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Modeling the Survival of Chinook Salmon Smolts Outmigrating Through the Lower Sacramento River System

Ken B. NEWMAN and John RICE

To study the factors associated with the freshwater mortality of outmigrating chinook salmon, releases of tagged juvenile salmon were made at multiple locations in the Sacramento River each spring between the years 1979 and 1995. A midwater trawl located downstream of the release sites caught salmon soon after release and, 1 to 4 years later, samples taken from the catches of marine fisheries recovered other tagged fish. An extended quasi-likelihood model was fit to both the freshwater and the marine recoveries. A ridge parameter was included to stabilize the parameter estimates and to improve predictive ability. Overdispersion was due, at least in part, to heterogeneity in the trawl's capture efficiency, as well as to the complex aggregation of marine recoveries. Different dispersion parameters were used for the river and ocean recoveries because of the additional sources of variation experienced by ocean recoveries relative to river recoveries. Interpretation of estimated coefficients was delicate, given the correlation between some of the covariates, the biases introduced by the ridge parameter, and possible confounding factors. With these caveats in mind, we found the most influential covariate to be the temperature of the water into which the fish were released, with increasing temperatures having a negative association with recoveries. Three covariates were of particular interest to the biologists and water managers: water flow, position of a water diversion gate (open or closed) separating the mainstem from the central delta, and relative fraction of water exported for irrigation and urban consumption. The effects of flow were slightly positive but were confounded by salinity levels. The effect of the water diversion gate being open was to lower apparent survival for fish released above the gate, but apparent survival increased for fish released in the central delta into which the water was diverted. There was evidence that increasing the export-to-inflow ratio lowered survival, but the effect was slight and not statistically significant.

KEY WORDS: Band recovery; Extended quasi-likelihood; Overdispersion; Release-recovery; Ridge regression.

1. INTRODUCTION

The Sacramento–San Joaquin River system is the southern limit for chinook salmon (*Oncorhynchus tshawytscha*) and until the early portion of this century supported returns of chinook salmon numbering a million or more (Healey 1991). Since then, the number of adult salmon returning to spawn has decreased dramatically; during the mid-1970s, returns to the San Joaquin River averaged less than 4,000. There are a variety of reasons for the decline, including freshwater habitat loss and degradation, increased ocean fishing, and the export of water for human use. Water export from the lower portion of the river system, including the delta, is facilitated by water pumping stations, diversion gates, and hundreds of man-made canals. The diversion and export of water has drastically altered historic outmigration routes and lowered the likelihood of juvenile salmon successfully reaching the estuary and the ocean.

To identify water management schemes that will have less-adverse effects on juvenile salmon survival, the U.S. Fish and Wildlife Service (USFWS) has conducted numerous release-recovery studies in the lower portions of the Sacramento–San Joaquin River system since the 1970s. Juvenile chinook salmon, raised and tagged at a hatchery, were released at multiple locations throughout the system, under varying water conditions (e.g., flows low or high, a major diversion gate open or closed, export levels low or high), and trawls located downstream of the releases were used to recover the fish.

The release-recovery data from these studies have been the basis for several statistical models for survival through the delta developed by the USFWS, California Department of Water Resources, and other agencies. A recent approach (Kjelson, Greene, and Brandes 1989) was based on releases during the years 1978–1989 made at various locations near and downstream of Sacramento with subsequent recoveries by a midwater trawl operating near Chipps Island (Fig. 1). Kjelson et al. (1989) fit separate multiple regression models for reach-specific mortality through three geographic areas of the river system. The geography can be roughly characterized as a line from Sacramento to Courtland (reach 1). At Courtland the line branches into two segments, one segment arcing through the "central delta" (reach 2) and the other staying in the main river (reach 3), and the two segments then merge together just above Chipps Island. Just south of Courtland there is a removable diversion called the cross-channel gate which, when open, diverts water from reach 1 into reach 2, and when closed keeps the water flowing into reach 3. Three dependent variables—the reach-specific mortality indices scaled to [0, 1]—could not be directly observed and were estimated using a somewhat involved procedure. Details of the estimation procedure are not discussed here, but the accuracy of the estimates hinged on a critical assumption that at the intersection of reaches 1, 2, and 3 the percentage of fish travelling through reach 2 equalled the estimated percentage

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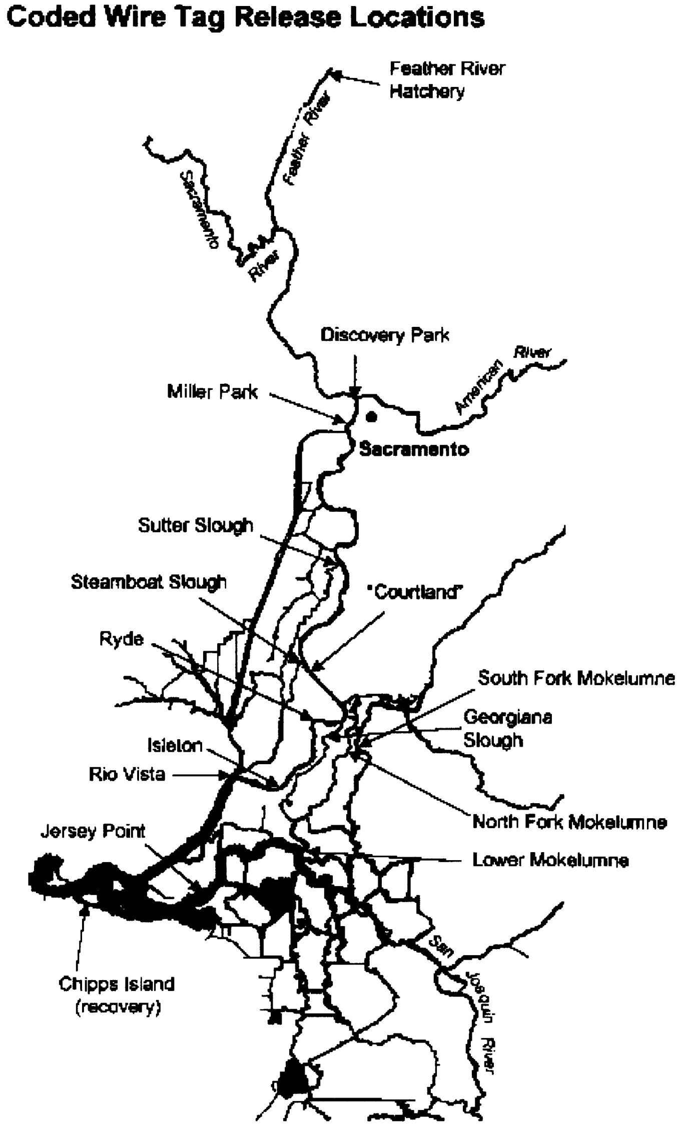

Figure 1. Release and Recovery Locations in the Lower Sacramento River System. The Feather River Hatchery is approximately 100 miles northeast of the recovery point at Chipps Island. Releases at Discovery Park and Miller Park are referred to as Sacramento releases. Releases at Sutter and Steamboat Sloughs are referred to as Slough releases. Releases at the three Mokelumne sites and Georgianna Slough are labeled Mokelumne-Georgiana releases.

of water entering that reach (i.e., fish "go with the flow"). The indices estimation procedure also required that paired releases be available for various endpoints of the reaches (with some ad hoc methods to deal with a lack of pairs for reach 1 estimation in particular). Covariates examined for inclusion into the model included measures of river flow, amount of water extracted from the river by pumping stations in the delta, water temperatures, fish size at time of release, and two different tide-related variables. Stepwise multiple regressions were used in each reach. Kjelson et al. (1989) concluded that increases in water temperature, fraction of water diverted from the Sacramento River, and total exports adversely affected juvenile chinook salmon survival. They also recommended that smolts be kept out of the central delta (reach 2), because the greatest mortality (based on the estimated mortality index) was observed there.

