Chipps Island. Then over a three to four year period, adult fish were recovered from samples of landings from ocean fisheries. The total number of ocean fishery recoveries, summed over many landing areas and years, was estimated from a spatially and temporally stratified random sample of landings and catches. The percentage of ocean catch that is sampled is roughly 20-25%. Additional recoveries of adult fish were made in freshwater fisheries, at hatcheries, and on spawning grounds (inland recoveries). The expanded ocean and inland recoveries were retrieved from a web-based database query system administered by Pacific States Marine Fisheries Commission (`www.rmpc.org`). The straying proportions, i.e., the fraction of inland recoveries that were not recovered at Coleman National Fish Hatchery, for Georgiana Slough and Ryde releases varied considerably between release pairs, but within release pairs the proportions were quite similar.

The combined water export levels, hereafter referred to as exports, from both the SWP and the CVP were averaged over a three day period starting the day after release in Georgiana Slough. The choice of three days was somewhat arbitrary, although linear correlations of three day average export levels with averages for 10 and 17 days were quite high (r=0.94 for 10 days and r=0.91 for 17 days). There is a certain degree of imprecision to defining an export variable with regard to fish outmigration because some fish take longer to out-migrate than others and the degree of exposure to the area influenced by the pumps will vary; e.g., the Georgiana Slough release in group 1 had one recovery at the SWP fish facility three months after release. Furthermore, export levels are not necessarily constant, even within a three day period, and day to day variation in export level is not captured by the use of an average. Water volumes entering the interior Delta are also affected by the position of the Delta Cross Channel gates, which when open increase the flow of water from the Sacramento River into the interior Delta. The gates were open on the day of the Georgiana Slough releases in the first two years of the study (1993 and 1994), and for one of the 1999 releases (Group 10), but otherwise closed for all other releases. Recognizing that it might be the amount of exports relative to total inflow from the Sacramento River (at Freeport) that could be more important than absolute exports, the export to flow ratio was also examined as a covariate; the relationship between the ratios and the absolute values, however, was positive and linear (r=0.83).

2.2 Assumptions and notation

Within and between releases, the fate of an individual fish, e.g., live or die, caught or not, was assumed independent of the fate of any other fish. For all fish released from one location at the same time, the survival and capture probabilities were assumed identical. In recognition of the paired release aspect of the studies, we further assumed that within a release pair the probability of capture at Chipps Island, and the recovery probabilities (a complicated combination of survival and capture probabilities) in the ocean fishery and inland areas were identical. For example, for release pair 1 (Table 1) the capture probability for a Ryde fish or a Georgiana Slough fish that has survived to Chipps Island is the same, but that probability can differ from that for release pair 2.

We further assumed that only fish released in Georgiana Slough were affected by exports. Ryde is located 2.5 miles downstream of the location on the main stem where water is diverted into the Georgiana Slough and releases at Ryde are further removed geographically from the export facilities. However, for two years there were sizeable numbers of Ryde fish recovered at the fish facilities (Table 1); these were potentially situations where flood tides carried some of the Ryde releases into the interior Delta at some upstream or downstream locations, e.g., Three Mile Slough (Figure 1), a channel several miles downstream that connects the Sacramento and San Joaquin Rivers in the Delta.

For a given release pair t, the numbers released at Ryde and Georgiana Slough are denoted $R_{Ry,t}$ and $R_{GS,t}$ and the associated recoveries at Chipps Island are $y_{Ry\rightarrow CI,t}$ and $y_{GS\rightarrow CI,t}$. Expanded ocean recoveries are $\hat{y}_{Ry\rightarrow Oc,t}$ and $\hat{y}_{GS\rightarrow Oc,t}$, and similarly expanded inland recoveries are $\hat{y}_{Ry\rightarrow IL,t}$ and $\hat{y}_{GS\rightarrow IL,t}$. Recovery fractions, defined as the ratios of number of recoveries to number released, will be denoted $\hat{r}$, with subscripts indicating release and recovery locations; e.g., $\hat{r}_{Ry\rightarrow Oc,t} = \hat{y}_{Ry\rightarrow Oc,t}/R_{Ry,t}$. Combined recovery fractions for more than one recovery location are denoted similarly; e.g., $\hat{r}_{Ry\rightarrow CI+Oc+IL,t} = (y_{Ry\rightarrow CI,t}+\hat{y}_{Ry\rightarrow Oc,t}+\hat{y}_{Ry\rightarrow IL,t})/R_{Ry,t}$.

Notation for the probability that a Ryde release is recovered at Chipps Island is $r_{Ry\rightarrow CI,t}$ and the recovery probability for ocean fisheries and inland recoveries combined is $r_{Ry\rightarrow Oc+IL,t}$. The corresponding probabilities of recovery for Georgiana Slough releases are denoted $\theta_t r_{Ry\rightarrow CI,t}$ and $\theta_t r_{Ry\rightarrow Oc,t}$, where θ_t is a release pair-specific constant. Given the assumption that within a release pair, the capture probabilities at Chipps Island are the same, θ_t is the ratio of the survival probability between Georgiana Slough and Chipps Island to the survival probability between Ryde and Chipps Island. How θ_t relates to export levels is the primary management question.

2.3 Non-Bayesian, non-hierarchical models

Two non-hierarchical models were fit. Both somewhat mimic Brandes and McLain's (2001) analyses in that a two step procedure was used: (a) an estimate of θ_t is calculated; (b) the estimate is regressed against exports. The first model is quite similar to Brandes and McLain's analysis in that only recoveries at Chipps Island are used, i.e., θ_t is estimated as the the ratio of recovery fractions at Chipps Island for Georgiana Slough and Ryde releases,

$$\hat{\theta}_{1,t} = \frac{\hat{r}_{GS\rightarrow CI,t}}{\hat{r}_{Ry\rightarrow CI,t}} \quad (1)$$

In contrast to Brandes and McLain (2001), recoveries were not scaled by estimated gear efficiency, because of the assumption that capture probabilities were identical within a release pair. A simple linear regression model using standardized exports was fit:

$$\hat{\theta}_{1,t} \sim \text{Normal}\left(\beta_0 + \beta_1 Exp_t^*, \sigma^2\right), \tag{2}$$

where $Exp_t^* = (Exp_t - \overline{Exp})/s_{Exp}$, Exp_t is the exports at time t, $\overline{Exp}$ is the average export level, and s_{Exp} is the standard deviation of exports. Assuming independence and identical probabilities of survival and capture for all fish in a single release, the number of fish recovered at Chipps Island is a binomial random variable, e.g., $y_{Ry\to CI,t} \sim \text{Binomial}(R_{Ry,t},\, r_{Ry\to CI,t})$. Given $R_{Ry,t}$ and $y_{Ry\to CI,t}$, $\hat{r}_{Ry\to CI,t}$ is the maximum likelihood estimate (mle) of $r_{Ry\to CI,t}$; similarly, $\hat{r}_{GS\to CI,t}$ is the mle of $\theta_t r_{Ry\to CI,t}$, and $\hat{\theta}_{1,t}$ is the mle for θ_t based on Chipps Island recoveries alone.

