

# Estimating spatial–temporal differences in Chinook salmon outmigration survival with habitat- and predation-related covariates

Mark J. Henderson, Ilysa S. Iglesias, Cyril J. Michel, Arnold J. Ammann, and David D. Huff

**Abstract:** Low survival rates of Chinook salmon (*Oncorhynchus tshawytscha*) smolts in California's Central Valley have been attributed to multiple biological and physical factors, but it is not clear which factors have the largest impact. We used 5 years of acoustic telemetry data for 1709 late-fall Chinook salmon smolts to evaluate the effect of habitat- and predation-related covariates on outmigration survival through the Sacramento River. Using a Cormack–Jolly–Seber mark–recapture model, we estimated survival rates both as a function of covariates (covariate model) and as a function of river location and release year (spatial–temporal model). Our covariate model was overwhelmingly supported as the preferred model based on model selection criteria, suggesting the covariates adequately replicated spatial and temporal patterns in smolt survival. The covariates in the selected model included individual fish covariates, habitat-specific covariates, and temporally variable physical conditions. The most important covariate affecting salmon survival was flow. We describe the importance of these parameters in the context of juvenile salmon predation risk and suggest that additional research on predator distribution and density could improve model estimates.

**Résumé :** Si les faibles taux de survie des saumoneaux de saumon chinook (*Oncorhynchus tshawytscha*) dans la vallée centrale de la Californie ont été attribués à différents facteurs biologiques et physiologiques, l'identité des facteurs exerçant la plus grande influence demeure incertaine. Nous avons utilisé 5 années de données de télémétrie acoustique pour 1709 saumoneaux de saumon chinook de la fin de l'automne pour évaluer l'effet de covariables associées à l'habitat et à la prédation sur la survie durant la dévalaison dans le fleuve Sacramento. En utilisant un modèle de marquage–recapture de Cormack–Jolly–Seber, nous avons estimé les taux de survie en fonction de covariables (modèle des covariables) et en fonction de l'emplacement dans le fleuve et de l'année du lâcher (modèle spatiotemporel). Le modèle de covariables s'est avéré, de loin, le modèle à privilégier sur la base de critères de sélection de modèles, ce qui donne à penser que les covariables reproduisent adéquatement les motifs spatiaux et temporels de survie des saumoneaux. Les covariables dans le modèle sélectionné comprennent des covariables associées aux poissons individuels, des covariables propres à l'habitat et des conditions physiques variables dans le temps. La covariable ayant la plus importante influence sur la survie des saumons est le débit. Nous décrivons l'importance de ces paramètres dans le contexte du risque de prédation de saumons juvéniles et suggérons que d'autres travaux sur la répartition et la densité des prédateurs pourraient améliorer les estimations découlant du modèle. [Traduit par la Rédaction]

## Introduction

Salmon smoltification and outmigration from freshwater rearing habitats is a time of increased mortality as fish undergo physiological changes and encounter new stressors (Connor et al. 2003; Welch et al. 2008; Nislow and Armstrong 2012). Much of the research on outmigration mortality has examined the effect of dam passage on survival (Skalski et al. 2001; Williams et al. 2001; Welch et al. 2008; Elder et al. 2016), with relatively few studies focusing on how other environmental conditions affect survival. Environmental conditions that have been linked to outmigration mortality include flow (Connor et al. 2003; Smith et al. 2003; Michel et al. 2015; Courter et al. 2016), temperature (Connor et al. 2003; Smith et al. 2003), turbidity (Gregory and Levings 1998; Smith et al. 2003), and predation (Beamesderfer et al. 1996; Friesen and Ward 1999;

Schreck et al. 2006). Some of these factors, such as water temperature and flow, are expected to increasingly affect juvenile salmon survival and population production as the climate changes (Jonsson and Jonsson 2009; Mantua et al. 2010; Katz et al. 2013; Russell et al. 2012). Many of the published correlations between outmigration survival and environmental characteristics have examined survival over relatively large temporal and spatial scales, whereas individual fish experience mortality at a particular time and place. To understand better how habitat- and predation-related covariates influence salmon smolt mortality, it is necessary to look at the conditions experienced by fish as they are migrating through a habitat.

Most Chinook salmon (*Oncorhynchus tshawytscha*) spawned in the Sacramento River have long outmigrations (~500 km) through multiple habitats, and it is believed that the precipitous decline of

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multiple salmon populations in this system is partially due to anthropogenic habitat modifications and poor outmigration survival (Yoshiyama et al. 1998; Katz et al. 2013; Michel 2019). Currently, survival of Chinook salmon smolts from the Sacramento River to the ocean is markedly lower than smolt outmigration survival from the Columbia and Fraser rivers in the Pacific Northwest region of the United States and Canada (Welch et al. 2008; Michel et al. 2015; Buchanan et al. 2018), but it is unclear what factors cause this increased mortality. Previous research has found that interannual variability in smolt survival is much greater in the Sacramento River than in the Sacramento–San Joaquin delta or the San Francisco Bay, suggesting that the river has a large influence on outmigration success (Michel et al. 2015). Within the river, outmigration survival rates vary both spatially and interannually (Singer et al. 2013; Michel et al. 2013). This spatial and temporal variability is likely driven by changes in the underlying environmental and habitat features comprising the river landscape.

Identifying the main factors that affect smolt mortality is important to establish restoration priorities and give managers quantitative data on how to optimize survival of threatened salmonids. This is especially important given recent findings that suggest outmigration survival has a larger effect on smolt-to-adult ratios than marine survival does (Michel 2019). To identify which factors had the largest influence on outmigration survival, we developed a series of mark–recapture models using 5 years of acoustic telemetry data for late-fall Chinook salmon. We then used model selection to identify which covariates had the largest influence on survival. Our analysis builds upon the research conducted by Singer et al. (2013) and Michel et al. (2015), whose primary objective was to identify temporal and spatial differences in the mortality of outmigrating juveniles. In contrast, our objective was to model survival solely as a function of covariates that were hypothesized to affect salmon survival through habitat modification and increased predation risk.

## Methods

### Study area

The northernmost extent of our study was the release location for late-fall run smolts at the Coleman National Fish Hatchery (Fig. 1). We included all detections of acoustically tagged fish from the release location to the ocean, but we only included covariates for reaches between the release location and the I-80 bridge in Sacramento. This was for two reasons: (i) hydrodynamic model estimates for temperature and flow below the city of Sacramento were not as reliable as the upstream estimates, and (ii) survival variability was much larger in the reaches upstream of Sacramento than in the Sacramento–San Joaquin delta or San Francisco Bay (Michel et al. 2015). Riverine habitat varied spatially across the ~300 km of Sacramento River that defined our study area. There was a general upriver to downriver gradient in habitat features associated with human influence. For example, diversion density, amount of armored bank, and agriculture and developed land use increased from the upper to lower reaches.

### Acoustic tagging

Late-fall run Chinook salmon were obtained from the United States Fish and Wildlife Service (USFWS) Coleman National Fish Hatchery, implanted with acoustic tags, and released annually during the winter months (December and January) from 2007 through 2011. Details regarding the surgical procedures and initial acoustic tag study design are documented in Michel et al. (2013) and Ammann et al. (2013). Briefly, small acoustic tags (Vemco 69 kHz, 7 mm diameter × 20.5 mm long, weighing 1.8 g in air and 1.0 g in water) were surgically implanted into the peritoneal cavity of anesthetized fish through a 12 mm incision. The incision was then closed with two simple interrupted stitches with nonabsorbable nylon cable-type suture. All fish were allowed to recover for a

minimum of 24 h before release. During the first year of this study (2007), smolts were tagged and released directly into Battle Creek, a tributary of the Sacramento River where the Coleman Hatchery is located (Fig. 1). From 2008 to 2010, tagged smolts were released concurrently from three locations along the mainstem Sacramento River: Jelly's Ferry, Irvine Finch, and Butte City to increase sample size of fish detected throughout the river and to estimate differences in survival between newly released fish and those released upstream (Fig. 1). In 2011, all fish were released at Jelly's Ferry due to a slightly reduced sample size. In addition to the acoustic tag data ( $n = 1350$ ) utilized in Michel et al. (2013) and Michel et al. (2015), we used acoustic tag data provided by the USFWS ( $n = 359$ ). These fish were tagged in accordance with the procedures described above, but released directly into Battle Creek in 2010 and 2011, simultaneous to the release of the remaining hatchery stock (batch released). The mean hatchery release during these dates was approximately 600 000 fish (range: 155 000–889 000).

