Hierarchical Modeling of Juvenile Chinook Salmon Survival as a Function of Sacramento–San Joaquin Delta Water Exports

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Abstract.—A multiyear study was carried out in the Sacramento–San Joaquin Delta system 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, the fish were recovered downstream by a midwater trawl, and over a 2–4-year period the fish were recovered in ocean fishery catches and spawning ground surveys. A Bayesian hierarchical model for the recoveries was fit that explicitly accounted for the between-release variation in survival and capture probabilities as well as the sampling variation in the recoveries. The survival of the interior delta releases was considerably lower than that of main-steam releases (mean ratio of survival probabilities, 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 that excluded exports. However, the signal-to-noise ratio, defined in terms of the export effect relative to environmental variation, was very low, and this could explain the indeterminacy in the results of the model selection procedures. Many more years of data would be needed to more precisely estimate the export effect. Whatever the factors that adversely affect survival through the interior delta, the fraction of out-migrants that enter the interior delta needs to be estimated in order to determine the overall effect of water exports on out-migrating Sacramento river Chinook salmon.

Survival experiments with juvenile Chinook salmon *Oncorhynchus tshawytscha* have been conducted in the Sacramento–San Joaquin Delta of California since the early 1970s (Kjelson et al. 1981, 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 Chinook salmon followed by later recovery of these fish. The 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 southern part of the delta (Figure 1) and provide water for municipal, agricultural, and domestic purposes to more than 23 million people throughout central and southern California. The delta is critical for the survival of salmon of Sacramento–San Joaquin origin, as all juvenile salmon must migrate through it to reach the Pacific Ocean. Two races of Central Valley Chinook salmon are listed under the Endangered Species Act (the winter

run as endangered [NMFS 1997] and the spring run as threatened), and two others (the fall and late-fall runs) are considered species of concern. The role of CVP and SWP water exports on the survival of juvenile salmon through the delta is of great interest to managers and stakeholders, and this was the primary reason for the survival experiments.

Previous analyses of survival experiments involving 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, at which many variables other than export levels may have affected survival.

In this paper we analyze release–recovery data from a more narrowly focused study of the effects of water exports, in which factors other than exports were to some degree controlled for by the temporal pairing of releases. Paired releases of juvenile late-fall-run Chinook salmon were made simultaneously in the interior delta and the main stem of the Sacramento River downstream from the Delta Cross Channel and Georgiana Slough (Figure 1). The interior delta is an area that out-migrating juvenile salmon can enter from the Sacramento River through either the Delta Cross
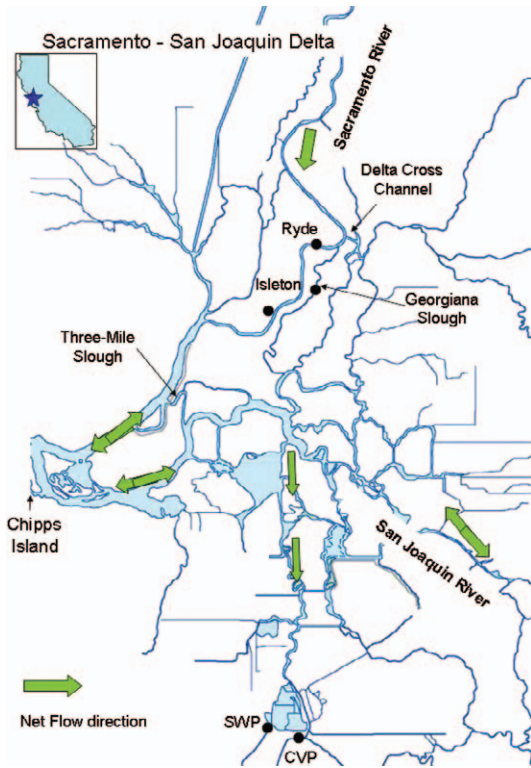
FIGURE 1.—Map of the Sacramento–San Joaquin Delta showing the Ryde and Georgiana Slough release locations, the Chipps Island recovery location, and the locations of two pumping stations with fish salvage facilities (SWP and CVP).

Channel (when the 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 into the main stem. Unlike in the 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 the levels of exports cannot be fixed or controlled by researchers because water demands take precedence. Another limitation is that the overall effect of exports on out-migrating salmon cannot be determined without knowing the proportion of such salmon that enter the interior delta.

Brandes and McLain (2001) analyzed paired re-lease–recovery data that involved releases of late-fall-run and fall-run fish. Their analytical procedure was to calculate freshwater recovery fractions (adjusted for estimates of capture efficiency) and regress those fractions against export levels. Based on the data available at the time, they found a statistically significant negative association between the survival of releases at Georgiana Slough (relative to that of releases at Ryde on the main-stem Sacramento River) and export levels (Figure 1).

One purpose of this paper was to update the analysis of Brandes and McLain (2001) incorporating more recent data but only using the late-fall-run stock. Late-fall-run fish are potential surrogates for winter-run Chinook salmon (Brandes and McLain 2001) since both runs out-migrate from November through May (Yoshiyama et al. 1998). A second purpose was to compare the results of the Brandes and McLain approach with those based on Bayesian hierarchical models (Carlin and Louis 1996; Gelman et al. 2004; for a fisheries release–recovery application, see Newman 2003). Hierarchical models offer several potential advantages for analyzing multirelease 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), one can specify a single distribution for the effects underlying the results for all release pairs. Another advantage is that such a "random effects" distribution characterizes the environmental variation in survival probabilities and the hierarchical approach makes this variation distinct from the 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 and recoveries (giving, for example, release pairs for which fewer fish were released less weight than those for which more fish were released).