For the second non-hierarchical model, θ_t was estimated using Chipps Island, ocean, and inland recoveries combined,

$$\hat{\theta}_{2,t} = \frac{\hat{r}_{GS\to CI+Oc+IL,t}}{\hat{r}_{Ry\to CI+Oc+IL,t}}. \tag{3}$$

Implicit to this calculation is the assumption that within a release pair the Chipps Island capture probabilities, the ocean recovery probabilities, and the inland recovery probabilities are identical. If total ocean and inland recoveries were known exactly and not estimated, the joint distribution of Chipps Island recoveries and combined ocean and inland recoveries would be multinomial, and $\hat{\theta}_{2,t}$ would be the mle for θ_t. However, with expanded recoveries, the distribution is more complex. To account for differences in sampling variation and to somewhat duplicate the hierarchical model, a weighted regression of the log of $\hat{\theta}_{2,t}$ against standardized exports was fit:

$$\ln\left(\hat{\theta}_{2,t}\right) \sim \text{Normal}\left(\beta_0 + \beta_1 Exp_t^*, se^2_{\ln[\hat{\theta}_{2,t}]}\sigma^2\right). \tag{4}$$

The weights were the inverse of the square of the standard errors of $\ln[\hat{\theta}_{2,t}]$, $se_{\ln[\hat{\theta}_{2,t}]}$, which were calculated using the delta method (cf Section 10.5, Stuart and Ord, 1987). The log transformation ensures that $\theta_{2,t}$ remains non-negative.

The primary inferential aim, for both models (Equations 2 and 4), is to estimate the slope coefficient β_1 and its standard error.

2.4 Hierarchical models

Hierarchical models (Carlin and Louis 1996) consist of two or more levels, each level accounting for a different type of variation. For these data, the first level accounts for sampling variation in the recoveries conditional on survival and capture probabilities, while the second level accounts for between release pair variation in the survival and capture probabilities. The second level reflects what is sometimes referred to as random effects. The prior distributions for the fixed and unknown parameters of the model (in the second level) make up the third level of the model.

2.4.1 Bayesian hierarchical model

A Bayesian hierarchical model (BHM) was formulated for the joint distribution of Chipps Island recoveries and the combined ocean and inland recoveries. The statistical distributions for each of the levels of the hierarchical model are shown below. The first level distributions are conditional on the second level variables, and similarly the second level is conditional on the third level.

Level 1:

$$y_{GS\to CI,t}, \hat{y}_{GS\to Oc+IL,t} \sim \text{Multinomial}\left(R_{GS,t}, \theta_{3,t} r_{Ry\to CI,t}, \theta_{3,t} r_{Ry\to Oc+IL,t}\right) \quad (5)$$

$$y_{Ry\to CI,t}, \hat{y}_{Ry\to Oc+IL,t} \sim \text{Multinomial}\left(R_{Ry,t}, r_{Ry\to CI,t}, r_{Ry\to Oc+IL,t}\right) \quad (6)$$

Level 2:

$$\ln(\theta_{3,t}) \sim \text{Normal}\left(\beta_0 + \beta_1 Exp^*, \sigma^2_\theta\right) \quad (7)$$

$$\text{logit}(r_{Ry\to CI,t}) \sim \text{Normal}\left(\mu_{r_{Ry\to CI}}, \sigma^2_{r_{Ry\to CI}}\right) \quad (8)$$

$$\text{logit}(r_{Ry\to Oc+IL,t}) \sim \text{Normal}\left(\mu_{r_{Ry\to Oc+IL}}, \sigma^2_{r_{Ry\to Oc+IL}}\right) \quad (9)$$

Level 3:

$$\beta_0, \beta_1, \mu_{Ry\to CI}, \mu_{Ry\to Oc+IL} \sim \text{Normal}\left(0, 1.0E+6\right) \quad (10)$$

$$\sigma_\theta, \sigma_{r_{Ry\to CI}}, \sigma_{r_{Ry\to Oc+IL}} \sim \text{Uniform}\left(0, 20\right) \quad (11)$$

As noted previously the joint distributions for Chipps Island recoveries and combined expanded ocean and inland recoveries cannot be multinomial due to estimation error in the expansions, thus the Level 1 formulation is an approximation. The log transformation of $\theta_{3,t}$ (in the Level 2 model) ensures that $\theta_{3,t}$ is non-negative. The logit transformations at Level 2 bounds $r_{Ry\to CI,t}$ and $r_{Ry\to Oc+IL,t}$ between 0 and 1; however, the resulting probabilities are so small that log transformations would have the same practical effect.

In contrast to the likelihood framework, the inferential objective in the Bayesian setting is to calculate the posterior distribution for the unknown parameters (Gelman, et al. 2004), i.e., to calculate

$$p(\Theta|Data) \propto p(Data|\Theta)p(\Theta)$$

where Θ is the vector of unknown constants, such as β_0 and β_1, and unknown random variables, such as θ_t, and $p(\Theta)$ is the prior distribution (here defined by Level 3). In this case primary interest is in the posterior distribution for β_1 and the probability that β_1 is negative is a measure of the degree of a negative association between exports and the relative survival of Georgiana Slough releases.

2.4.2 Sensitivity analysis

Sensitivity of the BHM to the choice of distributions and functional forms was assessed by alternative formulations for each level. At Level 1, to allow for possible dependence between fish within a release as well as extra-multinomial variation due to the fact that ocean and inland recoveries are sample expansions, negative binomial distributions were used for the Chipps Island and expanded ocean and inland recoveries from a given release. For example, the negative binomial model for recoveries at Chipps Island of releases from Ryde is the following.

$$y_{Ry \to CI} \sim \text{Negative Binomial}\left(k_{CI}, \frac{k_{CI}}{R_{Ry} r_{Ry \to CI} + k_{CI}}\right),$$

where k_{CI} is a non-negative constant that affects the degree of overdispersion (relative to a Poisson, or indirectly a Binomial, random variable). The larger k_{CI} is, the less the overdispersion.