The work of Kjelson et al. (1989) was closely scrutinized by numerous interested parties, and their methodology was criticized on a number of grounds. The assumptions and methods for estimating the indices, the application of standard linear regression to dependent variables ranging between 0 and 1, and the selection of covariates were major criticisms. In light of these criticisms, the interested parties chose to bring in statisticians previously unaffiliated with this work (namely, the authors) in an attempt to develop an alternative approach for modeling the release-recovery data. This article describes the resulting model. Although the approach here was quite different from that of Kjelson et al., some of our conclusions were quite similar—for example, the sizeable effect of water temperature.

2. THE DATA

Each spring, wild and hatchery-reared juvenile fall chinook salmon in the Sacramento River system begin their outmigration to the Pacific Ocean. The USFWS experiments mimic the outmigration process by releasing hatchery-reared juvenile chinook salmon during April and May. Each fish is marked externally by removing the adipose fin, and a small binary-coded tag, 1.1 mm in length and .25 mm in diameter (Nielsen 1992), is inserted in its snout. The tag codes are release-group specific. The marked and tagged fish are then trucked from a hatchery to a release location.

Some of these marked and tagged fish are recovered and killed soon after release by the midwater trawl at Chipps Island, usually within 2–3 weeks. The total number recovered by the trawl for a given release is denoted by y_r. Other marked and tagged fish are recovered as adult fish 1–4 years later in samples taken from the marine catch. Sampling of the marine catch is stratified by time (e.g., weekly or biweekly) and by port of landing, ranging from central California to northern British Columbia. Approximately 20%–25% of the marine catch is sampled, but the sampling fraction varies considerably from week to week and from port to port. The estimated number of total ocean recoveries, denoted by $\hat{y}_o$, is the sum over each of the strata of estimated recoveries. This can be approximately written as

$$\hat{y}_o \approx \sum_a \sum_t \sum_p e_{atp} y_{atp},$$

where y_{atp} is the number of recoveries of marked and tagged fish in stratum atp's sample; a denotes age, which ranges from 2 to 5 years; t denotes time period within a fishing season; p denotes landing area (usually a port); and e_{atp} is the inverse of the sampling fraction for a given stratum, also known as the expansion factor, which averages 4–5. An average expansion fraction, denoted by e_o, is used in the modeling of ocean recoveries:

$$e_o = \frac{\hat{y}_o}{\sum_a \sum_t \sum_p y_{atp}}. \tag{1}$$

Values of e_o ranged from 3.1 to 8.0, with a median of 4.4.

We modeled the river recoveries and the total expanded ocean recoveries from 101 groups of marked, hatchery-reared juvenile chinook groups. All of the fish were raised at the

Feather River Hatchery. The groups were released into the Sacramento River during the spring months of 1979–1995. The release locations varied both within and between years. The locations were broadly partitioned into seven areas (Feather River Hatchery, Sacramento, Courtland, Sutter and Steamboat Sloughs, Georgianna-Mokelumne, Ryde, and Jersey Point), where the ordering is approximately inversely proportional to the distance to the trawl (Fig. 1). The lower portion of the Sacramento River is a maze of sloughs and channels known as the delta. The San Joaquin River passes through the delta and empties into the Sacramento River. There is thus no single route for an outmigrating fish to take to the ocean, and the distance traveled from the point of release to the trawl can vary. With respect to location of release and year of release, the design was badly imbalanced. For example, there was only 1 release in both 1979 and 1982, but 17 releases in 1988. Similarly, there were only 2 releases from Feather River Hatchery (both in 1980), but 24 releases from Ryde.

The number of fish released per group ranged from 11,000 to 160,000, with a median of 51,000. The number of fish recovered by the trawl, y_r, ranged from 2 to 145, with a median of 32. The estimated number of fish recovered by the marine fishery, $\hat{y}_o$, ranged from 10 to 1,979, with a median of 280. The median trawl recovery rate was .00066, and the median estimated ocean fishery recovery rate was about 10 times larger, .0050.

Biologists and hydrologists identified a large set of covariates as possibly influencing the river survival of outmigrating salmon. After extensive discussion and analysis to minimize redundancy, the set was eventually reduced to the following 10 covariates:

1. Fish size (average length in mm)
2. Log-transformed median flow (ft^3/sec) during the outmigration period
3. Salinity of water as measured by resistance (μmho/cm)
4. River temperature at time of release (°F)
5. Temperature of the hatchery water on the day of release (°F)
6. Temperature shock, the difference between the temperature of water in the truck carrying the fish from the hatchery to the release location and the river temperature
7. A tide-related variable that measured the magnitude of the change in low-low and high-low tides and whether the delta was filling or draining
8. Turbidity of water (formazine turbidity units)
9. Position of the cross-channel gate located just below Courtland; 1 if open and 0 if closed
10. Ratio of amount of water exported to amount of water flowing in the mainstem.

3. METHODS

An extended quasi-likelihood model (Nelder and Pregibon 1987) was fit to the river recoveries y_r and the estimated total ocean recoveries $\hat{y}_o$. A ridge parameter was included to stabilize estimates of the coefficients. The number of river recoveries was a function of number released, R, the probability of surviving from point of release to the trawl, S, and the conditional probability of capture, p, by the trawl given survival. The estimated number of ocean recoveries was also a function of R, S, and p, as well as the marine survival probabilities, the harvest rates of the ocean fisheries, and the catch sampling fractions over the 4-year period after release. Our primary focus was on the covariates associated with S.

Before detailing the model formulation and estimation procedures, we briefly describe the classic multinomial formulation for modeling release-recovery data. We next give the additional assumptions and approximations tailored to accommodate the available data.

3.1 Multinomial Formulation for Recoveries

The classic formulation for release-recovery data is based on multinomial distributions. Its origins include the work of Darroch (1959), Cormack (1964), Jolly (1965), and Seber (1965), who developed procedures for estimating demographic parameters of open populations, populations with births, deaths, immigration, and emigration. Later work by Brownie, Anderson, Burnham, and Robson (1985) on models for the recovery of bands from dead birds (band-recovery models) and by Burnham, Anderson, White, Brownie, and Pollock (1987) on models for the recovery of tags from fish released above dams pertain more directly to the data analyzed herein. The available data do not exactly conform to the situations of Brownie et al. and Burnham et al., but it is useful to start with the simpler setting and delineate the points of departure.

For a given release, the fates of all fish are assumed independent and identically distributed. Assume that the total number of ocean recoveries is known, not estimated. For a release of size R, the distribution for y_r and y_o is trinomial,

$$\Pr(y_r, y_o|R) = \frac{R!}{y_r!\,y_o!\,(R-y_r-y_o)!}(Sp)^{y_r}(S(1-p)\pi)^{y_o} \times (1-Sp-S(1-p)\pi)^{R-y_r-y_o},$$

where π is the conditional probability of a fish being recovered by the marine fishery at any time and any place given that the fish survived the river and was not caught by the trawl. Thus π is a function of ocean survival probabilities and marine fishery harvest rates.