Acoustic receivers were located from the fish release sites in the upper Sacramento River to the Golden Gate Bridge at the entrance to the Pacific Ocean. We divided the Sacramento mainstem study region into 19 reaches demarcated by 20 acoustic receiver locations along the mainstem Sacramento River (Fig. 1). These reach locations were selected based on interannual consistency in receiver location throughout the 5-year study period; however, detections from inconsistently deployed receivers were retained to improve precision of survival and detection probabilities (see section on Mark–recapture analysis).

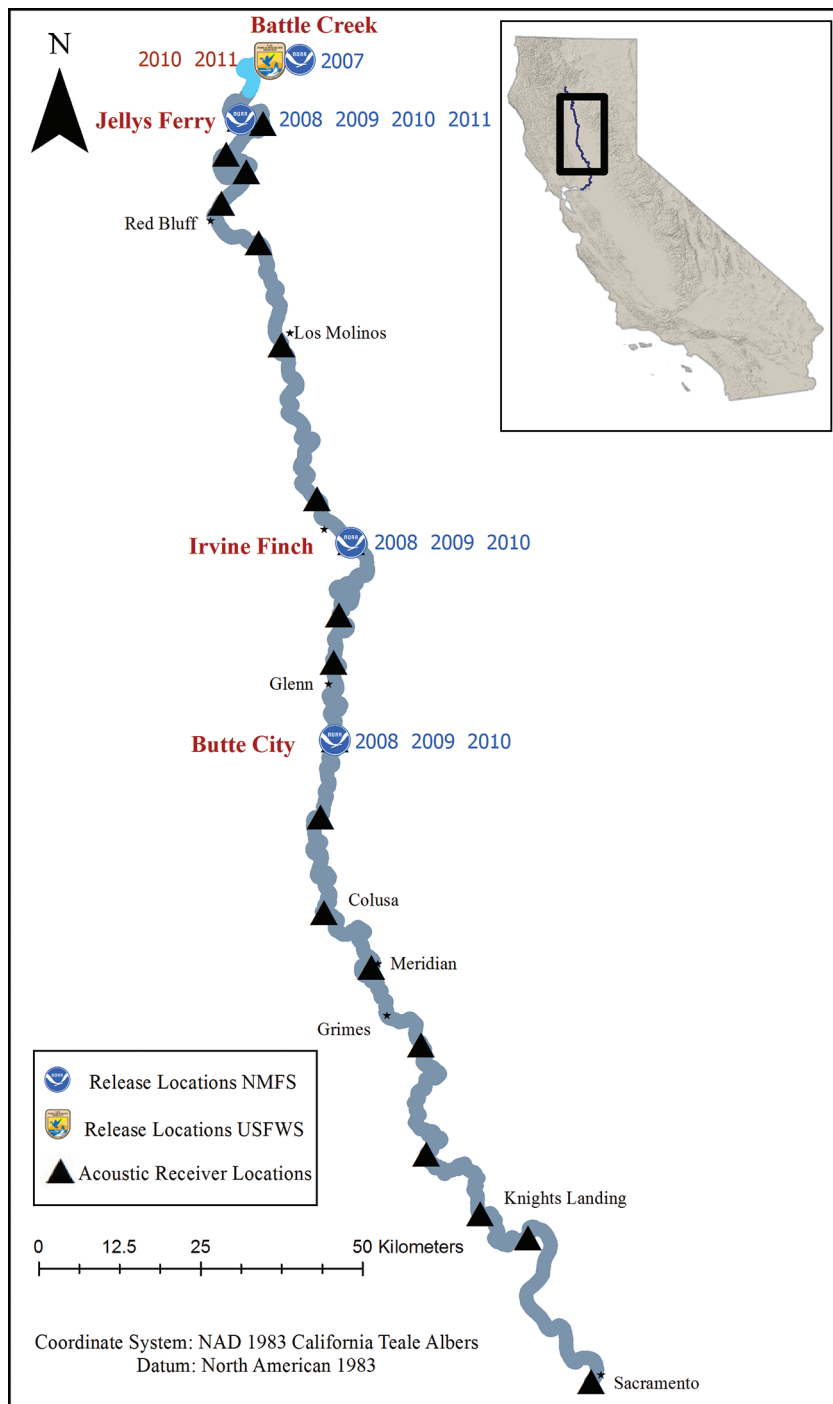
### Acoustic telemetry data processing

We used a series of algorithms to ensure our acoustic telemetry data did not include any false detections. The acoustic receivers automatically processed detection data by dropping incomplete codes from the detection file. To ensure that we removed any false detections due to acoustic pulse train collisions, we performed several additional quality control procedures. First, we removed all detections that occurred prior to the release date and time. We then removed all detections from fish that had only a single detection throughout the study. We required three or more detections within 10 days at a single receiver location to verify those detections were not the result of pulse train collisions. We also examined the encounter history of each individual fish and removed any detections that indicated upstream movements. Furthermore, we calculated the transit time between receivers (number of river kilometres between receivers divided by the difference in seconds between the last upstream detection and first downstream detection) and removed any detections resulting from a fish traveling at speeds greater than  $10 \text{ km} \cdot \text{h}^{-1}$  ( $2.78 \text{ m} \cdot \text{s}^{-1}$ ). We also assumed that any tag consistently detected at a single receiver location for more than 4 weeks, and not subsequently detected downstream, was a mortality. We selected the 4 weeks cutoff after a preliminary examination of the data indicated fish detected at a single location for more than 4 weeks were never detected at another receiver. These fish ( $n = 58$ ) were considered known mortalities (i.e., treated the same way as a harvested fish in a standard mark–recapture model) and did not have any impact on the estimated survival or detection probabilities downstream from where the presumed mortality occurred.

### Mark–recapture analysis

To estimate survival of outmigrating late-fall run Chinook salmon, we fit a Cormack–Jolly–Seber (CJS) survival model (Cormack 1964; Jolly 1965; Seber 1965) using the marked (Laake et al. 2013) and RMark package (Laake and Rexstad 2008; Collier and Laake 2013) within the R programming language (version 3.3.1; R Core Team 2017). We used the marked package for the initial model selection due to its computational efficiency and RMark for

**Fig. 1.** Map of the mainstem Sacramento River. Our study area extended from above Red Bluff in the north to the city of Sacramento in the south. Late-fall run Chinook salmon yearling smolts were released at Battle Creek, Jelly’s Ferry, Irvine Finch, or Butte City during the winter (December–January) of each of our study years. The locations of the 20 acoustic receivers that delineated our 19 river reaches are shown as triangles. [Colour online.]



parameter estimation due to better analytical functionality (see Appendix A). The CJS model was originally conceived to calculate survival of tagged animals over time by recapturing individuals and estimating survival and recapture probabilities using maximum likelihood. A spatial form of the CJS model can be used for species that migrate unidirectionally, and are recaptured, throughout a migratory corridor (Burnham 1987). Using this space for time substitution, we used individual fish encounter histories to estimate

the likelihood that a fish would survive and be detected at each receiver (Lebreton et al. 1992). In the standard formulation of the CJS model, detection probabilities are estimated for a single resampling occasion ( $i$ ) in time or space. However, our encounter histories included detections both from receivers at the reach boundaries as well as from receivers within the reach. Thus, our estimated detection parameter represents the probability of detection from receiver ( $i$ ) to receiver ( $i + 1$ ).