Methods

Data

The paired release–recovery data, including the numbers of fish released, the numbers recovered at various locations, and the water export levels at the times 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 inserted into its snout; to read such tags after implantation requires sacrificing the fish. The tag codes were batch specific, that is, 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 (Ryde or Isleton) and releases at both locations made within a day or two.

Within a few weeks of release, recoveries were made

TABLE 1.—Release and recovery data for juvenile Chinook salmon in the Sacramento–San Joaquin Delta. Abbreviations are as follows: R is the number of fish released, CI and $\widehat{Oc}$ are observed recoveries at Chipps Island and expanded recoveries in the ocean fisheries, $\widehat{FF}$ is expanded recoveries at fish salvage facilities, and $\widehat{IL}$ is expanded inland recoveries. Exports are 3-d averages (cfs) of the water exported from SWP and CVP, and E/F is the export–flow ratio over the same period.

Release date	Pair	Georgiana Slough					Ryde					E/F	Exports
		R	CI	$\widehat{Oc}$	$\widehat{FF}$	$\widehat{IL}$	R	CI	$\widehat{Oc}$	$\widehat{FF}$	$\widehat{IL}$		
Dec 2, 1993	1	33,608	5	79	248	12	34,650	37	293	10	36	0.68	10,434
Dec 5, 1994	2[a]	31,532	4	11	87	8	30,220	15	28	6	13	0.22	5,988
Jan 4–5, 1995	3[a]	31,328	2	102	837	53	31,557	13	266	231	138	0.40	10,403
Jan 10–11, 1996	4	33,670	5	146	768	9	30,281	21	239	12	23	0.55	9,523
Dec 4–5, 1997	5	61,276	2	7	153	4	46,756	22	42	18	11	0.51	10,570
Jan 13–14, 1997	6	66,803	18	240	24	51	49,059	48	167	0	70	0.06	3,887
Dec 1–2, 1998	7	69,180	12	172	28	44	48,207	30	183	0	102	0.04	1,868
Dec 29–30, 1998	8	68,843	12	151	48	54	48,804	17	156	0	88	0.09	1,984
Dec 10–11, 1999	9[a]	65,517	3	43	24	9	53,426	16	129	0	20	0.18	3,237
Dec 20–21, 1999	10[a]	64,515	21	149	82	32	49,341	19	160	4	66	0.26	4,010
Jan 3–5, 2002	11	77,053	18	240	390	116	52,327	34	521	18	418	0.12	7,789
Dec 5–6, 2002	12	90,219	1	68	700	11	49,629	18	148	42	34	0.46	5,007
Dec 9–10, 2003	13	68,703	5	51	306	8	45,981	13	127	24	69	0.18	4,016
Dec 8–9, 2004	14	72,082	10	11	0	1	50,397	28	20	0	0	0.25	6,092
Dec 8–9, 2005	15	70,414	6	35	165	1	51,017	23	49	12	1	0.68	10,837

[a] Ryde releases made at Isleton (see Figure 1).

in freshwater by a midwater trawl operating near Chipps Island (Figure 1). The trawl was towed at the surface almost daily for 4–6 weeks after the fish were released. Typically, ten 20-min tows were made each day between roughly 0700 and 1200 hours. Juvenile fish were also recovered at fish facilities located in front of the CVP and SWP pumping plants. These Chinook 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 be caught by the midwater trawl at Chipps Island. Then, over a 3–4-year period, adult fish were recovered from the landings of 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 the landings and catches. The percentage of ocean catch sampled was 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 the Pacific States Marine Fisheries Commission (www.rmpc.org). The straying proportions for the Georgiana Slough and Ryde releases (i.e., the fractions of inland recoveries that were not recovered at Coleman National Fish Hatchery) varied considerably between release pairs, but within release pairs they were quite similar.

The combined water export levels (hereafter referred to as exports) from both the SWP and CVP facilities were averaged over a 3-d period starting the day after the release in Georgiana Slough. The choice of 3 d was somewhat arbitrary, although linear correlations of 3-d average export levels with those for 10 and 17 d were quite high (0.94 and 0.91, respectively). There is a certain degree of imprecision in defining an export variable with regard to fish out-migration because some fish take longer to out-migrate than others and the degree of exposure to the area influenced by the pumps will vary (for example, in group 1 of the Georgiana Slough release there was one recovery at the SWP fish facility 3 months after release). Furthermore, export levels are not necessarily constant, even within a 3-d period, and the day-to-day variation in export level is not captured by an average. The 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 2 years of the study (1993 and 1994) and for one of the 1999 releases (group 10), but otherwise closed. Recognizing that the amount of exports relative to total inflow from the Sacramento River (at Freeport) could be more important than absolute exports, we also examined the export-to-flow ratio as a covariate; the relationship between the ratios and the absolute values, however, was positive and linear ($r = 0.83$).