The extended quasi-likelihood model that we used was a product of two independent overdispersed Poisson "distributions." As an intermediate step to that formulation, the trinomial distribution for y_r and y_o can be approximated with a product of independent Poisson distributions, where the Poisson parameters are products of release numbers and recovery rates,

$$y_r \sim \text{Poisson}(RSp) \quad (2)$$

and

$$y_o \sim \text{Poisson}(RS(1-p)\pi) \quad (3)$$

Given the large release numbers and the very low recovery rates for trawl and marine fisheries, Poisson approximations for the marginal distributions are reasonable. The assumption of independence is also tenable given that the median estimated covariance was $-.0000036$.

The only estimable parameters under the trinomial distribution or the Poisson approximations are the products, Sp and $S(1-p)\pi$. To make estimation of S possible and to conform with the classic formulations of Darroch (1959) and others, for each release made upstream of the trawl, a matching or paired release would be made just downstream of the trawl during the time period when surviving, but not caught, upstream releases would be passing. For a subset of upstream releases, such a pairing occurred and has been analyzed elsewhere (Newman 2000). Later, we compare the paired release results to our unpaired release analysis.

3.2 Partitioning Trawl Capture Probability p

Although S cannot be separately estimated based on the unpaired releases alone, the ratio of S's for any two release groups can be estimated by using additional information about the trawl effort to model p and by making the assumption of constant catchability. The assumption of constant catchability is that the trawl capture probability, p, is proportional to a measure of trawl fishing effort, f_r. Letting q denote the unknown constant of proportionality, also called the catchability coefficient,

$$p = qf_r. \tag{4}$$

This is a potentially strong assumption. If f_r is the same on two different occasions, then the trawl is assumed to have the same probability of capturing a passing fish even if, for example, the flow and turbidity differ greatly between the two occasions.

Trawl fishing effort is a relative measure between 0 and 1. It is defined as the fraction of river width swept by the trawl net crossed with the fraction of time the trawl was in operation during the period of salmon passage. For example, if the trawl net was stationary, covered half the river, and was left in the river 12 hours per day, then $f_r = .25$. The period of salmon passage began with the day of the first recovery and ended with the day of the last recovery for a release. For some releases, there likely were cases where salmon passed either before the designated first day or after the designated last day, but the day-to-day operation of the trawl was generally consistent enough within a given year so that the effect on f_r of failing to include those days should be minimal. The effort measures ranged from .07 to .25, with a median of .11.

With the probability of survival followed by capture by the trawl, Sp, estimated by y_r/R, (4) yields the following estimate of the ratio of survival probabilities for two releases, labeled I and II:

$$\frac{\widehat{S}_I}{\widehat{S}_{II}} = \frac{y_{rI}/(R_I f_{rI})}{y_{rII}/(R_{II} f_{rII})}. \tag{5}$$

Estimated ocean recoveries can also be used to estimate the ratio of survival probabilities between two releases assuming that p and π are the same for both releases, that is,

$$\frac{\widehat{S}_I}{\widehat{S}_{II}} = \frac{\hat{y}_{oI}/R_I}{\hat{y}_{oII}/R_{II}}. \tag{6}$$

For pairs of releases made in the same year, the assumption of equal p and π may not be too unreasonable. Year-specific estimates of S_I/S_{II} were made using (5) and (6) where the first release group was fixed as the first in the data file for the year and the second release group varied over the remaining releases for that year. A paired t test for equality of the estimates based on both equations indicated no difference in estimates (p value $= .45$).

3.3 Modeling Recoveries

Of primary interest to biologists and water resource managers was understanding how environmental and biological covariates were associated with survival probabilities, or in this case of unpaired release data, the ratio of survival probabilities for any two release groups. From (5), given a covariate-based model for y_r and known values of R and f_r, the effect of changes in covariate values on the ratio of survival probabilites can be studied. From (6), ocean recoveries provide information about survival ratios as well. The formulation given in (7)–(8) and (11) is a means of combining information from both sources.

The trawl and ocean recoveries were modeled by overdispersed Poisson regression models with log link functions. The models for the mean and variance structures are given first, and the rationale behind the formulation follows. Let μ_r and μ_o be the expected value of y_r and $\hat{y}_o$ for a given release, and let σ_r^2 and σ_o^2 be the corresponding variances. Rewrite π as $e_o\theta$, where e_o is defined in (1) and θ is defined to be the conditional probability of a fish being caught by the marine fisheries and being sampled given that it survived the river and was not caught by the trawl. The models used for the mean and variance structures were

$$\log(\mu_r) = \log(Rf_r) + \beta_0 + \beta_1 I_{River} + \sum_{j=2}^{m1} \beta_j x_j, \tag{7}$$

$$\log(\mu_o) = \log(Re_o) + \beta_0 + \sum_{j=2}^{m1} \beta_j x_j + \sum_{j=m1+1}^{m1+m2} \beta_j I_{Ocean,\,year_j}, \tag{8}$$

$$\sigma_r^2 = c_r \mu_r, \tag{9}$$

and

$$\sigma_o^2 = c_o \mu_o. \tag{10}$$

In (7)–(10), $\log(Rf_r)$ and $\log(Re_o)$ are offsets, I_{River} is an indicator variable for the recovery being by the trawl, $x_2, \ldots, x_{m1}$ are covariates shared by μ_r and μ_o, and $I_{Ocean,\,year_j}$ is an indicator variable for the recovery being an ocean recovery from a group released in one of $m2$ years. The coefficients c_r and c_o are (over)dispersion parameters.

The components of the model for μ_r in (7) can be equated to the terms of the Poisson rate parameter; using (2) and (4),

$$\begin{aligned}\log(\mu_r) &= \log(Rf_r) + \log(q) + \log(S)\\ &\equiv \log(Rf_r) + \beta_0 + \beta_1 I_{River} + \sum_{j=2}^{m1} \beta_j x_j.\end{aligned}$$

Equating the components of the model for μ_o in (8) to the terms of the Poisson rate parameter in (3), with $\pi = e_o\theta$, requires assuming that $1-p$ is 1.0:

$$\begin{aligned}\log(\mu_o) &= \log(R)+\log(S)+\log(1-p)+\log(e_o\theta)\\ &\approx \log(Re_o)+\log(S)+\log(\theta)\\ &\equiv \log(Re_o)+\beta_0+\sum_{j=2}^{m1}\beta_j x_j+\sum_{j=m1+1}^{m1+m2}\beta_j I_{Ocean,\,year_j}.\end{aligned}$$

The preceding two sets of equations imply that the contribution of $\log(q)$ is reflected in β_1 and one of the β_j, $j = m1+1,\ldots,m1+m2$, for the appropriate year models $\log(\theta)$. The motivation for the indicators, $I_{Ocean,\,year_j}$, was to separate the ocean recovery rate from the river survival probability S. Thus ocean recoveries, which result from a relatively large-scale process, can provide information about S over and above that provided by river recoveries, a relatively fine-scale process.