At Level 2, several alternative models were fit. One model removed exports from the model for $\ln(\theta_{3,t})$. A second used a logistic transformation of $\theta_{3,t}$, ensuring $0 \leq \theta_{3,t} \leq 1$, i.e., the Georgiana Slough to Chipps Island survival probability cannot exceed Ryde to Chipps Island survival probability. A third alternative was a multivariate normal distribution for the joint distribution of $\theta_{3,t}$, $r_{Ry \to CI,t}$, and $r_{Ry \to Oc+IL,t}$, which allowed for correlation among these parameters within each release pair. In particular, $\theta_{3,t}$ was log transformed and, largely to facilitate fitting, an extension of a logistic model was used to transform $r_{Ry \to CI,t}$ and

$r_{Ry\to Oc+IL,t}$, i.e., dropping the subscript t to reduce notation,

$$\begin{bmatrix} \theta^1 \\ \theta^2 \\ \theta^3 \end{bmatrix} \sim \text{MVN}\left(\begin{bmatrix} \beta_0 + \beta_1 Exp^* \\ \mu_{Ry\to CI} \\ \mu_{Ry\to Oc} \end{bmatrix}, \Sigma = \begin{bmatrix} \sigma_1^2 & \sigma_{1,2} & \sigma_{1,3} \\ \sigma_{2,1} & \sigma_2^2 & \sigma_{2,3} \\ \sigma_{3,1} & \sigma_{3,2} & \sigma_3^2 \end{bmatrix} \right)$$

where

$$\begin{aligned} \theta^1 &= \ln(\theta_3) \\ \theta^2 &= \ln\left(\frac{r_{Ry\to CI}}{1 - r_{Ry\to CI} - r_{Ry\to Oc+IL}} \right) \\ \theta^3 &= \ln\left(\frac{r_{Ry\to Oc+IL}}{1 - r_{Ry\to CI} - r_{Ry\to Oc+IL}} \right). \end{aligned}$$

A fourth alternative was to use the fraction of exports relative to total river flow, exports/flow, instead of the absolute level of exports. A fifth alternative was to remove random effects, i.e., the Level 2 models were deterministic.

For Level 3, various prior distributions were tried for the Level 2 fixed parameters. We used the inverse gamma distributions instead of uniform distributions (equation 11) for the variances of the random effects, i.e., σ^2_θ, $\sigma^2_{r_{Ry\to CI}}$, and $\sigma^2_{r_{Ry\to Oc+IL}}$. For the multivariate normal model, an inverse Wishart distribution was used as the prior for the variance-covariance matrix, Σ.

Not all possible combinations of models for each level were fit. During the fitting process it became clear that certain options at one level led to clearly poor fitting models; e.g., removing random effects at level 2 led to a drastic drop in model fit no matter what options were selected at other levels.

2.4.3 Model fitting, assessment, and comparison

To fit the BHMs we used the program `WinBUGS` (Lunn, et al. 2003), which generated samples from the joint posterior distribution for the parameters, random effects, and expected numbers of recoveries. `WinBUGS` is based on a technique known as Markov chain Monte Carlo, MCMC (Gilks, Richardson, and Spiegelhalter 1996), which is a computer simulation method where samples are generated from a Markov chain which has a limiting distribution equal to the distribution of interest, in this case the joint posterior distribution.

By a limiting distribution it is meant that the samples do not initially come from the desired distribution, but once "enough" samples are generated, the so-called burn-in period, all additional samples do come from the desired distribution. `WinBUGS` includes measures, e.g., the Brooks-Gelman-Rubin statistic (Brooks and Gelman,1998), based upon the results of simulating from multiple Markov chains with differing initial values, for determining an adequate burn-in period. Informally stated, given widely different starting values, the point at which the chains begin to overlap, i.e., begin mixing, is the necessary burn-in period, presumably the samples are coming from the limiting distribution and are not stuck at some local mode of the posterior distribution. Values near 1.0 for the Brooks-Gelman-Rubin statistic are evidence for convergence, with values below 1.1 often adequate (Gelman, et al. 2004, page 297). Three different chains, with differing initial values, were run in parallel and the summary statistics are based on the pooled output following burn-in.

Goodness of model fit, for a given model, was assessed by calculating Bayesian P-values (Gelman, et al. 2004) for each of the observations. The P-value is the proportion of time a predicted value exceeds the observed value:

$$\text{Bayesian P-value} \quad = \quad \frac{1}{L}\sum_{l=1}^{L} I(y_l^{pred} \geq y),$$

where $I()$ is an indicator function equaling 1 when the condition inside () is met. The predicted value, y_l^{pred} is found by simulating y from its probability distribution evaluated at the l^{th} parameter value in the MCMC sample. Ideally, the observed values will lie in the central portion of the simulated posterior predictive distribution, equally distributed around the median predicted values. A Bayesian P-value near 0 or 1 is indicative of a poor fit for the particular observation.

All the models were compared using the deviance information criterion, DIC (Spiegelhalter, et al. 2002). DIC can be viewed as a measure of overall model fit while penalizing for model complexity. When comparing two models, the model with the lower DIC value is estimated to have better predictive capabilities. Reversible jump MCMC (RJMCMC, Green 1995) was used to compare two models, one model with exports as a covariate (equation (7)) and one without exports. Given the data, a set of models, and a corresponding set of prior probabilities that a given model is the correct model (the prior model probability), RJMCMC calculates posterior model probabilities.

3 Results

The recovery fractions for Georgiana Slough releases were consistently less than the fractions for Ryde releases, with the exception of the fraction recovered at the fish facilities (Figure 2). The means of the ratios of recovery fractions equalled 0.26, 0.46, and 0.37 for Chipps Island, ocean fisheries, and inland recoveries, respectively. Conversely, at the fish facilities, Georgiana Slough releases were about 16 times more likely to be recovered. Also, the recovery fraction of fish facility recoveries from the Georgiana Slough releases tended to increase, from about 0.001 to 0.025 , as exports went from 2000 cfs to 10000 cfs, although there was considerable variability at any given level of exports (Figure 3). This suggested a higher probability of ending up at the pumps with increasing exports. In contrast, the fraction of Ryde releases ending up at the fish facilities, with group 3 an exception and a case with high exports, was less than 0.001 (generally supportive of the assumption that Ryde releases were unaffected by exports).

3.1 Non-hierarchical analyses

The release pair specific point estimates, $\hat{\theta}_1$ and $\hat{\theta}_2$, and corresponding standard errors are shown in Table 2. As expected, given the additional information provided by ocean and inland recoveries, the standard errors for $\hat{\theta}_2$ tended to be smaller than those for $\hat{\theta}_1$. That difference in standard errors was smaller for the most recent releases (groups 14 and 15) which likely have incomplete inland recovery information for older aged returns. Between release group variation in the estimates of θ_t was quite large, with values ranging from 0.13 to 0.80 (based on $\hat{\theta}_2$).

The fitted models of θ_t as a function of exports (equations 2 and 4) are the following:

$$\begin{aligned}
\hat{\theta}_{1,t} &\approx \text{Normal}\left(0.265 - 0.086 Exp_t^*, 0.18^2\right) \\
\ln\left(\hat{\theta}_{2,t}\right) &\approx \text{Normal}\left(-0.935 - 0.214 Exp_t^*, 3.88^2\right).
\end{aligned}$$

P-values for a one-sided test of significance of the slope coefficient for exports, with the alternative $H_1 : \beta_1 < 0$, are 0.05 for the $\hat{\theta}_1$ model and 0.04 for the $\ln(\hat{\theta}_2)$ model. Neither model fit particularly well, however; the R^2 values were 0.19 and 0.21 for the $\hat{\theta}_1$ and $\ln(\hat{\theta}_2)$ models, respectively.

3.2 Bayesian hierarchical model

For each model the burn-in time was 50,000 iterations, per chain, a further 150,000 iterations, per chain, were carried out, and every tenth realization was used for the posterior samples. The negative binomial model was an exception, due to somewhat slow computational speed, burn-in was 50,000 iterations followed by 50,000 sample iterations. Evidence for convergence to the posterior distribution were Brooks-Gelman-Rubin statistics for all parameters between 1.0 and 1.03, plots of the parameters for the three chains against simulation number (traceplots) that showed considerable overlap and movement in chain values (consistent with good mixing), and DIC values that were stable between different runs.