Assumptions and Notation

Within and between releases, the fate of an individual fish (live or die, be caught or not) was assumed to be independent of that of any other fish. For all fish released from a given location at a given time, the survival and capture probabilities were

assumed to be identical. In recognition of the paired-release aspect of the study, we further assumed that within a release pair the probability of capture at Chipps Island and the recovery probabilities (complicated combinations of the survival and capture probabilities) in the ocean fishery and inland areas were identical. For example, for release pair 1 (Table 1) the capture probability is the same for a Ryde fish and a Georgiana Slough fish that has survived to Chipps Island, but that probability can differ from the probability for release pair 2.

We further assumed that only fish released in Georgiana Slough were affected by exports. Ryde is located 2.5 mi (1 mi = 1.61 km) downstream of the location on the main stem where water is diverted into Georgiana Slough, and releases at Ryde are further removed geographically from the export facilities. However, for 2 years sizeable numbers of Ryde fish were recovered at the fish facilities (Table 1); it may be that flood tides carried some of the Ryde releases into the interior delta at some upstream or downstream locations such as Three Mile Slough (Figure 1), a channel several miles downstream that connects the Sacramento and San Joaquin rivers.

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

The notation for the probability that a Ryde release will be recovered at Chipps Island is $r_{\text{Ry}\to\text{CI},t}$ and that for the probability that it will be recovered in either the ocean fisheries or inland recoveries is $r_{\text{Ry}\to\text{Oc}+\text{IL},t}$. The corresponding probabilities of recovery for Georgiana Slough releases are denoted $\theta_t r_{\text{Ry}\to\text{CI},t}$ and $\theta_t r_{\text{Ry}\to\text{Oc},t}$, 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 and the survival probability between Ryde and Chipps Island. How it relates to export levels is the primary management question.

Non-Bayesian, Nonhierarchical Models

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

$$\hat{\theta}_{1,t} = \frac{\hat{r}_{\text{GS}\to\text{CI},t}}{\hat{r}_{\text{Ry}\to\text{CI},t}} \qquad (1)$$

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

$$\hat{\theta}_{1,t} \sim \text{Normal}(\beta_0 + \beta_1 \text{Exp}_t^*, \sigma^2), \qquad (2)$$

where $\text{Exp}_t^* = (\text{Exp}_t - \overline{\text{Exp}}/s_{\text{Exp}}$, Exp_t is exports at time t, $\overline{\text{Exp}}$ 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, that is, $y_{\text{Ry}\to\text{CI},t} \sim \text{Binomial}(R_{\text{Ry},t}, r_{\text{Ry}\to\text{CI},t})$. Given $R_{\text{Ry},t}$ and $y_{\text{Ry}\to\text{CI},t}$, $\hat{r}_{\text{Ry}\to\text{CI},t}$ is the maximum likelihood estimate (mle) of $r_{\text{Ry}\to\text{CI},t}$; similarly, $\hat{r}_{\text{GS}\to\text{CI},t}$ is the mle of $\theta_t r_{\text{Ry}\to\text{CI},t}$ and $\hat{\theta}_{1,t}$ is the mle for θ_t based on Chipps Island recoveries alone.

For the second nonhierarchical model, θ_t was estimated from Chipps Island, ocean, and inland recoveries combined, that is,

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

Implicit in this calculation is the assumption that within a release pair the Chipps Island capture, ocean recovery, and inland recovery probabilities are identical. If the total ocean and inland recoveries were known exactly and not estimated, the joint distribution of Chipps Island recoveries and the combined ocean and inland recoveries would be multinomial, and $\hat{\theta}_{2,t}$ would be the mle for θ_t. However, with the expanded recoveries, the distribution is more complex. To account for the 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, that is,

$$\log_e(\hat{\theta}_{2,t}) \sim \text{Normal}(\beta_0 + \beta_1 \text{Exp}_t^*, \text{se}^2_{\log_e[\hat{\theta}_{2,t}]}\sigma^2). \quad (4)$$

The weights were the inverses of the squares of the standard errors of $\log_e(\hat{\theta}_{2,t})$, $\text{se}_{\log_e[\hat{\theta}_{2,t}]}$, which were

calculated using the delta method (see section 10.5 in Stuart and Ord 1987). The log transformation ensures that $\theta_{2,t}$ remains nonnegative.

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

Hierarchical Models

Hierarchical models (Carlin and Louis 1996) consist of two or more levels, each level accounting for a different type of variation. For our data, the first level accounts for the sampling variation in the recoveries conditional on the survival and capture probabilities, the second level for the variation in the survival and capture probabilities between release pairs. 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.

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 the different levels of the hierarchical model are shown below. The first-level distributions are conditional on the second-level variables, and similarly for the second-level distributions.

Level 1:

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

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

Level 2:

$$\log_e(\theta_{3,t}) \sim \text{Normal}(\beta_0 + \beta_1 \text{Exp}^*, \sigma_\theta^2) \quad (7)$$

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

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

Level 3:

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

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

As noted previously, the joint distributions for the Chipps Island recoveries and the combined expanded ocean and inland recoveries cannot be multinomial

owing 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 nonnegative. The logit transformations in level 2 force $r_{\text{Ry}\to\text{CI},t}$ and $r_{\text{Ry}\to\text{Oc}+\text{IL},t}$ to lie between 0 and 1; however, the resulting probabilities are so small that log transformations would have the same practical effect.