The assumption $p=0$ for $\log(\mu_o)$ is at odds with the formulation of the model for $\log(\mu_r)$, but the effect of p on μ_r is considerably greater than the effect of $1-p$ on μ_o. The paired release analysis (Newman 2000) yielded estimates of p in the range of .001 to .002 and estimates of π an order of magnitude larger. Assuming, for example, $R = 50{,}000$, $S = .1$, $p = .002$, and $\pi = .01$, then $\mu_r = 10$ and $\mu_o = 49.9$, whereas assuming $p = 0$ implies $\mu_o = 50.0$.

Overdispersed Poisson regression models, using a log-link with $\log(R)$ as an offset and a single overdispersion parameter, have been used for ocean recoveries of tagged salmon by others (Cormack 1993). The use of two dispersion parameters is sensible given the very different recapture settings, the river trawl, and the widely ranging marine fisheries. Cormack (1993) argued that overdispersion is reasonable with fishery count data in general due to possible schooling and, in particular, for the special case of total estimated ocean recoveries, which is a complicated aggregation of estimates over many samples. Cormack also suggested extended quasi-likelihood as a possible approach for such fisheries data. A further reason for overdispersion is the heterogeneity in the capture probabilities, p (Baker, Speed, and Ligon 1995), over and above that accounted for by estimated trawl effort.

3.4 Covariate Details

It was reasonable to assume that distance from the trawl affected survival. Because distance from point of release to the trawl cannot be precisely measured, indicator variables were used for the seven release locations, with Jersey Point (the location closest to the trawl) as the default.

The effects of cross-channel gate position, export-to-inflow ratio, and turbidity on survival probabilities were believed to differ for fish released in the mainstem above the gate (Feather River Hatchery, Sacramento, and Courtland) and those released in the central delta (Georgianna-Mokelumne and Jersey Point). Furthermore, it was believed that fish released at Sutter and Steamboat Sloughs and Ryde would be largely unaffected by these covariates. The central delta contains the two largest water pumping stations; thus fish in the central delta could potentially be more disoriented than mainstem releases by the flow dynamics created by the pumps. When the gates are open, more water enters the central delta, which also could have a different effect on fish released in the central delta.

Gate position, export levels, and differences in the geography of the delta and mainstem can cause differences in turbidity levels. Thus a "mainstem" turbidity measurement was used for Feather River Hatchery, Sacramento, Courtland, and Ryde releases, whereas a "delta" turbidity measurement was used for Georgianna-Mokelumne and Jersey Point releases. No direct turbidity measurements were available for the Sutter and Steamboat Slough releases, and the turbidity covariate was set to 0 for those releases.

To allow for site-specific differential effects of the cross-channel gate position, export-to-inflow ratio, and turbidity, these variables were crossed with the release site indicator variables. The interactions of gate position and export-to-inflow ratio with location are prefixed "Upper" for the three sites above the gate and "Delta" for the two sites in the central delta. For example, *Upper.Gate* is the product of the indicator variable for gate position and sum of the indicators for Feather River Hatchery, Sacramento, and Courtland releases. The release site indicators and covariates interacting with release site are referred to as site-dependent covariates; the remaining covariates, are as site-independent covariates. The resulting model for $\log(\mu_r)$ and $\log(\mu_o)$ includes 35 covariates:

$$\begin{aligned}\log(\mu) = {}&\log(Rf_r)I_{River}+\log(Re_o)(1-I_{River})+\beta_0+\beta_1 I_{River}\\ &+\beta_2 Size+\beta_3\log(Flow)+\beta_4 Salinity\\ &+\beta_5 Release.Temp+\beta_6 Hatchery.Temp+\beta_7 Shock\\ &+\beta_8 Tide+\beta_9 I_{FRH}+\beta_{10}I_{Sac}+\beta_{11}I_{Slough}+\beta_{12}I_{Court}\\ &+\beta_{13}I_{Ryde}+\beta_{14}I_{Mk\text{-}Georg}+\beta_{15}Upper.Exp.Inflow\\ &+\beta_{16}Delta.Exp.Inflow+\beta_{17}Upper.Gate\\ &+\beta_{18}Delta.Gate+\beta_{19}Mainstem.Turbid\\ &+\beta_{20}Delta.Turbid+\beta_{21}I_{Ocean,\,1979}+\cdots\\ &+\beta_{35}I_{Ocean,\,1994}.\end{aligned} \tag{11}$$

3.5 Parameter Estimation

To estimate the coefficients of (11) and the two dispersion parameters, the extended quasi-likelihood function was maximized using iteratively weighted least squares (IWLS). The number of coefficients of (11) to estimate, 36, was large relative to the number of observations, 202, thus a ridge parameter, λ, was included to stabilize the estimates. Ridge estimators have been applied to generalized linear models, particularly logistic models (e.g., le Cessie and van Houwelingen 1992), but we are unaware of any applications to extended quasi-likelihood models. The ridge parameter was applied only to β_2 through β_{35}, whereas the intercept terms β_0 and β_1 were not shrunk. The value of λ was chosen on the basis of the ridge trace for the coefficients (in particular, β_2–β_{20}) and a leave-one-out cross-validation for a trimmed average of the squared Pearson residual, $(y-\hat{y})^2/\hat{y}$.

The IWLS algorithm was much the same as that used for fitting most generalized linear models (McCullagh and Nelder 1989). The coefficients were estimated by

$$\hat{\beta} = (X'WX+\Lambda)^{-1}X'WZ,$$

where X was the 202 by 36 design matrix of standardized covariates, W was a diagonal matrix of weights, Λ was a diagonal matrix containing the ridge parameter, and Z was the working dependent variable. The components of Z were reduced by the offset; for the ith river and ocean recoveries,

$$z_{ri} = \log(\hat{\mu}_{ri}) - \log(R_i f_{ri}) + \frac{y_{ri} - \hat{\mu}_{ri}}{\hat{\mu}_{ri}}$$

and

$$z_{oi} = \log(\hat{\mu}_{oi}) - \log(R_i e_{oi}) + \frac{y_{oi} - \hat{\mu}_{oi}}{\hat{\mu}_{oi}},$$

where the fitted values, $\hat{\mu}$, were estimated from (11) (using standardized covariates), substituting current estimates, $\hat{\beta}$, for β.

The weights were updated every iteration and estimated by $\hat{\mu}_r/\hat{c}_r$ and $\hat{\mu}_o/\hat{c}_o$ (McCullagh and Nelder 1989, eq. 2.12), where $\hat{c}_r$ and $\hat{c}_o$ are the estimated dispersion parameters. In turn, the dispersion parameters were estimated by the deviances for river and ocean recoveries divided by error degrees of freedom, in this case $202 - 35 = 167$ (McCullagh and Nelder 1989, sec. 10.5.2).

Using a Taylor approximation, the covariance matrix for $\hat{\beta}$ is approximately

$$\text{var}[\hat{\beta}] \approx (X'WX + \lambda I)^{-1} X'W \text{var}[Z] W'X (X'WX + \lambda I)^{-1},$$

where $\text{var}[Z] = \Phi W^{-1}$, with Φ being a diagonal matrix of dispersion values.