All the BHMs with a multinomial distribution for the observations (Level 1) and random effects (Level 2) had nearly equal DIC values (Models #1-#6 in Table 3). Spiegelhalter, et al. (2002) support the rule of thumb that models within 1-2 of the minimal DIC value deserve consideration (as used by Burnham and Anderson (1998) for AIC). Notably, this set included a model without exports. The results were robust to the choice of the prior for the random effects standard deviation (σ), either uniform or inverse gamma. Either covariate, exports or exports/flow, led to equivalent DIC values. Posterior means for $\theta_{3,t}$ were much the same for these models.

The Bayesian P-values were essentially identical for these multinomial, random effect models. Fifty-three of the 60 total observations, 88%, had Bayesian P-values that fell inside of the middle 90% of posterior predictive distributions. There were too few observed recoveries (P=0.02 to 0.04) for two cases ($y_{Ry\rightarrow CI,1}$ and $y_{Ry\rightarrow CI,6}$), and too many observed recoveries (P=0.95 to 1.00) for five others ($y_{GS\rightarrow CI,5}$, $y_{GS\rightarrow CI,9}$, $y_{GS\rightarrow CI,12}$, $\hat{y}_{Ry\rightarrow Oc+IL,14}$ and $\hat{y}_{GS\rightarrow Oc+IL,14}$).

Replacing the multinomial distribution with the negative binomial distribution (Model

#7) or excluding random effects (Model #8) led to sizeable increases in DIC values (Table 3), especially for the latter model. Many of the Bayesian P-values for the non-random effects model were close to 0 or 1. The negative binomial model's parameters, k_{CI} and k_{Oc} were quite large (posterior means of 214 and 279), indicating little evidence for overdispersion.

Referring now to model #1 (although the results are nearly identical for models #2-#6), the recovery probabilities for Ryde releases at Chipps Island were an order of magnitude lower than those for the ocean fisheries and inland recoveries; the median for $r_{Ry \to CI}$ was 0.0004 versus 0.0038 for $r_{Ry \to Oc+IL}$. Given that recovery probabilities are the product of survival and capture probabilities, $r_{Ry \to CI} \approx 0.0004$ seems reasonable for the Chipps Island trawl based on independent estimates of Chipps Island trawl capture probabilities on the order of 0.001 to 0.002 (Newman 2003). The correlations between θ, $r_{Ry \to CI}$, and $r_{Ry \to Oc}$, on the transformed scales, were weakly positive: between θ and $r_{Ry \to CI}$ the posterior mean for $\sigma_{1,2}$ was 0.21, between θ and $r_{Ry \to Oc}$ $\mathrm{E}[\sigma_{1,3}]$ was 0.18, and between $r_{Ry \to CI}$ and $r_{Ry \to Oc}$ $\mathrm{E}[\sigma_{2,3}]$ was 0.25. Thus, within a release pair, when survival was higher for one segment, it tended to be higher for the other segments.

For all models with exports the posterior mean value for β_1 was negative, indicative of a negative association between θ and exports. For Models #1-#5, $\Pr(\beta_1 < 0)$ ranged from 0.86 to 0.92. The variation in the relationship with exports, however, was quite large as both the size of $\mathrm{E}[\sigma_\theta]$ and the plot of predicted θ values against exports (Figure 4) indicate. While the plot shows the decline in mean θ as exports increases (e.g., when exports are at 2000 cfs, mean θ is 0.54, and when exports are at 10,000 cfs, mean θ is 0.34), the range of individual values is very wide. Upper bounds on θ for export levels less than 7200 exceed 1.0, allowing for the possibility that Georgiana Slough releases could occasionally have higher survival than Ryde releases.

Given the similarity in DIC values amongst Models #1 - #6, and primary interest being the effect of exports, reversible jump MCMC was applied to just two models differing only in terms of the inclusion (Model #2) or exclusion (Model #6) of exports . The posterior probability for the model including exports was only 1% compared to 99% probability for the model without exports, thus apparently scant evidence for a relationship between θ and exports. However, such results could be due to the low signal-to-noise ratio, as measured by the posterior mean for β_1 to the posterior means for σ_θ, $\sigma_{r_{Ry \to CI}}$, and $\sigma_{r_{Ry \to OC+IL}}$. Repeated simulations of 15 sets of recoveries with the actual release numbers and export levels were made using Model #2 (equations 5-11) with the posterior mean values for the parameters (e.g., E[β_1]= -0.17). Despite the fact that the true model did have θ as a function of exports, RJMCMC typically yielded the posterior probabilities for this model in the range of 1-3%. Even doubling the number of release pairs and extending the range of export levels to plus or minus two standard deviations of observed values did not change these results. However, if the environmental variation was artificially decreased (e.g., by an order of magnitude), then RJMCMC gave posterior probabilities for the correct model (the model with exports) ranging from 90 to 99%.

3.3 Non-hierarchical versus hierarchical

The posterior means and standard deviations of θ_t from the BHMs (#1-#6) were quite similar to the (approximate) maximum likelihood estimates, $\hat{\theta}_{2,t}$, and the standard errors (Table 2). This indicates that the influence of the prior distributions on the Bayesian results was slight. The posterior standard deviations of θ_t were generally slightly less than the standard errors, presumably a result of the "borrowing of strength" from other release-recovery data that informs the estimates.

Model-based predictions of θ_t as a function of exports were quite similar for the BHM (equations 5-11) and the non-hierarchical model (equation (4)), but the prediction intervals for the BHM were considerably wider (Figure 4). The observed variation in estimates of θ_t (shown in Figure 4) seems more consistent with the wider BHM prediction intervals than the non-hierarchical model intervals.

4 Discussion

We conclude that, for a paired release, the survival to Chipps Island of Georgiana Slough releases is considerably less than the survival to Chipps Island of Ryde releases. The ratios of recovery fractions to Chipps Island, ocean fisheries, and inland sites for Georgiana Slough releases to Ryde releases were consistently much less than 1.0 (Figure 2), and the posterior means and the maximum likelihood estimates of θ_t were at most 0.8 (Table 2). The posterior median of θ_t was 0.35 (from a model without exports, BHM #6).

Factors in addition to exports that could cause lower relative survival for Georgiana Slough releases include water temperature, predation, and pollution (Moyle 1994). Increasing water temperatures have been associated with increasing mortality through the Delta (Baker, et al. 1995). For the paired releases we have analyzed, however, water temperatures at release were very similar at Ryde and Georgiana Slough within a release pair. Regarding predation, Stevens (1966) found more salmon in the stomachs of striped bass located in the so-called flooded islands portion of the Delta (south of the Georgiana Slough release point) relative to that for the stomachs of striped bass in the Sacramento River.