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

$$p(\Theta|\text{Data}) \propto p(\text{Data}|\Theta)p(\Theta),$$

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 the 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 the negative association between exports and the relative survival of Georgiana Slough releases.

Sensitivity analysis.—The 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 the possible dependence between fish within a release as well as extramultinomial variation due to the fact that the 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 the recoveries at Chipps Island of releases from Ryde is

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

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

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

$r_{\text{Ry}\rightarrow\text{Oc+IL},t}$, that is (dropping the subscript t to reduce notation),

$$\begin{bmatrix} \theta^1 \\ \theta^2 \\ \theta^3 \end{bmatrix} \sim \text{MVN}\left(\begin{bmatrix} \beta_0 + \beta_1 \text{Exp}^* \\ \mu_{\text{Ry}\rightarrow\text{CI}} \\ \mu_{\text{Ry}\rightarrow\text{Oc}} \end{bmatrix}\right.,$$

$$\left.\Sigma = \begin{bmatrix} \sigma_1^2 & \sigma_{1,2} & \sigma_{1,3} \\ \sigma_{2,1} & \sigma_2^2 & \sigma_{2,3} \\ \sigma_{3,1} & \sigma_{3,2} & \sigma_3^2 \end{bmatrix}\right)$$

where

$$\theta^1 = \log_e(\theta_3)$$

$$\theta^2 = \log_e\left(\frac{r_{\text{Ry}\rightarrow\text{CI}}}{1 - r_{\text{Ry}\rightarrow\text{CI}} - r_{\text{Ry}\rightarrow\text{Oc+IL}}}\right)$$

and

$$\theta^3 = \log_e\left(\frac{r_{\text{Ry}\rightarrow\text{Oc+IL}}}{1 - r_{\text{Ry}\rightarrow\text{CI}} - r_{\text{Ry}\rightarrow\text{Oc+IL}}}\right).$$

A fourth alternative was to use the ratio of exports to total river flow instead of the absolute level of exports. A fifth alternative was to remove the random effects, that is, to make the level 2 models deterministic.

For level 3, various prior distributions were tried for the fixed parameters in level 2. We used the inverse gamma distributions instead of uniform distributions (equation 11) for the variances of the random effects, that is, σ_θ^2, $\sigma_{r_{\text{Ry}\rightarrow\text{CI}}}^2$, and $\sigma_{r_{\text{Ry}\rightarrow\text{Oc+IL}}}^2$. 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 the models for each level were fit. During the fitting process it became clear that certain options at one level led to clearly poorly fitting models (e.g., removing the random effects at level 2 led to a drastic drop in model fit no matter what options were selected at the other levels).

Model fitting, assessment, and comparison.—To fit the BHMs we used the program WinBUGS (Lunn et al. 2000), which generated samples from the joint posterior distribution for the parameters, random effects, and expected numbers of recoveries. Win-BUGS is based on a technique known as Markov chain–Monte Carlo (MCMC; Gilks et al. 1996), which is a computer simulation method in which samples are generated from a Markov chain that 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 that when "enough" samples have been 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 on 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., to begin mixing) is the necessary burn-in period; at that point, presumably, the samples are coming from the limiting distribution and are not stuck at some local mode of the posterior distribution. Values of the Brooks–Gelman–Rubin statistic that are near 1.0 are evidence for convergence, values below 1.1 often being adequate (Gelman et al. 2004:297). Three different chains with differing initial values were run in parallel and the summary statistics are based on the pooled output after burn-in.

For a given model, the goodness of fit 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, that is,

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

where $I(\cdot)$ is an indicator function that equals 1 when the condition inside $(\cdot)$ is met. The predicted value, y_l^{pred}, is found by simulating y from its probability distribution evaluated at the lth 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.

The models were compared using the deviance information criterion (DIC; Spiegelhalter et al. 2002). The DIC can be viewed as a measure of overall model fit while penalizing model complexity. When two models are compared, the one with the lower DIC value is judged 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.

