Chinook salmon smolt mortality zones and the influence of environmental factors on out-migration success in the Sacramento River Basin

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Abstract

A small percentage of imperiled Chinook salmon in the Central Valley survive the passage from natal habitat to the ocean, yet managers charged with ameliorating this loss struggle to identify specific causes amongst the myriad potential contributing factors. We incorporated a breadth of individual fish attributes, environmental covariates and reach specific habitat types into mark-recapture survival models in order to gain a holistic perspective on which factors are most influential in determining outmigration success for hatchery origin late-fall run yearling smolts. Reach-specific survival estimates within the Sacramento mainstem revealed high levels of spatial heterogeneity in the landscape of mortality, with a general trend of increased survival through the lower reaches. River flow, hatchery release strategy (whether or not fish were released in a large group), fish condition and swim speed were strongly correlated with survival dynamics, suggesting potential causative mechanisms. Habitat features, specifically diversion density, off-channel habitat availability and sinuosity were also correlated to survival, but to a lesser extent than flow and individual covariates. Of the numerous mortality factors we included, spanning multiple spatial scales, flow correlated the strongest with out-migration success, providing further evidence of the importance of flow and water management practices to the out-migration mortality of hatchery origin Chinook salmon in the Central Valley.

Introduction

Historically, steep montane tributaries conveyed water, unencumbered, through the mainstem Sacramento River. Juvenile salmon utilized vast expanses of seasonal habitat to rear and grow before emigrating to sea. Loss of habitat, combined with overfishing and water diversion have contributed to precipitous declines in Chinook salmon populations (Yoshiyama et al. 1998, Yoshiyama et al. 2000), potentially portending extinction of salmon in California (Katz et al. 2013). Factors impeding recovery include continual habitat loss, sustained extraction of water for consumptive and agricultural use, and out-migration mortality of smolts (CDFW 2015).

Out-migration is oft considered the most perilous stage in the Chinook salmon life-cycle (Healey 1991). Overall survival of smolts from the Sacramento River through the Sacramento-San Joaquin Delta and on to the San Francisco Estuary and the Pacific is low compared to other salmon watersheds (Michel et al. 2015). Whereas survival through the Sacramento-San Joaquin delta is consistently low (Kjelson and Brandes 1989, Baker and Morhardt 2001, Newman and Brandes 2010, Buchanan et al. 2013, Singer et al. 2013), survival through the Sacramento River mainstem fluctuates more than other regions and increased survival in this region can increase overall survival to the ocean (Michel et al. 2013). Further, while Chinook salmon smolt survival in the delta has been extensively studied and manipulated in order to identify effective management actions within locations of considerable mortality, there is a paucity of comparable information for the Sacramento River mainstem. Thus, our research focuses on identifying potential drivers of out-migrating smolt mortality in the Sacramento River and identifying large-scale areas within the river where mortality rates are consistently high. Small improvements in the survival of early life stages can enhance adult returns (Baker and Morhardt 2001) and as such, the identification of factors that affect smolt mortality could provide managers with direction on how to improve survival (Perry et al. 2013, Singer et al. 2013).

In order to evaluate which factors may contribute to out-migration mortality, it is imperative to consider out-migrant behavior. Chinook smolts in the Sacramento River and delta have been shown to emigrate nocturnally and hold during the day (Zajanc et al. 2012, Chapman et al. 2013). Chapman et al. (2013) found that while nocturnal migration dominated overall, the

proportion of nocturnal movement varied by river region (with almost exclusive nocturnal migration in upper reaches). Zajanc et al. (2012) offered evidence that the probability and duration of holding by juvenile Chinook salmon is influenced by specific nearshore habitat types such as large woody debris, cover and substrate type; although temporal and spatial factors had a greater overall effect. Thus, smolt holding behavior can be facilitated by environmental interactions driven at the basin wide and habitat level scales. Weins (2002) highlight the need to explore stream fish habitat associations across a broad riverscape in order to be meaningful for management. We incorporate scale in our analysis by examining smolt survival with respect to environmental factors influenced by broad, basin-wide level dynamics such as flow and temperature, as well as reach-specific habitat features such as shaded riverine aquatic cover, diversion structures and bank habitat, all of which can influence survival.