**Table 1.** A description of the covariates included in the mark–recapture model.

Category	Covariate	Range	Definition	Hypothesized relationship with survival
Individual	Fish length <sup>a</sup>	135–204 mm	Fork length	Larger fish may exceed gape width of predators
	Fish condition <sup>a</sup>	0.59–1.32	Fulton's <i>k</i>	Increased condition improves predator escape capability
	Transit speed <sup>b</sup>	0.02–8.25 km·h <sup>-1</sup>	Reach-specific transit speed	Faster fish have less exposure to predators
Release group	Batch release <sup>b</sup>	Binary	Tagged fish released concurrently with large hatchery releases	Predator swamping
	Release reach <sup>a</sup>	Binary	Difference in survival between newly released fish and those released upstream	Newly released hatchery fish are naïve and susceptible to predation
	Annual flow <sup>c</sup>	179–499 cm·s <sup>-1</sup>	Mean flow measured at Bend Bridge throughout outmigration (December–March)	Increased flows produce more habitat and predator refugia throughout the river
Reach-specific	Sinuosity <sup>d</sup>	1.04–2.74	River distance divided by Euclidean distance	More natural habitats have more predator refugia
	Diversion density <sup>e</sup>	0–1.05 number·km <sup>-1</sup>	No. of diversions per reach length	Increased predator densities near diversions
	Adjacent cover density <sup>f</sup>	0.2%–0.76%	Percentage of nonarmored river bank with adjacent natural woody vegetation	Increased cover produces more predator refugia
	Off-channel habitat density <sup>f</sup>	0%–1.62%	Off-channel habitat within 50 m of river expressed as percentage of river area	Increased off-channel habitat produces more predator refugia
Time-varying	Temperature <sup>g</sup>	6.2–12.9 °C	Mean water temperature per reach	Increased temperatures results in increased predation due to higher metabolic demands of predators
	Interannual reach flow <sup>g</sup>	215–447 cm·s <sup>-1</sup>	Mean water flow per reach	Higher flows within a reach will produce more habitat and predator refugia within that reach
	Intra-annual reach flow <sup>g</sup>	129–902 cm·s <sup>-1</sup>	Mean water flow per reach and year	Higher intra-annual flows (e.g., precipitation or dam releases) decrease predation due to increased turbidity and increased predator refugia

<sup>a</sup>Measured during tagging and release.

<sup>b</sup>Observed travel times and mixed effects model estimates.

<sup>c</sup>California Water Data Library.

<sup>d</sup>National Hydrography Dataset.

<sup>e</sup>Passage Assessment Database — verified by field survey.

<sup>f</sup>Department of Water Resources.

<sup>g</sup>River Assessment for Forecasting Temperature (RAFT) model.

### Spatial–temporal model

Prior to fitting a covariate model, we fit a model that estimated a different survival for every reach in every year. This spatial–temporal model provided a means to evaluate how well our covariate model replicated outmigration survival. We assumed that differences between the spatial–temporal model and the covariate model were the result of unaccounted variance due to missing covariates. Owing to the inherent complexity of the Sacramento River ecosystem, it was not feasible to measure or estimate all potential covariates that influence salmon survival. For example, there is no hydrodynamic model currently capable of estimating turbidity levels throughout the river.

The spatial–temporal smolt survival estimates were converted to survival per 10 km values to allow for comparisons between reaches via

$$\Phi_{10} = \sqrt[10]{\Phi_R}$$

where  $\Phi_{10}$  is the survival estimate per 10 km,  $\Phi_R$  is survival per reach, and  $l$  is reach length divided by ten.

### Covariate model

We included multiple individual, release group, reach-specific, and time-varying covariates in our analysis to identify the factors contributing to the mortality of outmigrating smolts. Each of the covariates included in the analysis had an a priori hypothesized relationship with smolt survival (Table 1).

The individual covariates we included were length, condition, and transit speed. Fish size has been known to influence juvenile salmon survival (Zabel and Achord 2004); thus, we included both length and condition factor (Fulton's  $k = (W/L^3) \cdot 100$ ) as individual covariates. Length was hypothesized to affect survival through predator gape limitation, whereas condition factor is an indicator of fish health and stamina. We also included individual fish transit speed within each reach, which we estimated with a mixed effects model (see details below), because faster fish would have less exposure to predators.

Release group effects included release group size, a release reach effect, and the mean annual flow at Bend Bridge (see Fig. 1 for location) in the release year. We included a binary group covariate for release group size to distinguish fish released in synchrony with thousands of other hatchery fish from those released in small (e.g., 50–100 fish) batches based on the hypothesis that

large releases would result in increased survival due to predator swamping (Fritts and Pearsons 2008; Furey et al. 2016). To test the hypothesis that the potential survival advantage of large releases would diminish as fish diffused downstream, we also included an interaction between release group size and distance from release site. We included a release reach effect to test whether survival in the first reach after release differed from fish released upstream of the release site. We hypothesized survival rate in the release reach would be lower because newly released hatchery fish are naïve and more susceptible to predation (Alvarez and Niecieza 2003; Huntingford 2004; Jackson and Brown 2011). The final release group-specific covariate was the mean annual flow measured at the Bend Bridge gauge during the months of smolt outmigration (December–March). This covariate was included to test whether survival decreased in low flow (e.g., drought) conditions. Bend Bridge was selected to represent mean annual flow because it was upstream of the major tributaries and diversions and was collinear with the flow measurements throughout the river.

The reach-specific covariates included in the model were sinuosity, diversion density, adjacent cover density, and off-channel habitat density. We selected these features because we hypothesized they would influence survival by affecting predation risk. More natural habitats with increased sinuosity, adjacent cover density, and off-channel habitat density are hypothesized to provide more predator refuge (reviewed by Roni et al. 2014). Furthermore, agricultural and municipal water diversions along the Sacramento River pose a risk to outmigrating salmon through direct entrainment (Hanson 2001; Kimmerer 2008; Mussen et al. 2014), as well as indirectly by providing structure for salmonid predators (Sabal et al. 2016). We hypothesize that the latter has more of an effect on Chinook smolt survival since the diversions are typically not in operation during the months of outmigration. These reach-specific data were derived from GIS layers available from multiple sources (Table 1) and plotted in a geographic information system (using ESRI ArcGIS 10.3). Because we were using static GIS layers, we were unable to determine whether the available off-channel habitats were connected to the main stem under different flow regimes. We were also unable to measure interannual differences in adjacent cover density.

The time-varying covariates we included in the model were flow and temperature, which we obtained from the river assessment for forecasting temperature (RAFT) model. The RAFT model is a one-dimensional physical model that estimates temperature and flow every 15 min at a 2 km spatial resolution (Pike et al. 2013). We included temperature as a covariate because predator metabolisms and predation rates increase at higher temperatures (Petersen and Kitchell 2001). We included multiple aspects of flow (see below) derived from the RAFT model because flow is important to smolt survival (Kjelson and Brandes 1989; Cavallo et al. 2013; Zeug et al. 2014; Michel et al. 2015; Courter et al. 2016). We associated values for each of these variables with each tagged fish in space and time at the 2 km spatial resolution and then calculated the reach-level means for each fish for each variable. We assumed that RAFT model predictions were accurate (i.e., we did not propagate RAFT model uncertainty into the mark–recapture model) based on results from model validations (Pike et al. 2013; Daniels et al. 2018).

Owing to the importance of flow to outmigrating salmon survival, we fit a variety of models with different flow standardizations to test which aspects of flow had the largest influence on survival. We scaled (subtracted the mean and divided by the standard deviation) the time-varying estimates of flow in two ways: (i) by reach and (ii) by year and reach. We scaled by reach to detect within-reach patterns of survival relative to **interannual** flow

conditions. In other words, is reach-specific survival dependent on whether flows are above or below average compared with other years? Since this parameter could distinguish between annual differences in flow (i.e., low-flow versus high-flow year), we did not include the annual flow at Bend Bridge in any models that included flow scaled only by reach. Thus, we could test whether the spatially explicit estimates of flow added any additional information beyond a single measure of mean annual flow. The year and reach scaling tested whether **intra-annual** changes in flow within a reach were important to salmon survival. In other words, we wanted to determine whether periods of higher flows within a reach, such as those after large precipitation events, would increase survival relative to periods of lower flows within the same year. This hypothesis was based on previous studies that have observed large increases in survival due to controlled changes in flow rate (Cavallo et al. 2013; Courter et al. 2016). Scaling by both year and reach removes the effect of annual differences in flow such that it is impossible to distinguish high-flow years from low-flow years with this parameter. Thus, models in which flow was scaled by year and reach could also include the mean annual flow at Bend Bridge. We also fit models that included an interaction between the mean annual flow and the time-varying flow standardized by year and reach to test the hypothesis that precipitation events would have a larger impact on survival in years with lower flows. We tested this hypothesis based on work by Courter et al. (2016) that suggested flow has a large impact on survival in reaches with relatively low flow but has a negligible impact in reaches with high flow.