Regarding the relationship between the relative survival and export levels, the point estimates of export effects were consistently negative, and for the BHMs, the probability that the effects are negative was 86 to 92%. However, the signal-to-noise ratio is low enough that DIC values and posterior model probabilities indicate that the predictive ability of models without exports is equivalent to that of models which include exports. Environmental variation is large enough that a failure to find a stronger association could be a function of inadequate sample size. Previous analyses (Newman 2008, page 72) of the relationship between number of paired releases and precision of the estimated slope parameter for exports showed that 100 paired releases were needed (based on β_1= -0.57 for a logistic transformation of θ) to yield a coefficient of variation of 20%. The RJMCMC analysis of simulated data were consistent with those findings.

Exports do affect Georgiana Slough releases more than Ryde releases as the fraction of Georgiana Slough releases recovered at the CVP and SWP fish salvage facilities increases with increasing exports (Figure 2). The intent of the salvage operations is to increase survival by relocating those fish away from the pumping facilities, and perhaps there is in fact some mitigating effect. However, at the SWP facilities there is an enclosed area, Clifton Court Forebay, where fish suffer mortality, due at least to predators (Gingras 1997), prior to entering the salvage facilities. Experiments with marked salmon in the vicinity of the SWP fish facility have yielded estimates of "pre-salvage" mortality in the range of 63-99%, with an average of 85% (Gingras 1997), although the quality of these estimates has been called into question (Kimmerer 2008).

A tangential question is whether or not the fish facility recovery fractions are related to exports or the export to flow ratio, i.e., the absolute or the relative level of exports. Over the range of values observed in these studies, exports and export/flow are linearly associated

(Pearson correlation coefficient = 0.83), thus it is difficult to disentangle the effects of the two factors. Deliberate fixing of export levels at varying levels of flows would be one means of trying to determine if it is the absolute level or the relative level of exports that affects the fraction of Georgiana Slough releases recovered at the fish salvage facilities. Current water management policies and operational standards, however, make such manipulations difficult to conduct. Export levels are largely determined by state and federal water project agencies based on water demand, Delta conditions, Delta water quality and operational standards as well as endangered species biological opinions. Due to this lack of randomization of export levels and the relatively low numbers of releases, the effect of exports may be confounded by other conditions that cause survival to increase or decrease. The pairing aspect of the design does potentially control such confounding factors.

Given the low signal-to-noise ratio, instead of repeating coded-wire-tag release-recovery experiments for many more years, releases of fish with acoustic tags combined with strategically placed receivers, is recommended. Such a system could provide more precise information about when and where mortality is occurring, yielding estimates of reach-specific survival (Muthukumarana, Schwarz, and Swartz, 2008). How much of an effect the interior Delta mortality has on the total population of Sacramento River juvenile Chinook salmon, whatever the causes, depends upon the fraction of the out-migrating population that moves into the interior Delta. Using coded-wire-tag release-recovery data, Kimmerer (2008) estimated that the overall mortality is 10% at the highest export levels assuming a pre-salvage mortality of 80% at the fish facilities. Pilot studies using acoustic tags have recently been carried out to estimate the proportion of out-migrants entering the Delta (Perry, et al., xxxx), and once this proportion is identified, the benefits of preventing fish from entering the interior Delta can be estimated more accurately.

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References

Baker, P.F., Speed, T.P., and Ligon, F.K. 1995. Estimating the influence of temperature on the survival of Chinook salmon smolts (*Oncorhynchus tshawytscha*) migrating through the Sacramento-San Joaquin River Delta of California. Canadian Journal of Fisheries and Aquatic Sciences, 52: 855–863.

Brandes, P.L., and McLain, J.S. 2001. Juvenile Chinook salmon abundance, distribution, and survival in the Sacramento-San Joaquin Estuary. Pages 39–136 in R. Brown editor. Contributions to the Biology of Central Valley Salmonids , Fish Bulletin 179, Vol 2.

Brooks, S P. and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics, 7: 434–455.

Burnham, K.P., and Anderson, D.R. 1998. Model Selection and Inference: A Practical

Information-Theoretic Approach. Springer-Verlag, New York, New York.

Carlin, B.P., and Louis, T.A. 1996. Bayes and Empirical Bayes Methods for Data Analysis, Chapman and Hall, New York, New York.

Gelman, A., Carlin, J.B., Stern, H.S., and Rubin, D.B. 2004. Bayesian Data Analysis, 2nd Ed., Chapman and Hall, New York, New York.

Gilks, W.R., Richardson, S., and Spiegelhalter, D.J. 1996. Markov chain Monte Carlo in Practice, Chapman and Hall, New York, New York.

Gingras, M. 1997. Mark/recapture experiments at Clifton Court forebay to estimate pre-screening loss to entrained juvenile fishes: 1976-1993. IEP Technical Report No. 55 [Internet]. November 1997. Available from `http://iep.water.ca.gov/report/reports.html`.

Green, P.J. 1995. Reversible jump Markov chain Monte Carlo computation and Bayesian model determination. Biometrika, 82: 711–732.

Kimmerer, W.J. 2008. Losses of Sacramento River Chinook salmon and delta smelt (*Hypomesus transpacificus*) to entrainment in water diversions in the Sacramento-San Joaquin Delta. San Francisco Estuary and Watershed Science. [Internet]. Vol. 6, Article 2. Available from:
`http://repositories.cdlib.org/jmie/sfews/vol6/iss2/`.

Kjelson, M.A., and Brandes, P.L. 1989. The use of smolt survival estimates to quantify the effects of habitat changes on salmonid stocks in the Sacramento-San Joaquin River, California, p. 100-115. In C.D. Levings, L.B. Holtby, and M.A. Henderson [ed.] Proceedings of the National Workshop on the effects of habitat alteration on salmonid stocks. Can. Spec. Publ. Fish. Aquatic. Sci. 105.

Kjelson, M.A., Raquel, P.F., and Fisher, F.W. 1981. Influences of freshwater inflow on chinook salmon *Oncorhynchus tshawytscha* in the Sacramento-San Joaquin Estuary, pp. 88-108. In R.D. Cross and D.L. Williams [ed.] Proceedings of the National Symposium Freshwater Inflow to Estuaries. U.S. Department of the Interior, Fish and Wildlife Service, FWS/OBS-81/04. Vol. 2.

Kjelson, M.A., Raquel, P.F., and Fisher, F.W. 1982. Life history of fall-run juvenile chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin Estuary, California, p. 393-411. In V.S. Kennedy [ed.] Estuarine Comparisons. Academic Press, New York, NY.

Lunn, D.J., Thomas, A., Best, N., and Spiegelhalter, D. 2000. WinBUGS – a Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing, 10:325–337.

Moyle, P.B. 1994. The decline of anadromous fishes in California Conservation Biology. 8: 869–870

Muthukumarana, S., Schwarz, C.J., and Swartz, T.B. 2008. Bayesian analysis of mark-recapture data with travel time-dependent survival probabilities. Canadian Journal of Statistics, 36: 5–21

Newman, K.B., and Rice, J. 2002. Modeling the survival of chinook salmon smolts outmigrating through the lower Sacramento river system. Journal of the American Statistical Association, 97: 983–993.