Numerous environmental factors are implicated in the survival of out-migrating Chinook salmon (Michel et al. (2013). Studies evaluating survival have revealed flow (Kjelson and Brandes 1989, Michel et al. 2015), temperature ((Kjelson and Brandes 1989, Newman and Rice 2002, Newman and Brandes 2010), water management practices (Kjelson and Brandes 1989, Brandes and McLain 2001, Perry et al. 2010, Cavallo et al. 2013) and predation (Cavallo et al. 2013) to be important mortality factors effecting the survival of tagged juvenile Chinook salmon transiting the Sacramento River and Sacramento- San Joaquin delta. Singer et al. (2013) and Michel et al. (2015) found evidence for differences in reach specific survival among years, with Michel et al. (2015) elucidating the role of hydrographic conditions in this result. Michel et al. (2013) recorded an effect of width to depth ratio and flow on movement rates of out-migrating smolts. While environmental variables affect the movement and survival of juvenile salmon in the Sacramento River and Sacramento-San Joaquin delta regions, there has yet to be a comprehensive study which incorporates the holistic interaction of reach-specific habitat features, basin scale environmental characteristics, as well as individual fish attributes, to explicitly detail survival in the Sacramento mainstem.

Directed management efforts to improve the survival of salmon smolts during outmigration are mired by the challenge of determining which elements, and at which scale, environmental factors exert the greatest influence on survival. Our study examines the spatial heterogeneity of mortality across an out-migration landscape, in order to resolve the existence and stability of mortality zones. We also systematically compare the impact of environmental covariates (flow, temperature, depth and velocity), habitat features (riverine cover, off channel habitat, diversion structures, bank type and adjacent land use) and individual fish covariates (fish condition, length and hatchery release strategy), in order to determine which factors, driven by processes occurring at disparate scales, have the greatest impact on survival. Finally, based on established relationships between juvenile Chinook salmon mortality rates and specific environmental factors, we posit potential mechanistic hypothesis for these observed relationships and propose potential management directions to improve out-migration success in the Central Valley.

Methods

Study Area

Although the historical northern extent of late-fall run in the Sacramento Basin likely stretched beyond present day Keswick and Shasta dams (Fisher 1994, Yoshiyama et al. 2001), our northernmost extent was the standard release location for late-fall run smolts at the Coleman National Fish Hatchery (see figure 1). Tracing the outmigration of tagged smolts, our study area included three major river segments: the upper, middle and lower Sacramento River as defined in Chapman et al. (2013). Upper reaches are composed of shallow riffles, gravel bars and deep

pools, the middle is defined by areas of deeper water with sand banks and large woody debris, and the lower reaches are channelized, with extensive levees, rip-rap and water diversion. Although previous work on late-fall run outmigration in the Central Valley utilized the entire outmigration extent, including the delta and estuary (see Michel et al. 2015 and Singer et al 2013), we focus here on the Sacramento mainstem portion of the outmigration corridor, as the riverine portion has received less attention, but is crucial for understanding population level changes in downstream migration success.

Acoustic tagging

Late-fall run Chinook salmon, obtained from the United States Fish and Wildlife Service - Coleman National Fish Hatchery, were implanted with acoustic tags and released annually for five years (2007-2011). For details regarding the surgical procedures undertaken and initial acoustic tag study design, please see (Michel et al. 2013, Michel et al. 2015). During the first year of this study (Dec-Jan 2007), smolts were tagged and released directly into Battle Creek. For subsequent years, each winter (Dec-Jan), tagged smolts were released concurrently from three locations along the mainstem Sacramento River: Jelly's Ferry, Irvine Finch and Butte City, and in 2011 all fish were released at Jelly's Ferry (see figure 1). In addition to the acoustic tag data utilized in Michel et al. (2013) and Michel et al. (2015), we utilized acoustic tag data collected by the USFWS. The USFWS fish were tagged in accordance with the same procedures as above, but released directly into Battle Creek in 2010 and 2011, and concurrent to the release of the remaining hatchery production (batch released), while the NMFS fish were released separately (table 1). Upon release, smolts passed through a series of acoustic receivers (again see Michel et al. (2013) and Michel et al. (2015) for more details), which extended from the release locations in the upper and middle Sacramento River, to the interface with the Pacific Ocean. We divided the Sacramento mainstem study region into 19 reaches demarcated by the location of 20 acoustic receivers, which had consistent locations between each of our study years.