Results

The recovery fractions for the Georgiana Slough releases were consistently less than those for the Ryde releases, with the exception of the fraction recovered at
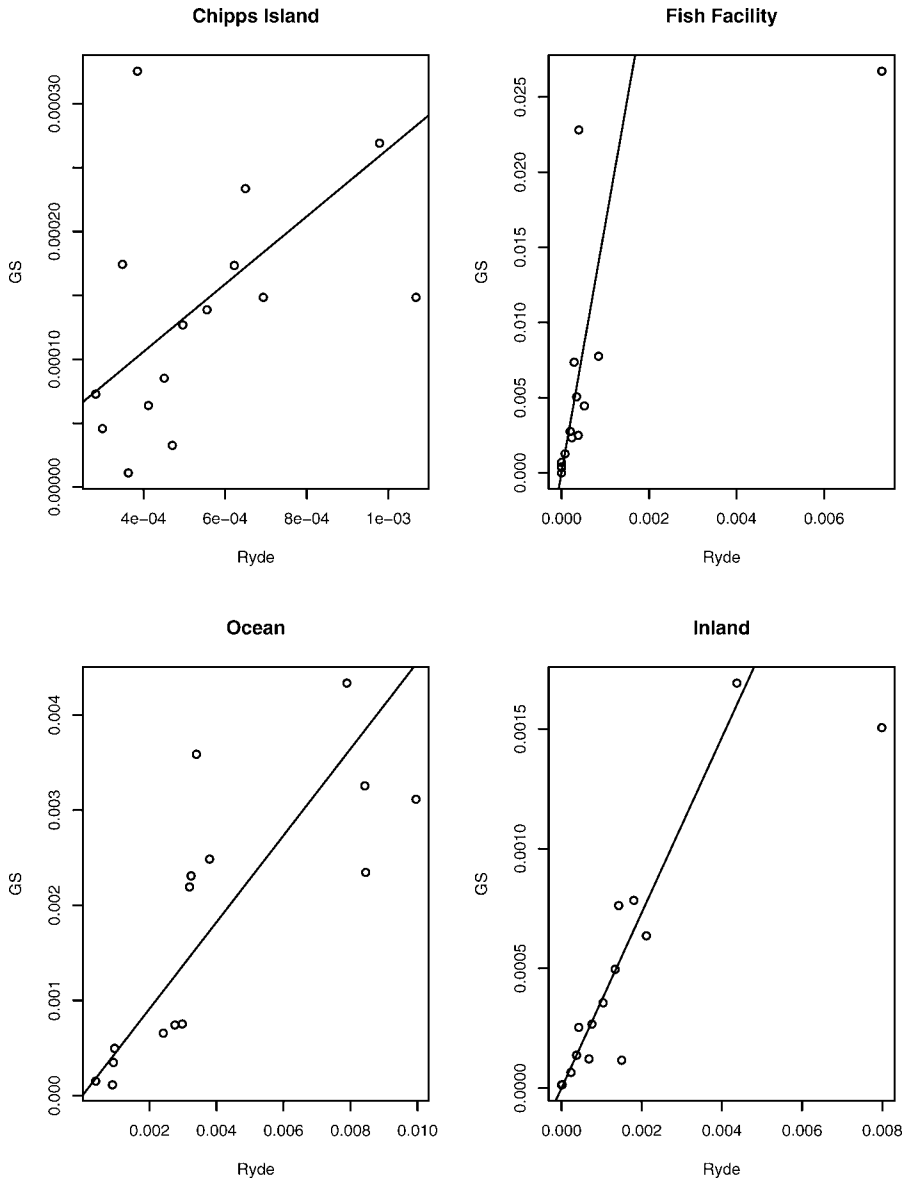
FIGURE 2.—Comparison of the recovery fractions at Chipps Island, in the ocean fisheries, at the fish salvage facilities, and among inland recoveries for Georgiana Slough and Ryde releases, by release pair. The straight lines have slopes equal to the means of the ratios of the recovery fractions.

the fish facilities (Figure 2). The means of the ratios of the recovery fractions equaled 0.26, 0.46, and 0.37 for the 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 fraction of fish facility recoveries from the Georgiana Slough releases tended to increase (from about 0.001 to 0.025) as exports increased from 2,000 cfs to 10,000 cfs (1 cfs = 0.028

m^3/s), 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 greater exports. In contrast, the fraction of the Ryde releases ending up at the fish facilities was less than 0.001 (group 3—a case with high exports—being an exception); these results are generally supportive of the assumption that Ryde releases were unaffected by exports.
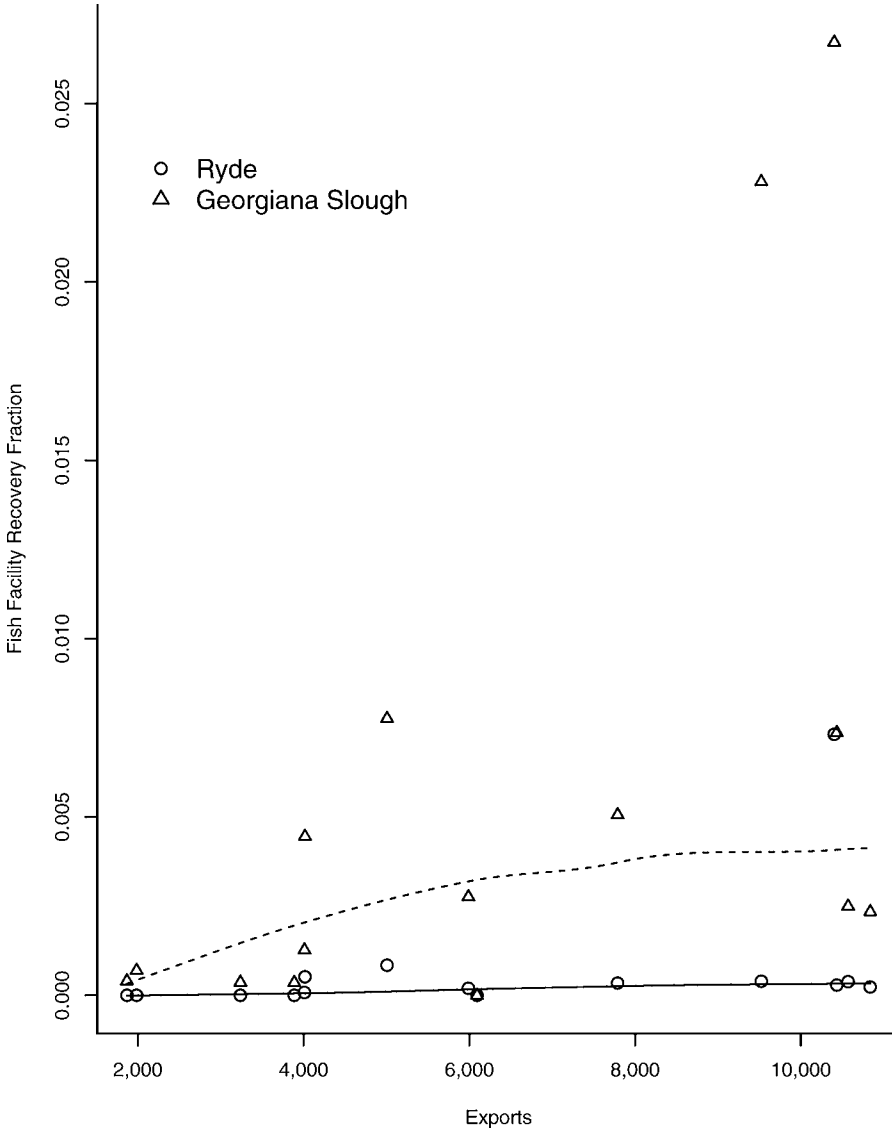
FIGURE 3.—Expanded recovery fractions at the SWP and CVP fish facilities versus export level. The lines are loess smooths for the Georgiana Slough (dashed) and Ryde releases (solid).