Newman, K.B. 2003. Modelling paired release-recovery data in the presence of survival and capture heterogeneity with application to marked juvenile salmon. Statistical Modelling, 3: 157–177.

Newman, K.B. 2008. An evaluation of four Sacramento-San Joaquin River Delta juvenile salmon survival studies. Available from www.science.calwater.ca.gov/pdf/psp/PSP_2004_final/PSP_CalFed_FWS_salmon_studies_final_033108.pdf - 2008-05-13

NMFS. 1997. NMFS proposed recovery plan for the Sacramento River winter-run chinook. National Marine Fisheries Service, Southwest Regional Office.

Perry, R.W., Brandes, P.L., Sandstrom, P.T., Ammann, A., MacFarlane, B., Klimley, A.P., and Skalski, J.R. (xxxx- under review) Estimating migration and survival of juvenile Chinook salmon through the SacramentoSan Joaquin River Delta.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P., and van der Linde, A. 2002. Bayesian measures of model complexity and fit (with discussion). Journal of the Royal Statistical Society, Series B, 64:583–640.

Stevens, D.E. 1966. Food habits of striped bass, *Roccus saxatilis*, in the Sacramento-San Joaquin Delta. Fish Bulletin 136, California Department of Fish and Game, 68–96.

Stuart, A., and Ord, K. 1987. Kendall's Advanced Theory of Statistics, Distribution Theory, 5th Ed., Oxford University, New York, New York.

Yoshiyama, R.M., Fisher, F.W., and Moyle, P.B. 1998. Historical abundance and decline of Chinook salmon in the Central Valley Region of California. North American Journal of Fisheries Management, 18:487-521.

Table 1: Release and recovery data. R are the number released, CI and $\widehat{Oc}$ refers to observed recoveries at Chipps Island and expanded recoveries in the ocean fisheries. $\widehat{FF}$ refers to expanded recoveries at fish salvage facilities and $\widehat{IL}$ are expanded inland recoveries. Ryde releases were occasionally made at Isleton (denoted by *). Exports are a three day average (cfs) for the sum of water exported from SWP and CVP and E/F is the export to flow ratio over that same period.

Release		Tag Codes		Georgiana Slough					Ryde						
Date	Pair	Georg.Sl.	Ryde	R	CI	$\widehat{Oc}$	$\widehat{FF}$	$\widehat{IL}$	R	CI	$\widehat{Oc}$	$\widehat{FF}$	$\widehat{IL}$	E/F	Exports
12/02/93	1	06-45-21	06-45-22	33,668	5	79	248	12	34,650	37	293	10	36	0.68	10,434
12/05/94	2	05-34-25	05-34-26*	31,532	4	11	87	8	30,220	15	28	6	13	0.22	5,988
01/04-05/95	3	06-25-25	06-25-24*	31,328	2	102	837	53	31,557	13	266	231	138	0.40	10,403
01/10-11/96	4	05-41-13	05-41-14	33,670	5	146	768	9	30,281	21	239	12	23	0.55	9,523
12/04-05/97	5	05-50-50	05-50-60	61,276	2	7	153	4	46,756	22	42	18	11	0.51	10,570
01/13-14/97	6	05-50-49	05-50-62	66,893	18	240	24	51	49,059	48	167	0	70	0.06	3,887
12/01-02/98	7	05-23-08	05-23-20	69,180	12	172	28	44	48,207	30	183	0	102	0.04	1,868
12/29-30/98	8	05-23-12	05-23-21	68,843	12	151	48	54	48,804	17	156	0	88	0.09	1,984
12/10-11/99	9	05-51-30	05-51-32*	65,517	3	43	24	9	53,426	16	129	0	20	0.18	3,237
12/20-21/99	10	05-51-31	05-51-33*	64,515	21	149	82	32	49,341	19	160	4	66	0.26	4,010
01/03-05/02	11	05-07-76	05-07-67	77,053	18	240	390	116	52,327	34	521	18	418	0.12	7,789
12/05-06/02	12	05-10-98	05-11-67	90,219	1	68	700	11	49,629	18	148	42	34	0.46	5,007
		05-11-68													
12/09-10/03	13	05-17-71:72	05-17-81:82	68,703	5	51	306	8	45,981	13	127	24	69	0.18	4,016
12/08-09/04	14	05-22-92:93	05-22-80:81	72,082	10	11	0	1	50,397	28	20	0	0	0.25	6,092
12/08-09/05	15	05-27-84:87	05-27-88:91	70,414	6	35	165	1	51,017	23	49	12	1	0.68	10,837

Table 2: Comparison of release pair-specific fitted values of θ, the ratio of the Georgiana Slough survival probability to the Ryde survival probability. The non-Bayesian, non-hierarchical results are the maximum likelihood estimates and standard errors based on the Chipps Island recoveries alone ($\hat{\theta}_1$) and combined Chipps Island, ocean, and inland recoveries ($\hat{\theta}_2$). The Bayesian hierarchical values are the posterior distribution means and standard deviations from the BHM with a multivariate normal distribution at Level 2 and θ modeled as a function of exports.

	Non-Bayesian Non-Hierarchical				Bayesian Hierarchical	
Group	$\hat{\theta}_1$	SE	$\hat{\theta}_2$	SE	$E[\theta_{3,t} \mid \text{Data}]$	SD
1	0.14	0.07	0.27	0.031	0.28	0.031
2	0.26	0.14	0.39	0.097	0.38	0.084
3	0.15	0.12	0.38	0.035	0.38	0.035
4	0.21	0.11	0.51	0.050	0.50	0.049
5	0.07	0.05	0.13	0.040	0.16	0.041
6	0.28	0.08	0.80	0.065	0.79	0.064
7	0.28	0.10	0.50	0.044	0.51	0.043
8	0.50	0.19	0.59	0.054	0.58	0.052
9	0.15	0.10	0.27	0.042	0.28	0.041
10	0.85	0.27	0.63	0.060	0.62	0.057
11	0.36	0.10	0.26	0.016	0.26	0.016
12	0.03	0.03	0.22	0.029	0.23	0.029
13	0.26	0.14	0.20	0.029	0.22	0.029
14	0.25	0.09	0.32	0.082	0.32	0.076
15	0.19	0.09	0.42	0.081	0.38	0.070

Table 3: Summary of Bayesian hierarchical models. Level 1 column specifies distributions (Mn = Multinomial and NB = Negative Binomial). Level 2 column has models for $\theta_{3,t}$ with N denoting Normal distribution; models for $r_{Ry \to CI,t}$ and $r_{Ry \to CI,t}$ were those shown in Equations (8) and (9) except for Multivariate Normal (MVN) and model without random effects. Level 3 column specifies prior distribution for the random effects variance; σ (U for Uniform), σ^2 (IG for Inverse Gamma), and Σ in the MVN model (IW[I,4] for Inverse Wishart with I=Identity matrix).