Table 1: Release locations for all tagged late-fall run Chinook salmon yearling smolts. Fish were tagged by either NOAA-NMFS (National Marine Fisheries Service), Southwest Fisheries Science Center, or by the USFWS (United States Fish and Wildlife Service). All fish regardless of year were tagged at the Coleman National Fish Hatchery, located along Battle Creek- a tributary to the Sacramento River.

Study year	Release locations
2007	All NMFS tagged fish released into Battle Creek
2008	All NMFS tagged fish released from Jelly's Ferry, Irvine Finch and Butte City
2009	All NMFS tagged fish released from Jelly's Ferry, Irvine Finch and Butte City
2010	All NMFS tagged fish released from Jelly's Ferry, Irvine Finch, and Butte City USFWS tagged fish released into Battle Creek with main hatchery production
2011	All NMFS tagged fish released exclusively from Jelly's Ferry USFWS tagged fish released into Battle Creek with main hatchery production

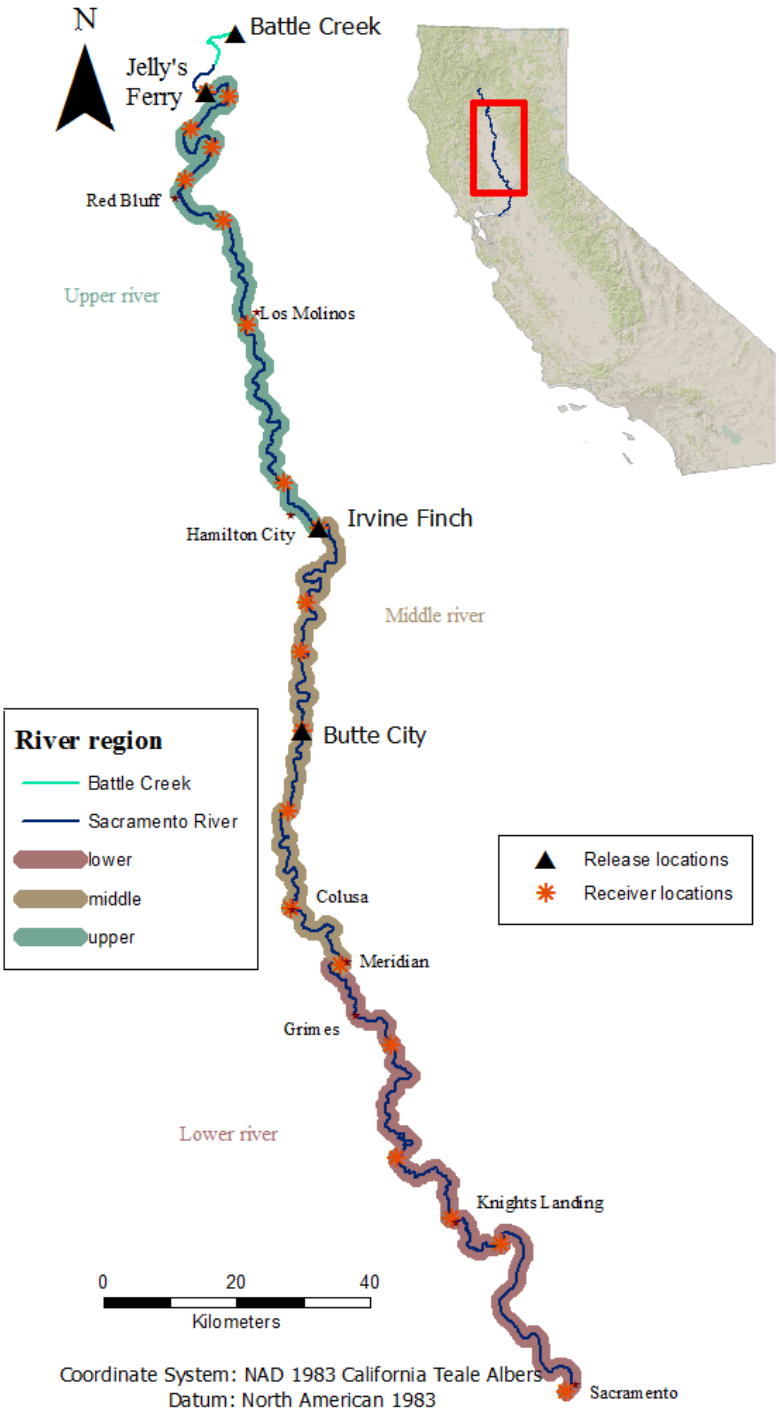

Fig 1: Map of the mainstem Sacramento River study area. Late-fall run Chinook yearling smolts were released at Battle Creek, Jelly's Ferry, Irvine Finch or Butte City during our study period (water years 2007- 2011). While the Southern extent of our study area ended at the I-80 bridge near Sacramento, smolts must continue their outmigration through the delta and eventually the San Francisco Bay before entering the Pacific Ocean.

Habitat and environmental factors

In order to incorporate physical habitat features and environmental factors in survivorship models, we first had to establish basic hydrography for the Sacramento River. We utilized the most recent National Hydrography Database (NHD), high-resolution data to create our river hydrography layer. The Sacramento River has meandered considerably through time in response to varying flow conditions and bank erosion (Larsen 2007). This dynamism meant that many GIS layers depicting the course of the Sacramento River were incongruous to one another when data came from disparate years and sources. Our NHD Flowline was thus necessarily edited to match our other environmental data layers by manually editing the NHD flowlline layer to match 2009 imagery from the National Agriculture Imagery Program aerial.