Nonhierarchical 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 the ocean and inland recoveries, the standard errors for $\hat{\theta}_2$ tended to be smaller than those for $\hat{\theta}_1$. The difference in standard errors was smaller for the most recent releases (groups 14 and 15), for which there is probably incomplete inland recovery information for the older-age returns. The variation in the

estimates of θ_t was quite large between release groups, 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

$$\hat{\theta}_{1,t} \approx \text{Normal}(0.265 - 0.086\text{Exp}_t^*, 0.18^2)$$

and

$$\log_e(\hat{\theta}_{2,t}) \approx \text{Normal}(-0.935 - 0.214\text{Exp}_t^*, 3.88^2).$$

The *P*-values for a one-sided test of the significance

TABLE 2.—Comparison of release-pair-specific fitted values of the ratio of the survival probability of Georgiana Slough releases to that of Ryde releases (θ). The non-Bayesian, nonhierarchical results are maximum likelihood estimates and standard errors based on 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 model with a multivariate normal distribution at level 2 and θ modeled as a function of exports. See text for more details.

	Non-Bayesian, nonhierarchical				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

of the slope coefficient for exports with the alternative hypothesis that $\beta_1 < 0$ are 0.05 for the $\hat{\theta}_1$ model and 0.04 for the $\log_e(\hat{\theta}_2)$ model. Neither model fit particularly well, however; the R^2 values were 0.19 and 0.21 for the two models, respectively.

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; owing to the somewhat slow

computational speed for that model, the burn-in time was 50,000 iterations, and this was followed by 50,000 sample iterations. There were three types of evidence for convergence to the posterior distribution: Brooks–Gelman–Rubin statistics between 1.0 and 1.03 for all parameters; plots of the parameters for the three chains against the simulation number (trace plots) showing considerable overlap and movement in chain values (which would be consistent with good mixing); and DIC values that were stable between runs.

All of 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 the Akaike information criterion). Notably, this set included a model without exports. The results were robust to the choice of the prior for the standard deviation of the random effects (σ), either the uniform or inverse gamma distribution. Either covariate, exports or exports/flow, led to equivalent DIC values. The 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 observations (88%) had Bayesian P-values that fell within the middle 90% of the posterior predictive distributions. There were too few observed recoveries ($P = 0.02$–0.04) for two cases ($y_{\text{Ry}\rightarrow\text{CI},1}$ and $y_{\text{Ry}\rightarrow\text{CI},6}$) and too many observed recoveries ($P = 0.95$–1.00) for five others ($y_{\text{GS}\rightarrow\text{CI},5}$, $y_{\text{GS}\rightarrow\text{CI},9}$, $y_{\text{GS}\rightarrow\text{CI},12}$, $\hat{y}_{\text{Ry}\rightarrow\text{Oc+IL},14}$, and $\hat{y}_{\text{GS}\rightarrow\text{Oc+IL},14}$).

Replacing the multinomial distribution with the negative binomial distribution (model 7) and excluding random effects (model 8) led to sizeable increases in the DIC values (Table 3), especially for the latter

TABLE 3.—Summary of Bayesian hierarchical models. The level 1 column specifies the distributions (Mn = multinomial, NB = negative binomial). The level 2 column shows models for $\theta_{3,t}$, N denoting the normal distribution and MVN the multivariate normal distribution; the models for the recovery probabilities ($r_{\text{Ry}\rightarrow\text{CI},t}$ and $r_{\text{Ry}}\rightarrow\text{IL},t$) are those shown in equations (8) and (9) in the text except for the MVN model (1) and the model without random effects (8). The level 3 column specifies the prior distribution for the random effects variance; U = uniform, IG = inverse gamma, and IW(I, 4) = inverse Wishart, I being the identity matrix.