The ratio of the survival rates for two releases, labeled I and II, can be estimated as follows. Let $\mathbf{x}_I^*$ and $\mathbf{x}_{II}^*$ be column vectors of the (standardized) covariate values for the two releases. Then

$$\widehat{\text{E}}\left[\frac{S_I}{S_{II}}\right] = \exp\left((\mathbf{x}_I^* - \mathbf{x}_{II}^*)'\hat{\beta}\right). \tag{12}$$

In practice, only those covariates with differing values need to be specified, because of cancellation of the values for the other covariates. Release numbers and trawl effort levels are also irrelevant. The estimate for variance of the ratio is

$$\begin{aligned} \text{var}\left[\widehat{\text{E}}\left[\frac{S_I}{S_{II}}\right]\right] &= \text{var}\left[\exp\left((\mathbf{x}_I^* - \mathbf{x}_{II}^*)'\hat{\beta}\right)\right] \\ &\approx \left[\exp\left((\mathbf{x}_I^* - \mathbf{x}_{II}^*)'\hat{\beta}\right)\right]^2 (\mathbf{x}_I^* - \mathbf{x}_{II}^*)' \\ &\quad \times \text{var}[\hat{\beta}](\mathbf{x}_I^* - \mathbf{x}_{II}^*) \\ &= \left(\frac{\widehat{S_I}}{\widehat{S_{II}}}\right)^2 (\mathbf{x}_I^* - \mathbf{x}_{II}^*)'\text{var}[\hat{\beta}](\mathbf{x}_I^* - \mathbf{x}_{II}^*). \end{aligned} \tag{13}$$

The variance of a predicted ratio follows from the "double-variance" formula and the assumed overdispersed Poisson distribution.

4. RESULTS

4.1 Choice of Ridge Parameter

The ridge parameter was set to 30 on the basis of the cross-validation scores for prediction errors, ridge traces of $\hat{\beta}$, and changes in the sum of the estimated variances of the $\hat{\beta}$'s. The λ choice from cross-validation scores was quite sensitive to the degree of trimming and to whether the scores were based on all recoveries or on river recoveries alone. This was partially due to two releases with a relatively large number of ocean recoveries. The choice was clearer for ridge traces; the changes in coefficients were relatively minor for $\lambda > 30$. Also, the relative decrease in total variance from $\lambda = 0$ to $\lambda = 30$ was 56%; increasing λ from 30 to 40 decreased total variance by only 6%.

4.2 Parameter Estimates and Interpretation

The estimated dispersion parameters were $\hat{c}_r = 11.90$ and $\hat{c}_o = 42.49$. The magnitudes of these parameters are large compared to commonly published values. If recoveries are seen as being generated from a hierarchic distribution, however, such as a beta-binomial, then such values are reasonable given the very large number of released fish. For example, if $Sp \sim \text{beta}(1.7, 2409.4)$ (which yields $\text{E}[Sp] = .0007$ and $\text{var}[Sp] = 2.9\text{e}{-07}$) and $y_r|Sp \sim \text{binomial}(50{,}000, Sp)$, then the overdispersion relative to a binomial is 21.7. If clusters smaller than the release number form, then the variance inflation falls between 1 and that of the beta-binomial.

Table 1 presents the estimated coefficients (denoted $\hat{\beta}_\lambda$) for the site-independent and site-dependent covariates. The release year effect coefficients for ocean recoveries are not shown; they are of minor interest, and interpretation is difficult due to the complex combination of factors that affect the probability of marine recovery. The estimated coefficients for the site-independent and site-dependent covariates are plotted in descending order, along with ±2 standard errors, in Figure 2. This provides an approximate means of visually separating

Table 1. Estimated Coefficients and Standard Errors (Subscripts) for the Standardized Covariates

Covariate	$\hat{\beta}$	$\hat{\beta}_\lambda$
Intercept	$-5.939_{.037}$	$-5.924_{.036}$
I_{River}	$.591_{.125}$	$.656_{.070}$
Site-independent variables		
Size	$.070_{.045}$	$.072_{.041}$
log(*Flow*)	$.144_{.083}$	$.104_{.059}$
Salinity	$.265_{.074}$	$.201_{.058}$
Release.Temp	$-.456_{.078}$	$-.375_{.059}$
Hatchery.Temp	$.031_{.070}$	$-.010_{.055}$
Shock	$-.032_{.066}$	$-.057_{.053}$
Tide	$-.104_{.040}$	$-.089_{.036}$
Site-dependent variables		
I_{FRH}	$-.218_{.054}$	$-.200_{.038}$
I_{Sac}	$.011_{.116}$	$.007_{.054}$
I_{Slough}	$.028_{.068}$	$.036_{.045}$
I_{Court}	$.024_{.121}$	$.012_{.058}$
I_{Ryde}	$.048_{.109}$	$.067_{.053}$
$I_{Mk\text{-}Georg}$	$-.165_{.056}$	$-.168_{.048}$
Upper.Exp.Inflow	$-.153_{.091}$	$-.104_{.065}$
Delta.Exp.Inflow	$-.070_{.090}$	$-.039_{.063}$
Upper.Gate	$-.116_{.053}$	$-.130_{.046}$
Delta.Gate	$.195_{.091}$	$.142_{.064}$
Mainstem.Turbid	$-.057_{.061}$	$-.025_{.045}$
Delta.Turbid	$-.126_{.099}$	$-.069_{.064}$

NOTE: $\hat{\beta}_\lambda$ is the coefficient with $\lambda = 30$. $\hat{\beta}$ is the coefficient without a ridge parameter. The default site location is Jersey Point and default release year is 1995. The coefficients for the 15 release year indicators for marine fisheries recoveries are not shown.

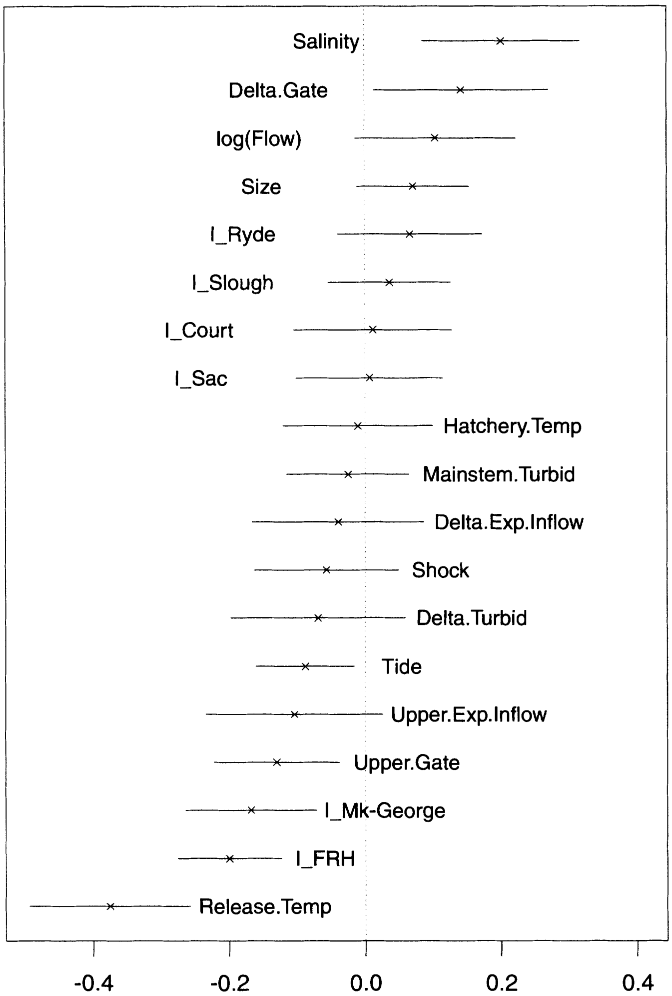

Figure 2. Estimated Coefficients for Site-Independent and Site-Dependent Covariates ± Two Standard Errors.

strong from weak effects in that coefficients with intervals including 0 would be considered weak. Given that the ridge parameter generally shrinks the estimates toward 0, these intervals likely are shifted more to the origin than correct 95% confidence intervals.