To estimate the effect of a covariate (e.g., flow) on fish survival throughout a reach, it is necessary to have a covariate value for every fish in every reach. When we did not detect an individual fish at a receiver, there was uncertainty as to when that fish might be within that reach and, thus, what covariate value should be used. To impute covariate data in locations where fish were not detected, we fit a mixed-effects model where the response was transit speed of individual fish detected at both upstream and downstream acoustic receivers of a single reach. Our independent covariates were release year, release week, reach, and fish condition. We also included a random intercept for each individual fish to account for individual behavioral variability. We fit the model using the “lme4” package (Bates et al. 2015) and selected the model with the lowest Akaike’s information criterion (AIC; Burnham and Anderson 2002). To verify that the mixed-effects model did not unduly violate any assumptions, we examined model diagnostics (QQplot and residuals) using the DHARMA package (Hartig 2018). We then used the results from the mixed-effects model based on detected fish to estimate the dates and times undetected fish were present within each reach.

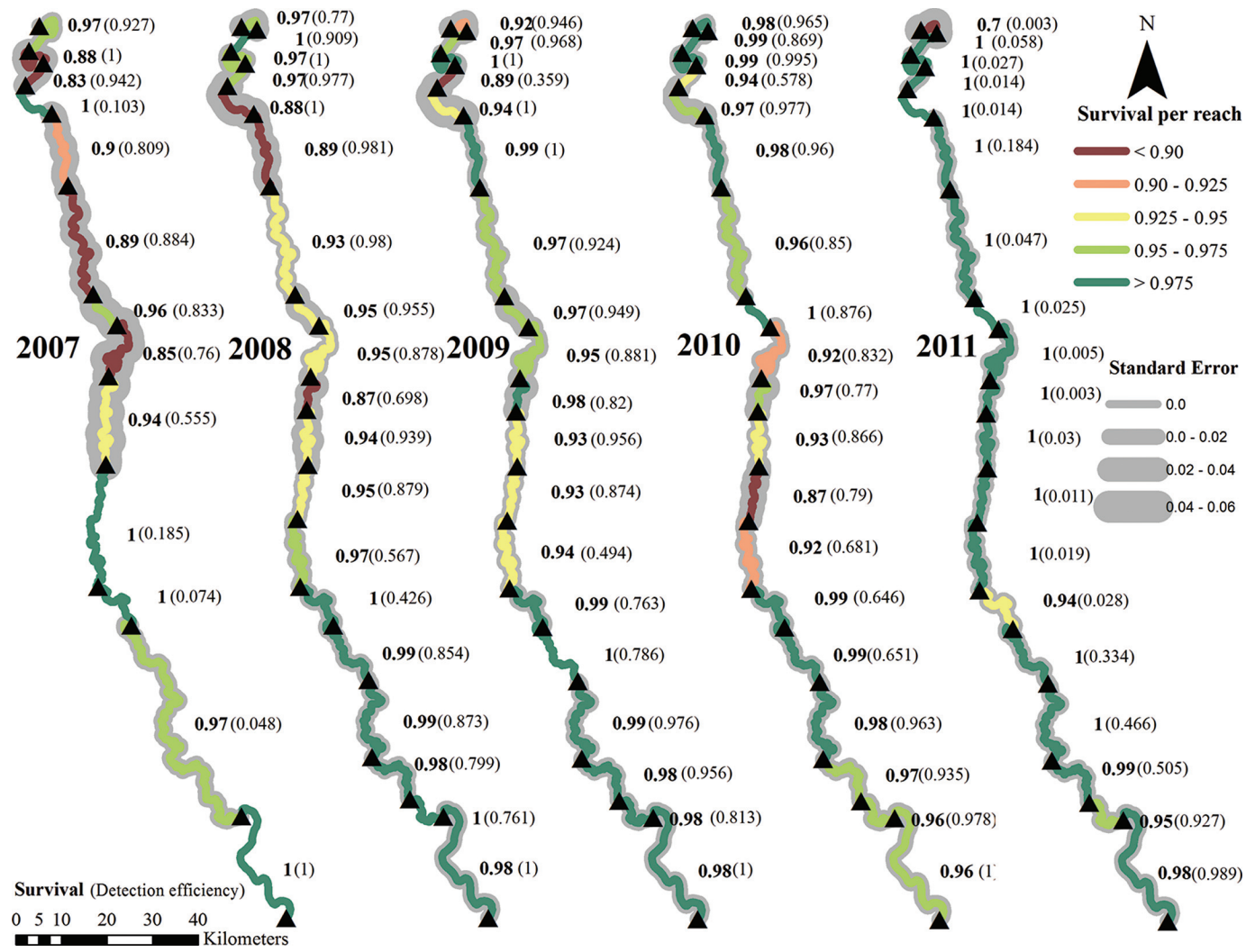
Prior to fitting the CJS models, all continuous covariates were standardized by subtracting the mean and dividing by the standard deviation. Standardized coefficients could then be interpreted as the estimated change in survival predicted from one standard deviation increase in the covariate value. We also conducted pairwise comparisons of all continuous individual, habitat, and physical covariates to determine whether any covariates were collinear (see online Supplementary material, Fig. S1<sup>1</sup>). From pairs that had correlation coefficients greater than 0.7 (Dormann et al. 2013), we selected a single covariate that we hypothesized would have the largest influence on survival based on results from previous studies.

### Model selection

We fit a series of CJS models to determine which covariates (individual, release group, reach-specific, or time-varying) had the greatest impact on outmigrating smolt survival. With the excep-

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2018-0212>.

**Fig. 2.** Map depicting reach-specific survival estimates (per 10 km) for 2008–2010. Colours represent per-reach survival risk, and standard error is represented as the grey buffer surrounding each reach. The values adjacent to each reach represent the survival estimate for a given reach (per 10 km) from our full survival model. [Colour online.]



tions of collinear variables and the restrictions noted above, we fit models with all possible combinations of covariates and selected the most appropriate models with adequate support using Quasi-Akaike’s information criterion (QAIC<sub>c</sub>) (Burnham and Anderson 2002). QAIC adjusts the AIC value based on an overdispersion parameter ( $\hat{c}$ ), which we estimated using the median  $\hat{c}$  method for the spatial temporal model within program MARK (White and Burnham 1999). If the observed data has no overdispersion,  $\hat{c}$  will be approximately equal to 1. Values of  $\hat{c}$  greater than 4 indicate the model structure is inadequate and does not account for a sufficient amount of variation in the data (Burnham and Anderson 2002). Our median  $\hat{c}$  was 1.45, indicating the model was satisfactory but slightly overdispersed. We selected the most appropriate model by examining the difference in QAIC values between each model and the model with the lowest QAIC ( $\Delta$ QAIC). We assumed models with  $\Delta$ QAIC < 2 had equal support (Burnham and Anderson 2002); thus, if multiple models had a  $\Delta$ QAIC < 2, we selected the one with the fewest parameters.

**Covariate plots**

To determine which covariates had the largest influence on survival, we plotted the  $\Delta$ QAIC between the selected covariate model and the same model without a single covariate. In the case of covariates that were included as main effects and in an inter-

action, we also removed the interaction. We will refer to these models as our covariate importance analysis.

We used marginal model plots to evaluate the effect of individual covariates on outmigrating smolt survival. To produce these plots, the  $\hat{\beta}$  parameter coefficients from the selected covariate model were used to simulate what survival would be for the 95% observed range of a single covariate. With the exception of reach length, covariates not included in the individual response plots were set to 0 for binomial covariates or to their mean for continuous covariates. Reach length was set to 10 km for all plots except the one that explicitly focused on the effect of reach length.