#	Level 1	Level 2	Level 3	$E[\beta_1]$	$Pr(\beta_1 < 0)$	$E[\sigma_\theta]$	DIC
1	Mn	$\ln(\theta_{3,t}), \ldots \sim \text{MVN}(\beta_0 + \beta_1 Exp^*_t, \ldots, \Sigma)$	$\Sigma \sim$ IW[I,4]	-0.194	0.92	0.53	460.0
2	Mn	$\ln(\theta_{3,t}) \sim \text{N}(\beta_0 + \beta_1 Exp^*_t, \sigma^2_\theta)$	$\sigma \sim$ U(0,20)	-0.170	0.89	0.50	460.0
3	Mn	$\ln(\theta_{3,t}) \sim \text{N}(\beta_0 + \beta_1 \frac{Exp}{Flow}_t, \sigma^2_\theta)$	$\sigma \sim$ U(0,20)	-0.706	0.86	0.51	460.0
4	Mn	$\ln(\theta_{3,t}) \sim \text{N}(\beta_0 + \beta_1 Exp^*_t, \sigma^2_\theta)$	$\sigma^2 \sim$ IG(0.001,0.001)	-0.166	0.90	0.48	459.9
5	Mn	$\text{logit}(\theta_{3,t}) \sim \text{N}(\beta_0 + \beta_1 Exp^*_t, \sigma^2_\theta)$	$\sigma \sim$ U(0,20)	-0.297	0.88	0.89	460.0
6	Mn	$\ln(\theta_{3,t}) \sim \text{N}(\beta_0, \sigma^2_\theta)$	$\sigma \sim$ U(0,20)	NA	NA	0.51	460.1
7	NB	$\ln(\theta_{3,t}) \sim \text{N}(\beta_0 + \beta_1 Exp^*_t, \sigma^2_\theta)$	$\sigma \sim$ U(0,20)	-0.168	0.89	0.46	487.0
8	Mn	$\ln(\theta_{3,t}) = \beta_0 + \beta_1 Exp^*_t$	NA	-0.079	0.99	NA	4281.8

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Figure 1: Map of the Ryde and Georgiana Slough release locations and the Chipps Island recovery location.

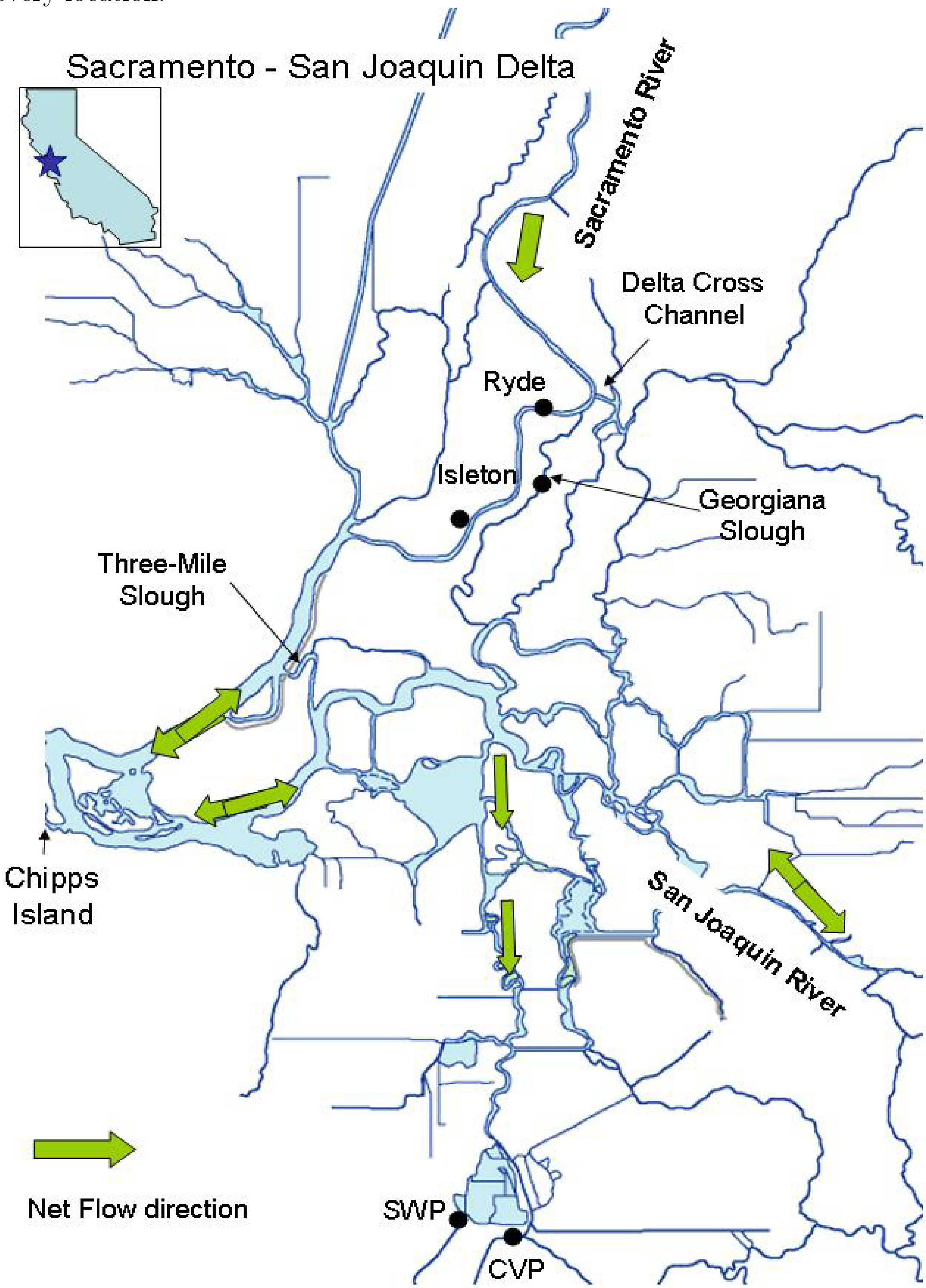


Figure 2: Comparison of recovery fractions at Chipps Island, in the ocean fisheries, in fish facility salvage, and from inland recoveries for Georgiana Slough and Ryde releases by release pair. Straight lines on plots have slope equal to mean of the ratios of recovery fractions.