The stronger positive effects for site-independent covariates are from increasing salinity and increasing flow. The interpretation is complicated, however, by the inverse (and nonlinear) relationship between flow and salinity—as flow increases, salinity decreases. When using the model for comparing releases under two different flow regimes, for example, reasonable levels of salinity need to be selected.

The stronger negative effects for site-independent covariates are from increasing the tide variable and increasing the release temperature. The detrimental effect of high release temperatures on survival through the delta has been documented elsewhere (Baker et al. 1995) and is consistent with the results of Kjelson et al. (1989).

With regard to site-dependent covariates, the relatively adverse effect of being released from Feather River Hatchery is no surprise, because this hatchery is significantly further upstream than any of the other sites. The adverse effect of being released in the Mokelumne-Georgianna area was consistent with a priori beliefs about fish being disoriented by being placed within the central delta as opposed to the mainstem, and thus being more vulnerable to pump mortality. This effect is complicated, however, by the apparently positive effect of the gate being open (*Delta.Gate*). This has been explained by some biologists as being due to the increased flow of mainstem water into the central delta, which reduces the disorientation of these releases, because most of the water will usually make its way back to the mainstem. The export to inflow effects were negative, but slight, for both upstream and delta releases.

4.3 Diagnostics

Following the recommendations of McCullagh and Nelder (1992) on model checking for generalized linear models, we checked for outliers, influential points, and collinearity, making necessary modifications for the ridge parameter and the two dispersion parameters. To detect influential points, a modification of Cook's distance measure (McCullagh and Nelder 1992, p. 407) was used,

$$D_i = (\hat{\beta}_{(-i)} - \hat{\beta})'(X'WX + \Lambda)(\hat{\beta}_{(-i)} - \hat{\beta})/m,$$

where $\hat{\beta}_{(-i)}$ is the column vector of coefficients with the ith observation removed and m is the number of parameters. One observation was significantly influential at the .05 level, a 1986 release from Ryde with an exceptionally large number of ocean recoveries, which primarily affected $I_{Ocean,1986}$.

Multicollinearity was moderate; the condition number without the intercept was 19. The largest correlations were between log(flow) and salinity, $r = -.71$, and between release temperature and shock, $r = .83$.

The fitted values are plotted against the observed values in of Figure 3(a). Figures 3(b) and 3(c) show the results separately for river and ocean recoveries. The increased variability of ocean recoveries is apparent from the residuals shown in Figure 3(d); the first 101 observations on the x-axis are the river recoveries, and the last 101 are the ocean recoveries. Standardized residuals were plotted against $2\sqrt{\hat{\mu}}$, the constant information scale; no pattern was present. Studentized residuals were plotted against the covariates; no problems were evident. However, plots of studentized residuals for the river recoveries against year of release showed that some unaccounted for year effects were present. This could mean that some omitted covariates, which varied between years, affected survival and/or gear effectiveness.

4.4 Comparing Releases With Lowest and Highest Fitted Recovery Rates

Given potential instability in estimates of individual coefficients, it is useful to compare the lowest and highest fitted rates at Chipps Island in terms of the corresponding covariate values to see whether, for example, values at opposite extremes of a covariate matched with extremes in recovery rates (Fig. 4). Fitted recovery rates were defined as fitted recoveries divided by release number and f_r. To focus attention on factors other than site effects, the release site effects were partially removed by dividing fitted recovery rates by $\exp(\hat{\beta}_9 I_{FRH} + \cdots + \hat{\beta}_{14} I_{Mk\text{-}Georg})$, and the highest 10 and lowest 10 by this measure were compared. Turbidity values were either mainstem or central delta values, depending on

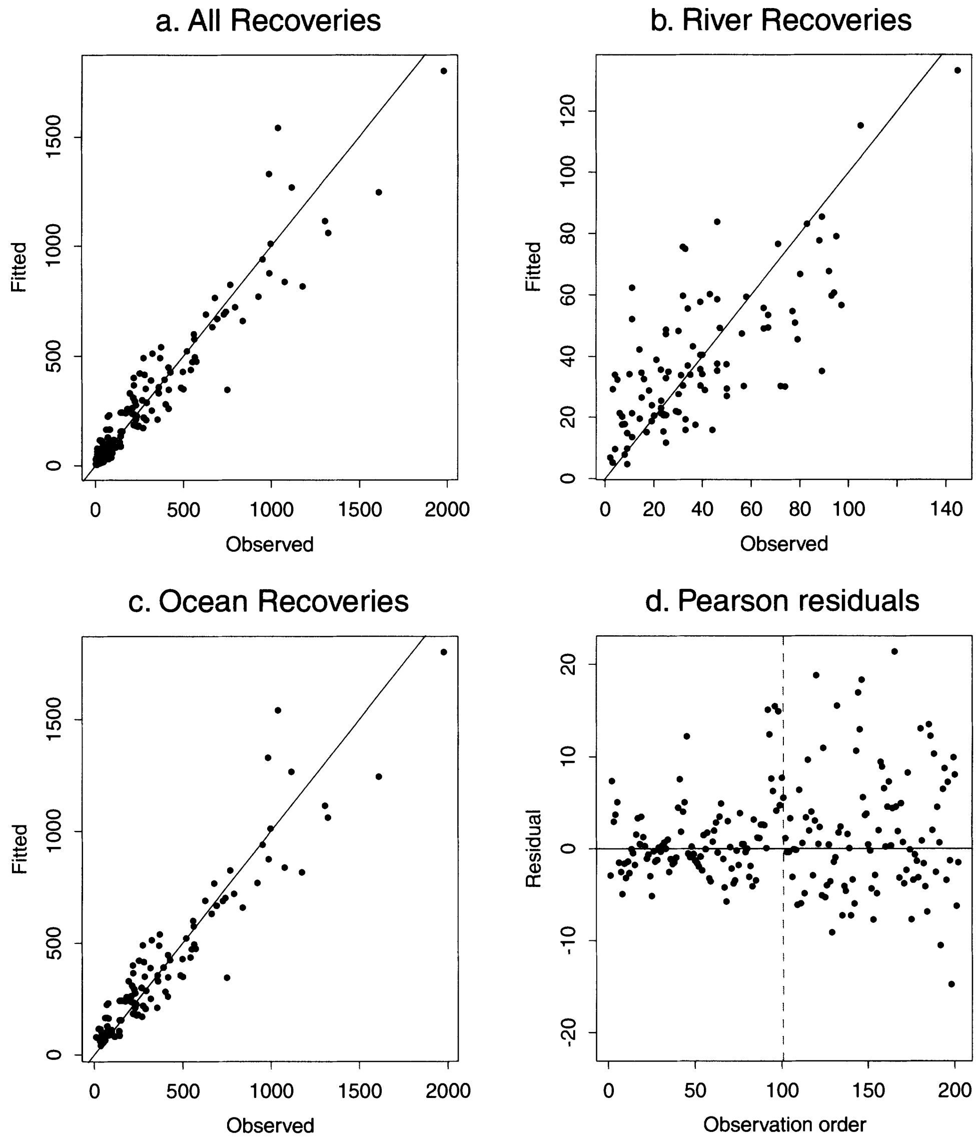

Figure 3. Fitted Versus Observed Recoveries for the Combined Recovery Sets and Separate Recovery Sets (A–C) and Pearson Residuals Plotted Against Fitted Values (d). In (d), the first 101 observations refer to the river recoveries, and the second 101 observations refer to the ocean recoveries.

the release location. The most noteable separations were for *Release.Temp*, *Hatchery.Temp*, and *Shock* (all somewhat correlated). Salinity and flow effects were clearly confounded; for example, the highest fitted recovery rate was with a very low flow but very high salinity, whereas the sixth highest rate was with a very high flow but very low salinity.