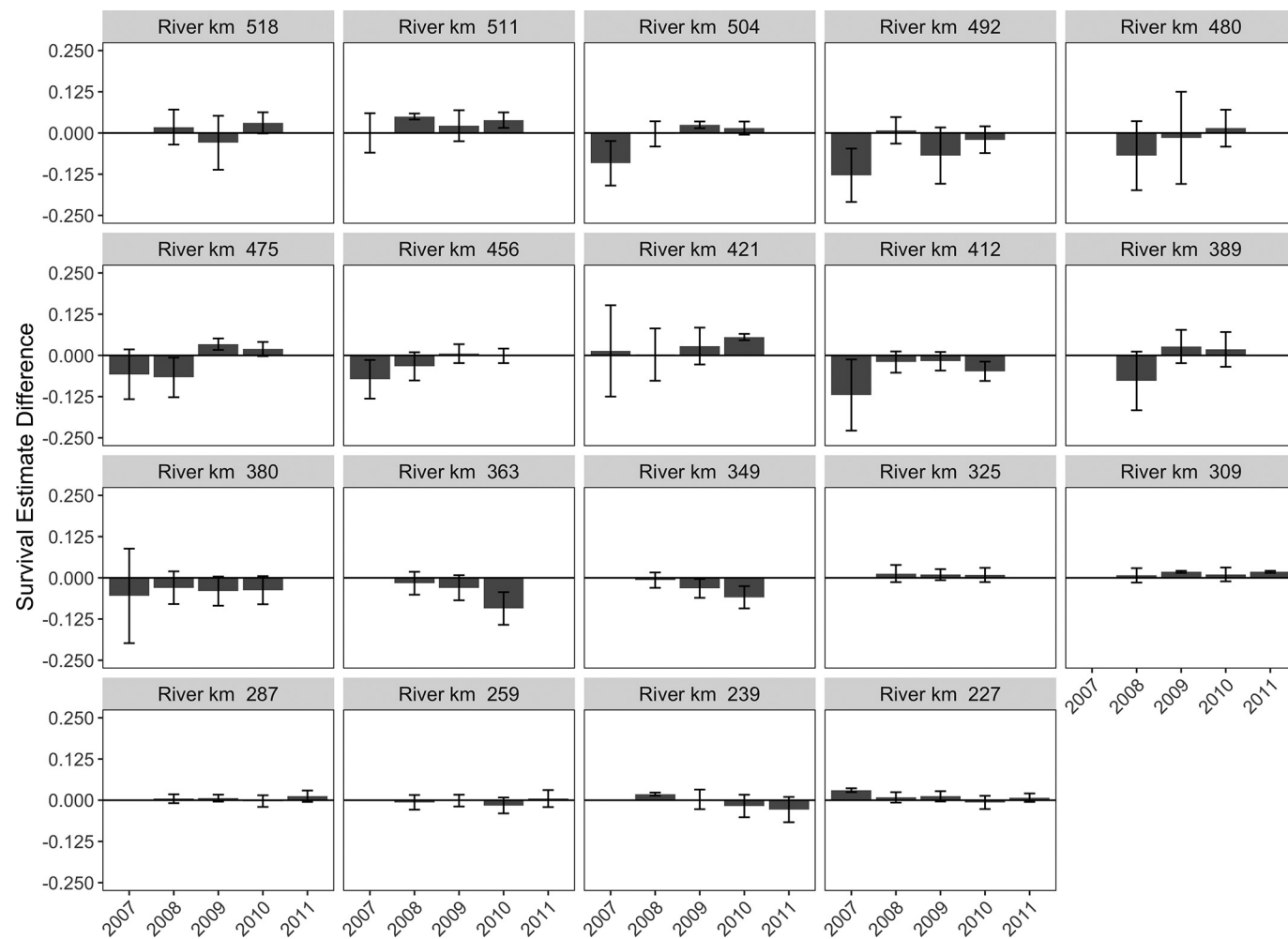
**Results**

**Spatial-temporal model**

Based on the model that included a reach by year interaction, we observed that survival was not consistent spatially or temporally. We saw a general trend of lower per-reach survival in the upper and middle reaches compared with the more downstream reaches, but the location and severity of mortality varied interannually (Fig. 2). The high flows in 2011 negatively impacted our detection efficiencies, rendering 12 receivers without reliable detection data; however, the detection efficiencies in the lower river and the estuary remained high and provided sufficient data to

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**Fig. 3.** Difference between survival estimates in the spatial–temporal model and the covariate model for each reach (labeled as the distance (River km) between the upstream boundary and the Golden Gate Bridge). Negative values represent occasions when the covariate model had a larger estimate of survival and was presumably missing covariates that increased smolt mortality. Error bars represent the 95% confidence interval estimated with the delta method.



estimate outmigration survival through the river. The receiver locations with low detection efficiencies often resulted in survival estimates of 1 due to numerical boundary issues.

#### Covariate model

The selected covariate model had 15 survival parameters and fit the data nearly as well as the spatial–temporal model that had 110 survival parameters. As a result, the covariate model had a much lower QAIC<sub>c</sub> value ( $\Delta\text{QAIC}_c = 55.90$ ), implying it was more parsimonious. Although the covariate model showed some deviation from the spatial–temporal model, especially in the most upstream reaches, these tended to be relatively small and not significantly different from zero (Fig. 3).

The top covariate model included a combination of an individual covariate (transit speed), group covariates (batch release, interaction between batch release and distance from release site, release reach, and the mean annual flow recorded at Bend Bridge), reach-specific covariates (reach length, sinuosity, and diversion density), and time-varying covariates that were estimated for when a fish passed through a specific reach (reach flow, interaction between reach flow and annual flow, and water temperature). Based on the standardized beta coefficients for the covariates (Table 2) and the results from the covariate importance analysis (Fig. 4), annual flow and reach length had the largest influence on survival. Flow was the most important covariate in predicting

outmigration success, with increased levels of annual flow correlating to increased smolt survival (Fig. 5a). Above average reach flows within a year (e.g., large precipitation events) helped improve survival much more in low-flow years than in high-flow years. As would be expected, longer reaches had lower survival rates (Fig. 5b). Based on the covariate importance analysis, the next most important variables affecting survival were diversion density, release reach, and the interaction between release group size and distance from release location. Survival increased relative to diversion density (Fig. 5c), was lower in the first reach after release (Fig. 5d), and increased for approximately the first 200 km from the release site when fish were released concurrently with thousands of hatchery fish (Fig. 5e). Finally, the covariates that had the least effect on survival were sinuosity (increase), transit speed (increase), and water temperature (decrease) (Figs. 5f–5h).

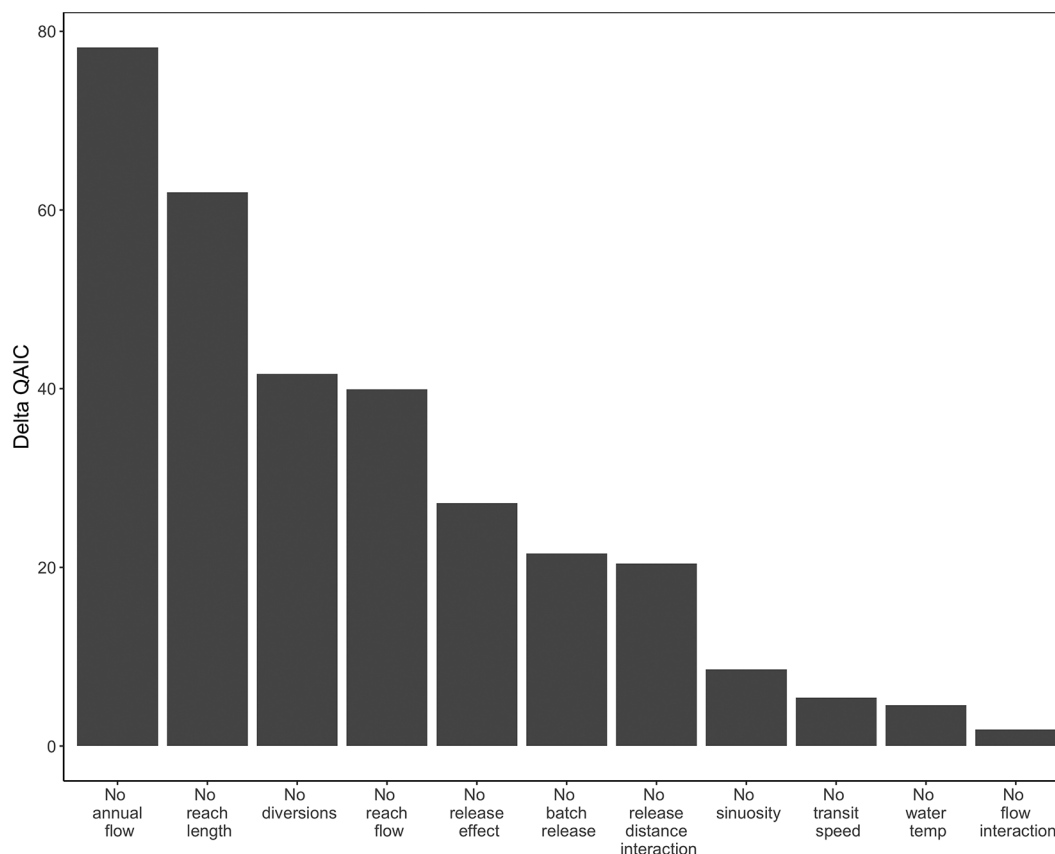
#### Discussion

Conservation of salmonid populations depends on understanding what physical and biological factors have the largest impact on mortality during different life history stages. Recent research has shown that the outmigration period may have the largest influence on smolt to adult survival rates and cohort strength (Michel 2019). Therefore, identifying the primary factors that affect survival of outmigrating smolts can help prioritize manage-

**Table 2.** Beta estimates (standard errors) of covariates included in mark–recapture models with a delta QAIC<sub>c</sub> < 2.