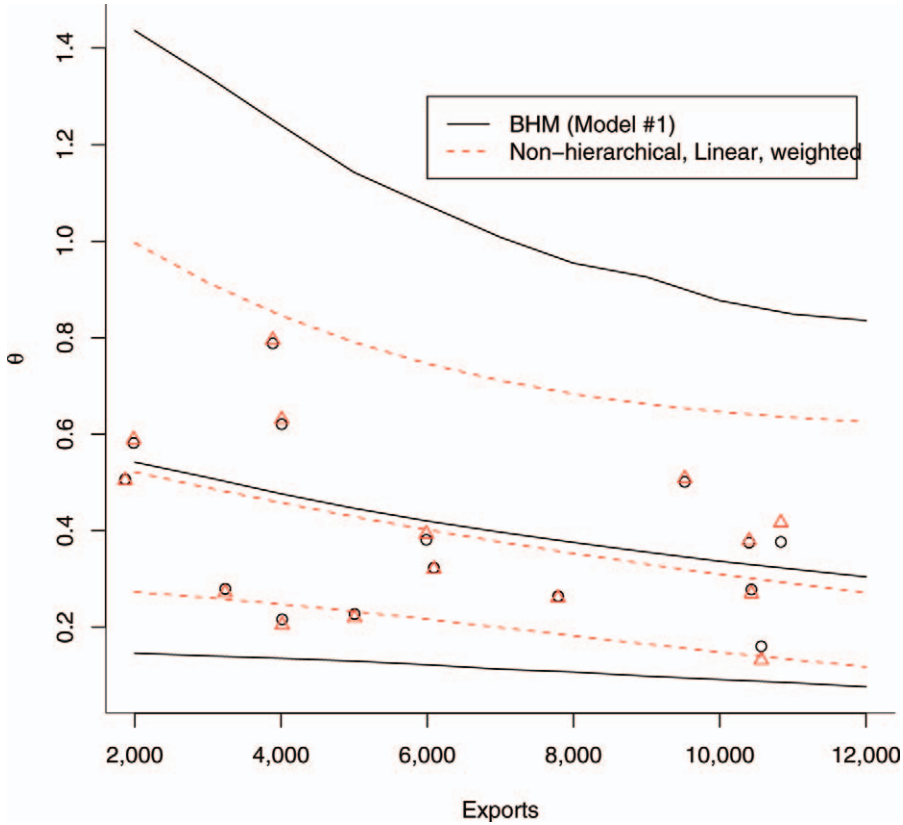| Model	Level 1	Level 2	Level 3	$E(\beta_1)$	$\Pr(\beta_1 < 0)$	$E(\sigma_\theta)$	DIC
1	Mn	$\log_e(\theta_{3,t}), ... \sim .\text{MVN}(\beta_0 + \beta_1 \text{Exp}^*_t, ..., \Sigma)$	$\Sigma \sim \text{IW}[I, 4]$	−0.194	0.92	0.53	460.0
2	Mn	$\log_e(\theta_{3,t}) \sim .N(\beta_0 + \beta_1 \text{Exp}^*_t, \sigma^2_\theta)$	$\sigma \sim U(0, 20)$	−0.170	0.89	0.50	460.0
3	Mn	$\log_e(\theta_{3,t}) \sim .N\left(\beta_0 + \beta_1 \dfrac{\text{Exp}}{\text{Flow}_t}, \sigma^2_\theta\right)$	$\sigma \sim U(0, 20)$	−0.706	0.86	0.51	460.0
4	Mn	$\log_e(\theta_{3,t}) \sim .N(\beta_0 + \beta_1 \text{Exp}^*_t, \sigma^2_\theta)$	$\sigma^2 \sim \text{IG}(0.001, 0.001)$	−0.166	0.90	0.48	459.9
5	Mn	$\text{logit}(\theta_{3,t}) \sim .N(\beta_0 + \beta_1 \text{Exp}^*_t, \sigma^2_\theta)$	$\sigma \sim U(0, 20)$	−0.297	0.88	0.89	460.0
6	Mn	$\log_e(\theta_{3,t}) \sim .N(\beta_0, \sigma^2_\theta)$	$\sigma \sim U(0, 20)$			0.51	460.1
7	NB	$\log_e(\theta_{3,t}) \sim .N(\beta_0 + \beta_1 \text{Exp}^*_t, \sigma^2_\theta)$	$\sigma \sim U(0, 20)$	−0.168	0.89	0.46	487.0
8	Mn	$\log_e(\theta_{3,t}) = \beta_0 + \beta_1 \text{Exp}_t$		−0.079	0.99		4,281.8

FIGURE 4.—Expected values and 2.5–97.5% prediction intervals for θ at different levels of exports produced by Bayesian hierarchical model (BHM) 1 (solid lines) and the nonhierarchical model (dashed lines) using Chipps Island and combined ocean and inland recoveries (equation 4). The circles denote posterior mean fitted values for θ from the BHM, the triangles maximum likelihood estimates.

model. Many of the Bayesian P-values for the nonrandom-effects model were close to 0 or 1. The negative binomial model's parameters, k_{CI} and k_{Oc}, were quite large (with posterior means of 214 and 279, respectively), providing little evidence for overdispersion.