4.5 Evaluating Release Strategies

We demonstrate how the model is used to evaluate the effect of different release strategies on survival through a simple example. Only two covariates differ between the strategies, gate position and export-to-inflow ratio; thus the rest are irrelevant to the calculation of the ratio.

- Strategy I: The gate is open, and export/inflow is .4
- Strategy II: The gate is closed, and export/inflow is .2

The only relevant coefficients are those for *Upper.Exp.In* and *Upper.Gate*, where the covariate for *Upper.Gate* when the gate is closed is 0. The calculations can be facilitated by simply using the difference in covariate values as new covariates. In particular, because the interest is in river survival for a given year, release year indicator variables can be ignored.

Using (12) with unstandardized variables and corresponding coefficients, the relative survival of the first strategy to the second strategy is

$$\widehat{\mathrm{E}}\left[\frac{S_I}{S_{II}}\right] = \exp((-.555 \times (.4 - .2)) + (-.287 \times (1 - 0)) = .67.$$

The estimated standard error in this case is .068 [using (13)], and the estimated prediction error is .822.

Comparisons such as this must be tempered with caution, however. Our model summarizes historical relationships and is relevant to prediction in such a passively observed system. But because a number of unmeasured variables may well be important, it is much less well suited to predicting what would happen if the system were directly manipulated (Box 1966).

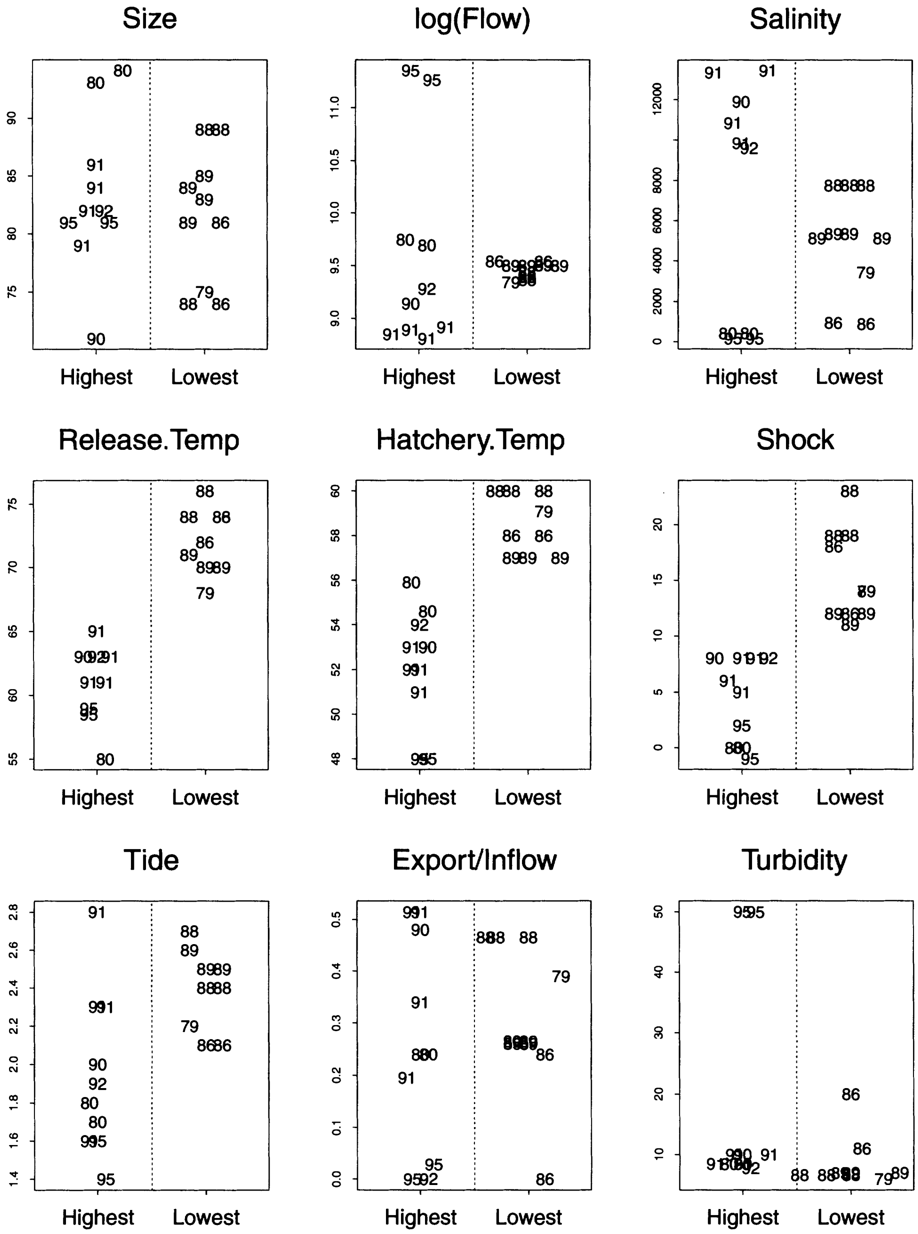

Figure 4. Covariate Values for the Releases With the 10 Highest and 10 Lowest Fitted Recovery Rates After Adjustment for Location of Release. (The plotting symbols denote the year of release.)

Thus it would be a mistake to take literally the numerical predictions of the model in the latter case; a more modest and realistic hope is that they point to beneficial management strategies.

Finally, a problem in practical application is not extrapolating beyond the data used to fit the model. With this many covariates, this is not a trivial matter. Besides not inputting values outside the joint range of the covariates, one must avoid selecting combinations that have not occurred or cannot occur; for example, high flows and high salinities cannot both occur.

5. DISCUSSION

Our approach to modeling recoveries is arguably an improvement over that taken by Kjelson et al. (1989). Our response variables are river recoveries and estimated ocean recoveries, rather than a complicated scaled index. The assumption of "going with the flow" is not made, and additional covariates are considered. One question, however, is whether including the ocean recoveries is beneficial. Other issues discussed here are the effect of using two dispersion parameters, the merit (if any) of using a ridge parameter, comparisons with alternative modeling approaches, and science and policy findings.

5.1 Influence of Ocean Recoveries

The model was refit using river recoveries alone, excluding I_{River} and the $I_{Ocean,year}$ indicators. The coefficients were quite similar to those based on river and ocean recoveries ($r = .90$), but the coefficients based on river recoveries alone were slightly larger in absolute magnitude (median change, .04). The increase in magnitude may be a reflection of departures from (4) as well as inaccuracies in the coarse ocean expansion factor, e_o. Including the ocean recoveries led to a decrease in the standard errors from 4% to 45%, with a median decrease of 17%—evidence that the relatively large-scale data provided by ocean recoveries provided information over that of the relatively small-scale data provided by river recoveries alone.