Covariate	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
Intercept	2.918 (0.050)	<b>2.900 (0.049)</b>	2.899 (0.049)	2.917 (0.050)	2.943 (0.049)	2.942 (0.049)	2.936 (0.049)
Battle Creek	-2.000 (0.141)	<b>-1.986 (0.140)</b>	-1.957 (0.141)	-1.969 (0.142)	-2.023 (0.141)	-1.992 (0.142)	-2.013 (0.141)
Sac–SJ Delta	-2.673 (0.096)	<b>-2.656 (0.095)</b>	-2.659 (0.095)	-2.678 (0.096)	-2.695 (0.096)	-2.698 (0.096)	-2.691 (0.096)
SF Bay	-2.888 (0.260)	<b>-2.868 (0.259)</b>	-2.899 (0.261)	-3.042 (0.240)	-2.926 (0.259)	-2.959 (0.261)	-2.913 (0.259)
Reach length	-0.463 (0.047)	<b>-0.446 (0.046)</b>	-0.444 (0.045)	-0.461 (0.047)	-0.445 (0.049)	-0.442 (0.049)	-0.457 (0.049)
Sinuosity	0.168 (0.050)	<b>0.147 (0.049)</b>	0.145 (0.049)	0.167 (0.050)	0.181 (0.051)	0.181 (0.051)	0.188 (0.051)
Adjacent cover	—	—	—	—	0.073 (0.053)	0.076 (0.053)	0.089 (0.052)
Diversion density	0.421 (0.057)	<b>0.382 (0.052)</b>	0.379 (0.052)	0.418 (0.057)	0.423 (0.056)	0.421 (0.056)	0.419 (0.056)
Off-channel habitat	0.118 (0.062)	—	—	0.120 (0.062)	0.143 (0.065)	0.147 (0.065)	0.147 (0.065)
Fish condition	—	—	0.050 (0.030)	0.054 (0.030)	—	0.054 (0.030)	—
Annual flow	0.404 (0.039)	<b>0.406 (0.039)</b>	0.405 (0.039)	0.402 (0.039)	0.387 (0.038)	0.387 (0.038)	0.396 (0.038)
Reach flow (year)	0.320 (0.047)	<b>0.320 (0.047)</b>	0.315 (0.047)	0.314 (0.047)	0.309 (0.047)	0.304 (0.047)	0.327 (0.046)
Annual flow: reach flow	-0.112 (0.046)	<b>-0.113 (0.046)</b>	-0.107 (0.046)	-0.106 (0.046)	-0.115 (0.046)	-0.109 (0.046)	-0.106 (0.046)
Temperature	-0.079 (0.041)	<b>-0.080 (0.041)</b>	-0.078 (0.041)	-0.077 (0.041)	—	—	—
Transit speed	0.079 (0.034)	<b>0.078 (0.034)</b>	0.081 (0.034)	0.083 (0.035)	0.069 (0.035)	0.073 (0.035)	—
Release reach	-0.821 (0.131)	<b>-0.857 (0.130)</b>	-0.865 (0.130)	-0.829 (0.131)	-0.781 (0.135)	-0.787 (0.135)	-0.781 (0.135)
Batch release	0.694 (0.147)	<b>0.701 (0.146)</b>	0.689 (0.147)	0.679 (0.147)	0.637 (0.143)	0.625 (0.143)	0.651 (0.143)
Batch release: distance	-0.003 (0.000)	<b>-0.003 (0.000)</b>	-0.003 (0.000)	-0.003 (0.000)	-0.003 (0.000)	-0.003 (0.000)	-0.003 (0.000)
Survival covariates	16	<b>15</b>	16	17	16	17	15
ΔQAIC <sub>c</sub>	0	<b>0.29</b>	0.71	1.20	1.27	1.38	1.63

**Note:** The Battle Creek, Sacramento–San Joaquin Delta (Sac–SJ Delta), and San Francisco Bay (SF Bay) covariates are beta estimates for the three reaches where habitat- and predation-related covariates were not included in the model. See Table 1 for definitions of the other covariates. The selected model is in bold.

**Fig. 4.** A barplot depicting the results of covariate removal analysis to determine the importance of each variable to the final model. Delta QAIC values represent the change in QAIC when specific variables are removed from the full model.

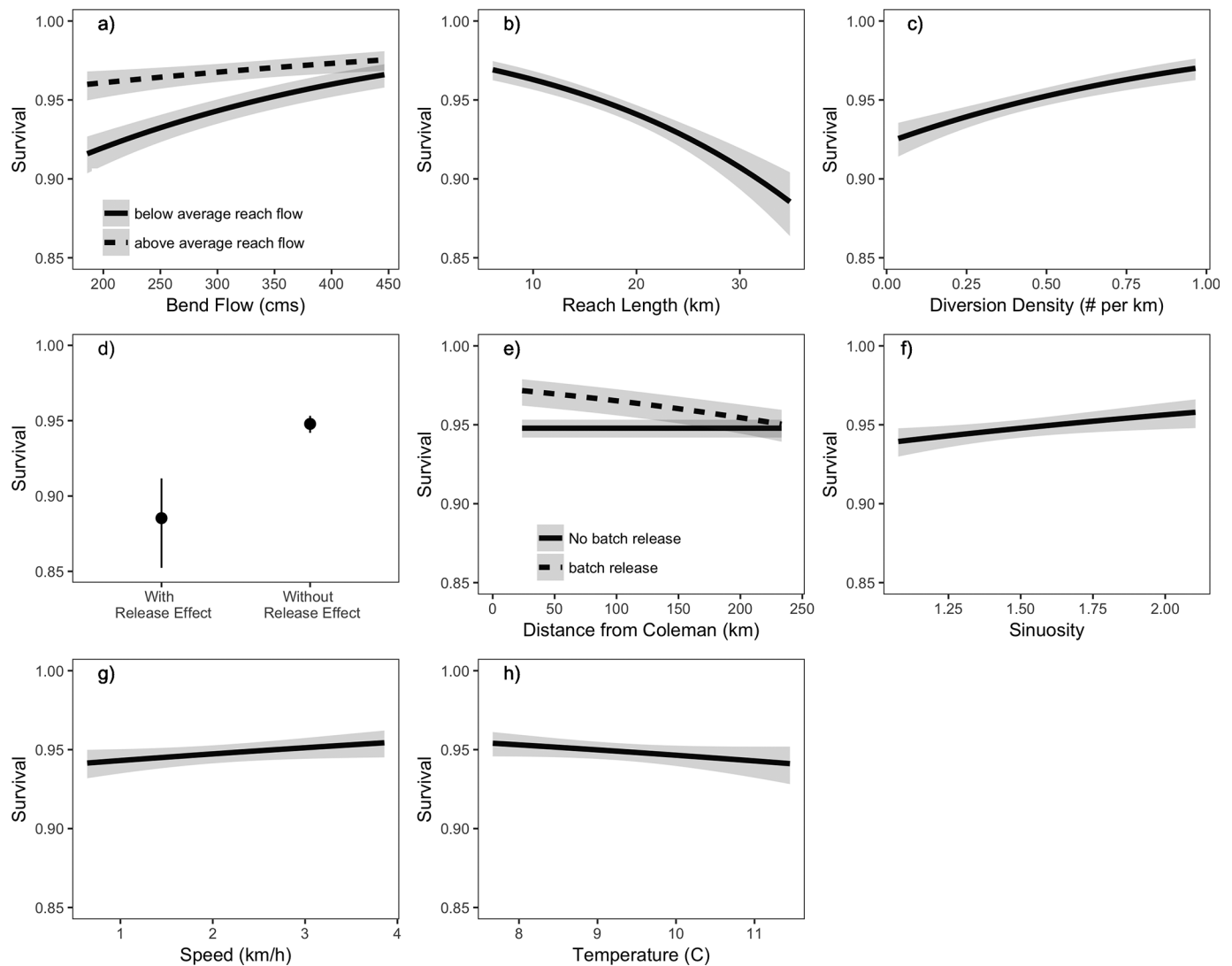
ment actions that will be most beneficial to the conservation of imperiled populations. While we could not include all possible sources of mortality in our analysis, we conclude that flow remains the single most influential factor for determining survival of late-fall Chinook salmon smolts outmigrating from California's Central Valley.