Referring now to model 1 (the results for which are nearly identical to those 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, an $r_{Ry \to CI}$ of that value seems reasonable for the Chipps Island trawl based on independent estimates of Chipps Island trawl capture probabilities on the order of 0.001–0.002 (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 $r_{Ry \to Oc}$ $E[\sigma_{1,3}]$ was 0.18; and between $r_{Ry \to CI}$ and $r_{Ry \to Oc}$ $E[\sigma_{2,3}]$ was 0.25. Thus, within release pairs, 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, indicating 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 $E(\sigma_\theta)$ and the plot of the predicted θ values against exports (Figure 4) indicate. While the plot shows a decline in the mean value of θ as exports increase (e.g., when exports are 2,000 cfs, the mean value of θ is 0.54, whereas when exports are 10,000 cfs, it is 0.34), the range of individual values is very wide. The upper bounds on θ for export levels less than 7,200 cfs exceed 1.0, allowing for the possibility that Georgiana Slough releases occasionally have higher survival than Ryde releases.

Given the similarity in DIC values among models 1–

6 and the fact that our primary interest was the effect of exports, we applied reversible jump MCMC to just two models that differed only with respect to the inclusion (model 2) or exclusion of exports (model 6). The posterior probability for the model including exports was only 1%, compared with 99% for the model without exports; thus, there is 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 ratio of the posterior mean for β_1 to the posterior means for σ_θ, $\sigma_{r_{Ry \to CI}}$, and $\sigma_{r_{Ry \to OC+CI}}$. Repeated simulations of 15 sets of recoveries with the actual release numbers and export levels were made with model 2 (equations 5–11) using the posterior mean values for the parameters (e.g., $E[\beta_1] = -0.17$). Despite the fact that the true model did have θ as a function of exports, RJMCMC typically yielded 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 ± 2 SDs of the observed values did not change these results. However, if the environmental variation were artificially decreased (e.g., by an order of magnitude), RJMCMC gave posterior probabilities for the correct model (the model with exports) ranging from 90% to 99%.

Nonhierarchical versus Hierarchical Models

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 nonhierarchical model (equation 4), but the prediction intervals for the BHM were considerably wider (Figure 4). The observed variation in the estimates of θ_t (shown in Figure 4) seems more consistent with the wider BHM prediction intervals than the nonhierarchical model intervals.

Discussion

We conclude that, for a paired release the survival to Chipps Island of Georgiana Slough releases is considerably less than that of Ryde releases. The ratios of the recovery fractions of the two releases at Chipps Island, in the ocean fisheries, and at the inland sites were consistently much less than 1.0 (Figure 2), and

the posterior means and 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 other than exports that could cause lower relative survival for Georgiana Slough releases include water temperature, predation, and pollution (Moyle 1994). Higher water temperatures have been associated with higher mortality through the delta (Baker et al. 1995). For the paired releases we analyzed, however, the temperatures at release were very similar at Ryde and Georgiana Slough. Regarding predation, Stevens (1966) found more salmon in the stomachs of striped bass *Morone saxatilis* located in the so-called flooded-islands portion of the delta (south of the Georgiana Slough release point) than in the stomachs of striped bass in the Sacramento River.

Regarding the relationship between relative survival and export level, the point estimates of the effects of exports were consistently negative and for the BHMs the probability that the effects are negative was 86–92%. However, as a result of the low signal-to-noise ratio, the DIC values and posterior model probabilities indicate that the predictive ability of models without exports is equivalent to that of models with exports. The environmental variation is large enough that our failure to find a stronger association could be a function of inadequate sample size. Previous analyses (Newman 2008:72) of the relationship between the number of paired releases and the precision of the estimated slope parameter for exports showed that 100 paired releases were needed (based on $\beta_1 = -0.57$ for a logistic transformation of θ) to yield a coefficient of variation of 20%. The RJMCMC analysis of simulated data was 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 some mitigating effect. However, at the SWP facility there is an enclosed area, Clifton Court Forebay, where fish suffer mortality due to predators (Gingras 1997) before entering the salvage facilities. Experiments with marked salmon in the vicinity of the SWP fish facility have yielded estimates of "presalvage" 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–flow ratio (i.e., the absolute or relative level of

exports). Over the range of values observed in these studies, exports and the export–flow ratio are linearly associated (Pearson correlation coefficient = 0.83), so that it is difficult to disentangle the effects of the two factors. Deliberate fixing of export levels at varying levels of flow would be one possible way of determining whether it is the absolute or the relative level of exports that affects the fraction of Georgiana Slough releases recovered at the fish salvage facilities. However, current water management policies and operational standards make such manipulations difficult to conduct. Export levels are largely determined by state and federal water project agencies based on water demand, conditions in the delta, water quality, and operational standards as well as endangered species biological opinions. Owing to the lack of randomization of export levels and the relatively low numbers of releases, the effects of exports may be confounded by other conditions that cause survival to increase or decrease. The pairing aspect of the design may control for such confounding factors, however.

Given the low signal-to-noise ratio, instead of repeating coded wire tag release–recovery experiments for many more years, we recommend releasing fish with acoustic tags and relocating them with strategically placed receivers. Such a system could provide more precise information about when and where mortality is occurring, yielding estimates of reach-specific survival (Muthukumarana et al. 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 on 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 presalvage 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. 2009, this issue), and once this proportion is identified, the benefits of preventing fish from entering the interior delta can be estimated more accurately.

Acknowledgments

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