5.2 Use of Two Dispersion Parameters

The effect of fitting a single dispersion parameter was a very slight change in the coefficients and a decrease in the standard errors for most of the coefficients, salinity and flow being exceptions. The estimated dispersion parameter was 25.67, midway between $\hat{c}_r$ and $\hat{c}_o$. The need for two dispersion parameters is apparent from Figure 3(d), however.

5.3 Ridge Versus Sequential Model Selection

Table 1 includes estimates of the β's and standard errors when a ridge parameter was not included. As expected, in most cases the ridge parameter tended to shrink $\hat{\beta}$ toward 0; for example, the coefficient for release temperature went from $-.456$ to $-.375$. One exception was the effect of the gate being open for upstream releases, *Upper.Gate*, for which the coefficient went from $-.116$ to $-.130$.

One reason for including a ridge parameter was to provide more stable (i.e., more precise) estimates of the coefficients. Inclusion of the ridge parameter decreased the standard errors, with a median relative decrease in standard error of 30%.

An alternative to a relatively large "full" model with a ridge parameter is to use sequential model selection procedures. The desired result would be a potentially simpler model with more precise estimates of the coefficients kept in the model. A problem with many model selection procedures, however, is that unstable coefficients can lead to instability in the choice of the final model. As Breiman (1996) demonstrated, in terms of prediction errors subset selection is superior to ridge when there are relatively few strong effects, whereas ridge does better when there are many relatively weak effects. The magnitude of the estimated coefficients (see Table 1) suggests many weak effects in the present case.

For the sake of comparison with the ridge model, both backward elimination and forward selection were applied. The criterion for elimination or inclusion was a variation of the Bayes information criterion (BIC) (Schwarz 1978), a "quasi-BIC" (QBIC) criterion (see Burnham and Anderson 1998 for a similar modification of the Akaike information criterion) defined as $\text{QBIC} = -\text{EQL} + m\log(n)/2$, where EQL is the extended quasi-likelihood value, m is the number of parameters, and n is the sample size. Model selection was restricted to models that included at least the river recovery indicator and the release year indicators for ocean recoveries. The river and ocean dispersion parameters were fixed at the values for the full model for both backward elimination and forward selection. The results were that the full model [eq. (11)] was the final model using both backward elimination (no covariates were dropped) and forward selection (all covariates were added).

5.4 Bayesian Analysis and Model Averaging

An alternative to including a ridge parameter for the purpose of reducing instability is model averaging (Raftery 1996; Burnham and Anderson 1998). In addition to providing predictions based on weighted average predictions from multiple models, a Bayesian analysis yields both posterior probabilities for various models and posterior probability distributions for the coefficients. If the posterior probabilities for the models are concentrated on a few simple models, then the Bayesian approach could prove simpler to interpret than the ridge procedure.

A Bayesian approach was applied to a group of 576 models, in which the most complex model was the full model, (11) and the simplest model included only the river recovery and ocean year indicators (Newman and Remington 2000). The dataset was nearly the same as that analyzed here; differences were that the recovery information was less complete and two other covariates, an annual pesticide measure and a trend term, were included. The prior distributions for covariates were those given by Raftery (1996) for generalized linear models. The S-PLUS program glib() (publicly available from Statlib), developed by Raftery and colleagues to estimate posterior model probabilities and coefficient distributions, was modified to include offsets and the two dispersion parameters, c_r and c_o. Three sets of priors for the models were examined: uniform priors (1/576), priors weighted proportional to the number of covariates (favoring complex models), and priors weighted inversely proportional to the number of covariates (favoring simpler models). Priors for the coefficients were normal mean 0 with three different standard deviations, 1.0, 1.65, and 5.0.

The release numbers were sufficient to dwarf the impact of model priors, but the standard deviations for the coefficients' priors did have an impact. A standard deviation of 5.0 led to simpler models with larger posterior probabilities than did standard deviations of 1.0 and 1.65. The conclusions were generally similar to those based on the ridge model, however. Release temperature and site indicators were present in the models with highest posterior probability. Cross-channel gate position and salinity were the next most important covariates, whereas export-to-inflow ratios and turbidity were not in any of the higher-probability models.

Bayesian model-averaged (BMA) point estimates of predicted survival ratios were nearly identical to those for the ridge model when the prior standard deviations were 1.0 or 1.65. When the prior standard deviation was 5.0, the BMA estimates were similar as long as the predictor covariate set was restricted to those found in the simpler models. But the standard errors for the BMA estimates were often around 50% larger than those based on the ridge procedure, consistent with the fact that model uncertainty is explicitly included in the Bayesian procedure. However, the Bayesian procedure did not lead to simpler models or interpretation, because many of the covariates were included in at least one of the models with the larger posterior probabilities.

5.5 Paired Release Analysis

The paired release experiments (Newman 2000) fit within the classic framework of Darroch (1959) and others and allow separate estimation of S and p, assuming that π is constant for the upstream and downstream pair. Here we examine the similarities and dissimilarities of the results of the analyses of the paired and unpaired release data. Comparisons must be tempered by the fact that the paired release analysis had a narrower scope of inference, fewer initial covariates (excluding, e.g., several of the release site indicators), and different link functions.

Sixty-one upstream releases were paired with 19 releases made downstream of the midwater trawl; that is, the same downstream release was often paired with two or more upstream releases. Most of the 61 upstream releases were among the 101 used for the unpaired ridge analysis, but the upstream releases were all mainstem releases from just 3 release sites, Sacramento, Courtland, or Ryde. An EQL version of a Brownie et al. (1985) band-recovery–type model was fit using three separate logistic link functions for S, p, and π (see Lebreton, Burnham, Clobert, and Anderson 1992 for examples of the use of separate link functions) and two dispersion parameters. The results discussed here are for the case in which separate p's were assumed for each upstream release. The QBIC value was used with backward elimination to select a single model.

The paired results were largely consistent with the unpaired results, although the estimated precision of the coefficients was higher for the paired analysis, which is sensible given the pairing and the more homogenous set of upstream releases. The most important consistencies were the highly significant and negative effect of increasing release temperature, the positive effect of flow, and the slightly negative (but insignificant) effect of the export-to-inflow ratio. The most important inconsistency was that gate position was not significant, according to the paired release analysis.

5.6 Science and Policy Findings and Implications

Management of the river during juvenile salmon outmigration is largely a matter of releasing water from upstream dams, opening or closing the cross-channel gate, and exporting water for human, agricultural, and industrial use. Increasing water releases from dams increases flow, of course, and over the range of observed flow values, the results of the analyses suggest that such increases improve survival probability. The magnitude of the effect is slight based on the unpaired release data, but more sizeable based on the paired release data. Releasing water will also sometimes lower water temperature, which is clearly beneficial to survival. Keeping the cross-channel gate closed during outmigration appears to help releases made upstream of the gate (although the paired release analysis with the more restricted dataset does not suggest this). Undoubtedly at some level, increasing the export-to-inflow ratio lowers survival probabilities, but over the range observed (0–50%) the estimated effect, though negative, was not significant. After working with the biologist and analyzing the existing data several different ways, we have recommended experimentation involving explicit manipulation of the river system (i.e., gate position, and export levels) over reasonable but extreme values of covariate space at fewer locations to gain more precise estimates of the effects of these factors.

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