#### Spatial and temporal survival heterogeneity

The spatial–temporal model indicated that survival through different reaches varied interannually, which is likely a result of the dynamic nature of the Sacramento River system. Overall, we can conclude from our reach-specific survival estimates that increased mortality rates occurred most frequently in the upper and



**Fig. 5.** Covariate response plots showing the effect of the individual covariates on the apparent survival rate through a 10 km reach. The grey shaded region represents the 95% confidence interval.



middle regions of the Sacramento River, and decreased rates occurred through the lower reaches. We compared the observed values for the covariates included in the selected model to determine whether fish had different behaviors in the upper reaches and whether any aspects of the physical habitat differed. The most striking difference between the upper reaches and the lower reaches was the diversion density. This implies that increased diversion density, and the coincident anthropogenic habitat modifications of the lower river, reduced mortality of outmigrating smolts. Much of the previous work that has examined the effects of habitat modification and restoration on salmonid populations has focused on egg incubation, freshwater–estuarine rearing, and available spawning habitat (reviewed in Roni et al. 2014) or the effects of fish passage on outmigration mortality (Skalski et al. 2001; Williams et al. 2001; Welch et al. 2008; Elder et al. 2016). We do not know of any studies that have explicitly looked at the effect of channel alteration on salmon outmigration survival. A valuable future study would be to examine whether channelized habitats have lower predator densities or whether the deeper waters make it easier for salmon to avoid predators.

In addition to the higher mortality rates in the upper reaches, the biggest discrepancies between the spatial-temporal model and the covariate model also occurred in the upper reaches. This

suggests our covariate model would benefit from including additional covariates that contributed to smolt mortality in the upper reaches. Based on previous research, we believe that including covariates such as turbidity and predator density would likely improve our explanatory power. Turbidity likely improves salmon survival by decreasing predation risk (Gregory and Levings 1998). Likewise, high predator densities in the upper and middle reaches may partially explain the increased mortality rates in these locations. Naïve, hatchery-raised fish are more susceptible to predation after release (Alvarez and Nieceza 2003; Huntingford 2004; Jackson and Brown 2011). This was reflected in our covariate model where newly released fish had a lower survival rate than fish released upstream. Including turbidity and predator density in a mark-recapture model could improve model fit and provide important information necessary to develop a purely mechanistic model to estimate outmigration mortality.

#### Time-varying covariates

Model selection for the covariate model provided insight into which time-varying physical covariates had the largest influence on survival of outmigrating late-fall Chinook salmon. Flow exerted the greatest overall effect on outmigration success, with increased annual flow positively related to increased smolt sur-

vival. Studies have repeatedly demonstrated that flow is the most important factor affecting survival of Chinook salmon (Connor et al. 2003; Smith et al. 2003; Zeug et al. 2014; Michel et al. 2015). In addition to the effect of annual flow, we also found that variability in flow within a reach affected survival rates, particularly in low-flow years. If flow within a reach was well above the annual average, as it would be after a precipitation event, there was relatively little (1.6% per 10 km) difference between survival in low- and high-flow years. In contrast, below average flows within a reach resulted in large (5% per 10 km) differences in survival between low- and high-flow years. This provides a potential explanation for results observed by Courter et al. (2016), where survival was highly dependent on flow within a low-flow (<125 cm·s<sup>-1</sup>) reach, but had no effect in a reach with higher flows (100–300 cm·s<sup>-1</sup>).

Our study also builds on previous work by including measurements of both spatially explicit flow and transit speed as covariates in our model. This allowed us to separate the effect of flow from transit speed, suggesting that there are features inherent to flow itself, not just its effect on travel time, which affects survival. Flow has been significantly reduced and homogenized in the Sacramento River system from historic levels (Buer et al. 1989), in particular during the winter months when runoff from storm events is captured behind dams. Flow magnitude affects the amount of off-channel and floodplain habitat available for juvenile salmon rearing (Nislow and Armstrong, 2012; Merenlender and Matella 2013). Fish residing in these habitats have accelerated growth rates that may aid individuals in predator avoidance and survival (Sommer et al. 2001; Limm and Marchetti 2009). Furthermore, the highest sediment loads for the Sacramento River were observed with the highest peak flows (Stern et al. 2016), which can increase turbidity rates and decrease predation rates (Gregory and Levings 1998). Whatever the specific mechanism, flow was clearly the most important factor influencing the outmigration success of late-fall run Chinook smolts in 2007–2011. Perhaps more importantly, the effect of flow propagates throughout a cohort's life history and can be used to estimate smolt-to-adult ratios (Michel 2019). Threshold flow values could be determined through combined controlled-release and tagged-release studies in the Central Valley.

We also found survival was higher at lower water temperatures. We hypothesize that this effect was the result of increased predator metabolism, and thus consumption, at increased temperatures (Petersen and Kitchell 2001). This effect was relatively minor (1.3% per 10 km) over the small range of temperatures we observed during the fall-run winter outmigration months. However, we expect this effect will be more pronounced for fall and winter run fish that are outmigrating during warmer months and may exhibit adverse responses to warmer temperatures (Baker et al. 1995; Lehman et al. 2017).

#### Release group covariates

Acoustically tagged fish had higher survival rates when they were released concurrently with thousands of hatchery fish. Based on the interaction between release size and distance from release location, this effect persisted for approximately 200 km from the release location. One explanation for this improved overall survival is the theory of “predator swamping”, whereby predators, inundated by prey, pose less of a threat to individual smolts. This effect has been demonstrated for Chinook salmon in the Yakima River (Fritts and Pearsons 2008) and juvenile sockeye salmon (*Oncorhynchus nerka*) in British Columbia (Furey et al. 2016). We examined the difference in arrival times at the acoustic receiver locations for each of the release groups and found that fish from the same release group arrived at the same location within approximately 24 h for the first 100 km (Supplemental Fig. S2<sup>1</sup>). After the first 100 km, the river has more channel alterations and fish arrival times were more dispersed. However, fish survival rates in these lower sections of the river were generally higher

than survival rates in the upstream reaches, most likely due to decreased predation rates in the channelized portions of the river.

#### Individual covariates

Predicted transit speeds were also an important factor, with increasing transit speeds corresponding to increased survival. For outmigrating yearling smolts, it is likely that transit speed in the context of our study is a proxy for duration of exposure to mortality factors. Previous studies have found that survival rates decline over longer migration distances (Bickford and Skalski 2000; Muir et al. 2001; Smith et al. 2002). However, these studies have primarily found that survival was related to distance traveled but not to travel time. Anderson et al. (2005) explained this apparent discrepancy by suggesting that survival was a function of both migration distance and predation risk. This provides further motivation to study the factors that influence the spatial distribution and density of salmon predators throughout the Sacramento River.

#### Reach-specific characteristics

Model selection results provided evidence that reach length, diversion density, and sinuosity were associated with outmigrating smolt survival. After accounting for all other covariates, survival was higher with increasing sinuosity, suggesting that more natural river conditions were better for smolt survival than the deeper and more armored portions of the river. This result is in contrast with our other finding that the highest survival rates were in the lower, more channelized sections of the river. We suspect that the larger covariate effect of diversion density accounts for the variation associated with increased survival in the lower reaches. Because the diversions are typically not operational during the period when late-fall Chinook are outmigrating, we suspect this effect is more a function of the habitat conditions in locations where diversions are more abundant. Diversions were highly correlated to other habitat variables typical of agricultural zones, namely depth, armored banks, and agricultural and developed land use (Supplemental Fig. S1<sup>1</sup>). Because we did not wish to obfuscate the results of our analysis, we withdrew these collinear factors from our modeling efforts, but the role of “diversions” on survival could be equally viewed as the role of depth, agriculture and developed land, and armored banks. These modified habitats may result in reduced predator densities and predation mortality.