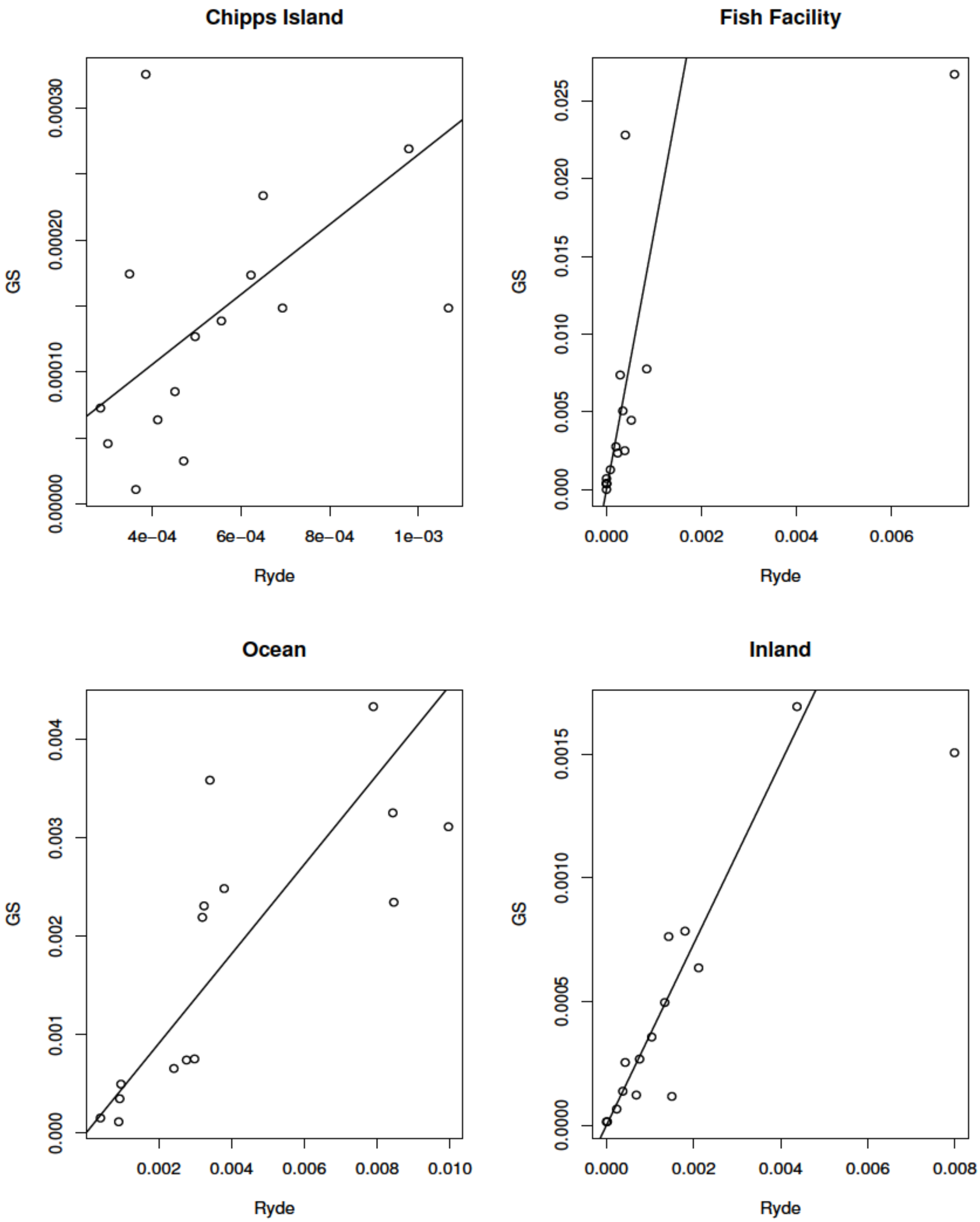
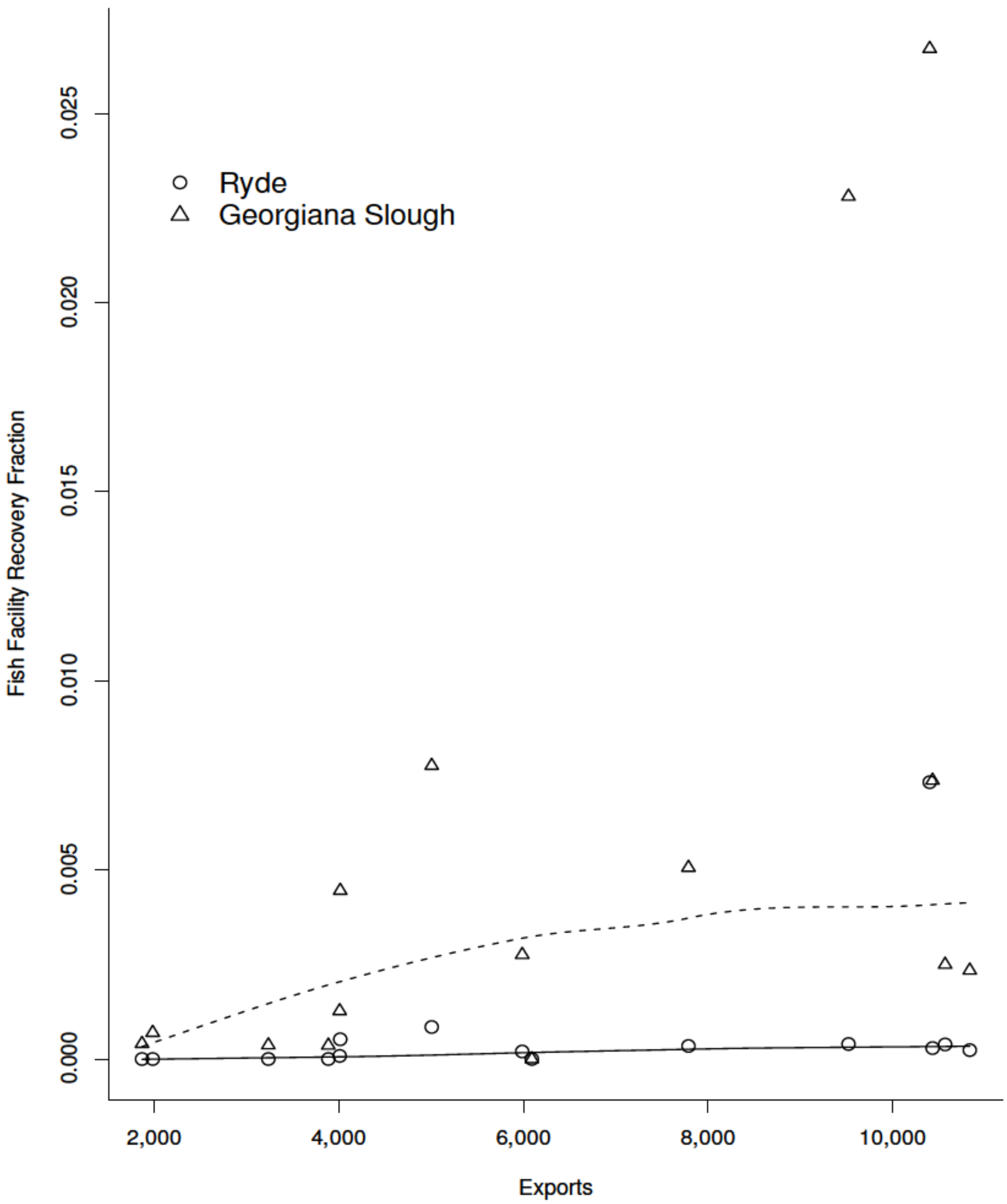


Figure 3: Expanded recovery fractions at the fish facilities near SWP and CVP plotted against the export level. Lines drawn on the plot are scatterplot smooths (dashed for Georgiana Slough; solid for Ryde).



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