#### Conclusions

Flow, diversion density, and release strategy had the strongest influence on survival of outmigrating, hatchery origin, late-fall run Chinook salmon during the 2007–2011 water years. For years with high flow, gains in in-river survival can lead to a threefold increase in total outmigration survival, while survival in the delta and estuary remain the same (Michel et al. 2015). There is limited natural habitat remaining for Chinook salmon in the Central Valley as a result of human activities, and increasingly managers are turning to habitat restoration efforts to restore salmon populations. When we compare physical covariates, metrics for habitat features, and individual covariates, flow remains the most important factor affecting outmigration survival of late-fall run hatchery-raised smolts. Although our study used hatchery fish, which have limitations as wild fish surrogates, these results suggest that maintaining flow during periods of salmon outmigration is an important step towards conserving Chinook salmon in the Central Valley.

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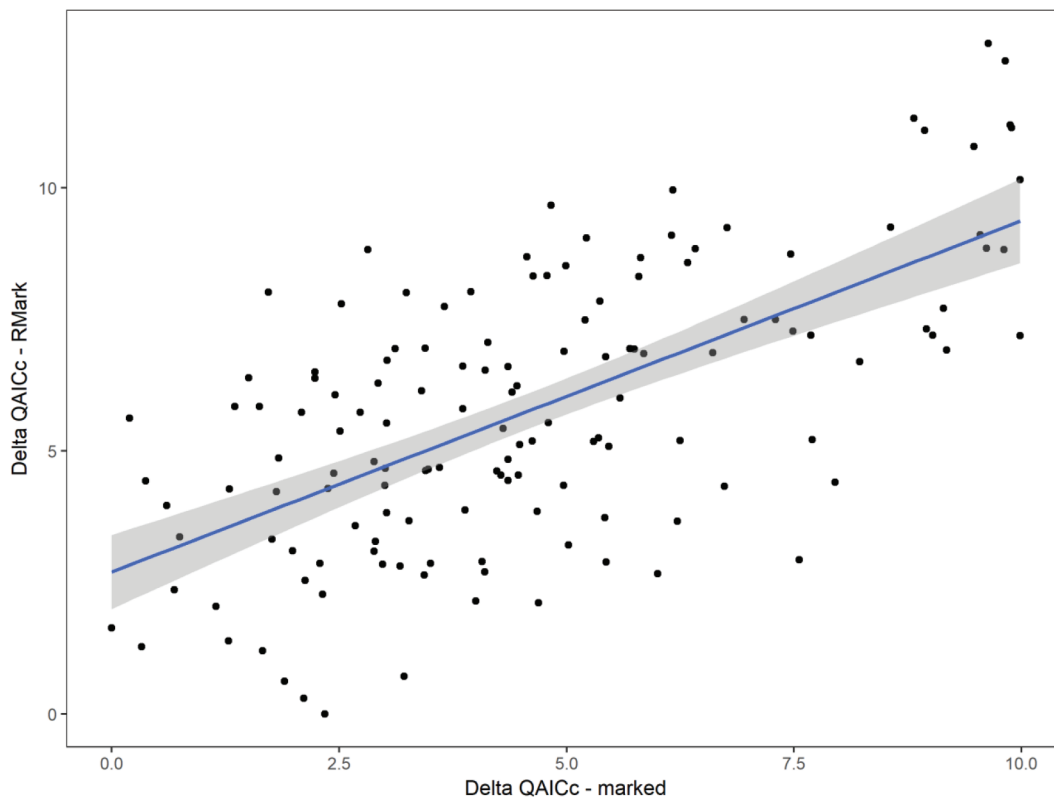
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## Appendix A

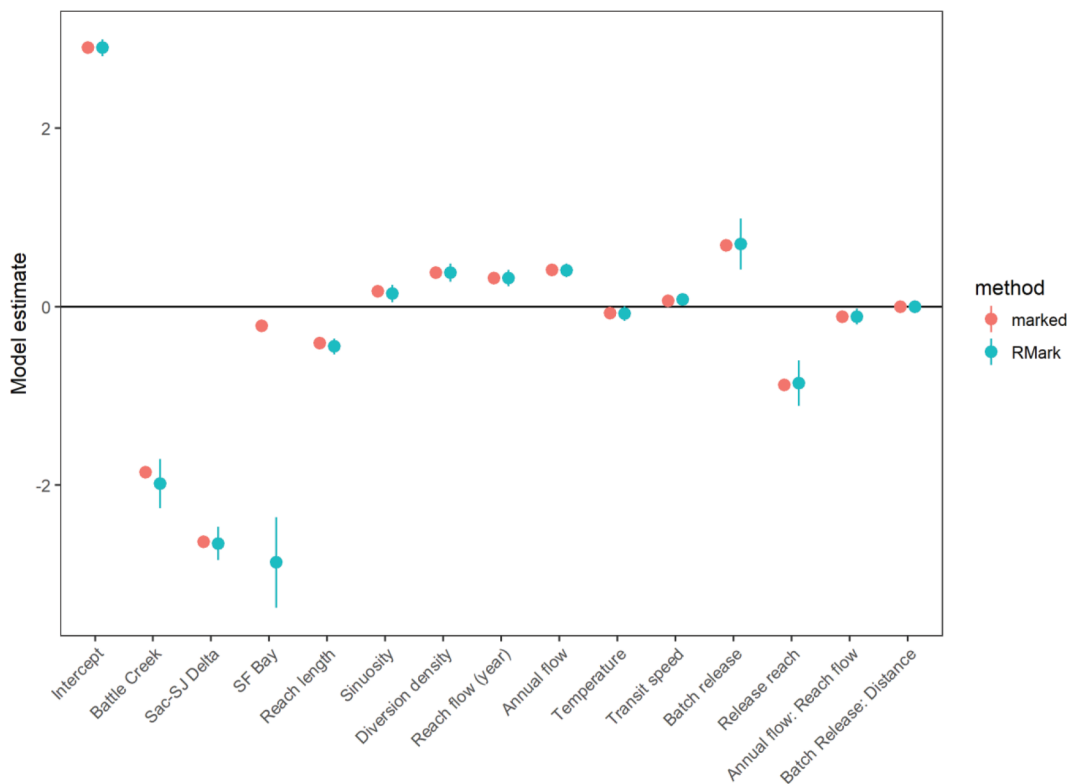
Owing to the large number of potential models ( $n = 8064$ ) and the long RMark execution times required for models with individual time-varying covariates, we first fit the models using the Automatic Differentiation Model Builder (ADMB) option available through the “marked” package (Laake et al. 2013). In contrast with RMark, the “marked” package fits models based on the hierarchical likelihood construction described by Pledger et al. (2003). Although we could successfully fit models and estimate QAIC<sub>c</sub> criterion using the “marked” package, we were unable to estimate standard errors for all model parameters due to indefinite Hessian matrices. This prompted concerns that these models were not converging properly and the QAIC<sub>c</sub> values were not accurate. To test this assumption, we refit all models with a  $\Delta\text{QAIC} < 10$  using RMark and compared the QAIC<sub>c</sub> values, and the model parameters, with those produced with “marked”. We then used the RMark results to select the model with the most appropriate combination of covariates and to calculate the final parameter estimates and confidence intervals.

The comparison between the model selection results from “marked” and RMark indicated that using “marked” for initial model selection was reasonable. The magnitude of the  $\Delta\text{QAIC}_c$  values showed good agreement (linear regression  $r^2 = 0.41$ ,  $p$  value  $< 0.001$ ; Supplemental Fig. S1), and the parameter estimates were nearly identical for the most parsimonious model (Supplemental Fig. S2). Thus, we concluded that using RMark for our final model selection, after using “marked” to identify the top candidate models, was a valid approach.

**Fig. A1.** Comparison of  $\Delta QAIC_c$  values for 141 CJS models fit with the R packages “marked” and “RMark”. These were all the models with a “marked”  $\Delta QAIC_c$  of less than 10.



**Fig. A2.** Parameter estimates for the selected model (see Table 2) estimated using the R packages “marked” and “RMark”. Error bars represent the 95% confidence interval, which was only estimated for the RMark models (see text). The only difference in parameter estimates occurred in the final study reach (SF Bay) and is a result of the different likelihood formulation used by the different packages. [Colour online.]



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