The California Department of Water Resources (DWR) provided a bankwidth layer (Adam Henderson, personal communication), which was created as part of the Central Valley Riparian Mapping Project in support of the Central Valley Flood Protection Program. This layer traces all visible surface water along the mainstem Sacramento River and was used as our baselayer for calculating habitat features within and adjacent to the Sacramento River.

The GIS- derived data we use to define habitat features in this study were static; the same values were used for each of the 5 years of our study. As such, we accept that our static descriptions of habitat do not necessarily reflect the conditions experienced by smolts during out-migration. However, as we were interested in describing physical habitat conditions for the entirety of the mainstem Sacramento River, and since many of these features do not change appreciably between years, we determined that this was the best available approximation of physical habitat. Dynamic environmental factors, the values of which were driven by basin-wide forcings, were modeled using existing River Assessment for Forecasting Temperature (RAFT) model output. RAFT is a 1-dimensional physical model that estimates temperature, flow, depth, and velocity every 15-minutes at a 2 km spatial resolution (Pike et al. 2013).

Habitat features: GIS

Data from each of the environmental factors, the source and limitations of which are outlined in table 2, were plotted in a Geographic Information System (using ArcGIS 10.3) and summarized by the 19 reaches we used to define our study reaches. River area, adjacent land use and off-channel habitat were calculated as area per reach. Shaded Riverine Aquatic Cover (SRA) and revetment (riprap) were summarized by reach as a measure of the length of bank with SRA and length of bank with revetment per reach. Densities of the number of diversions and number of tributaries were calculated per reach, and sinuosity was calculated for each river segment separately. In addition to mapping the landscape of habitat features in GIS, we explored the numerical relationships between environmental and habitat factors and river region (upper, middle and lower). All analysis and interpretation were conducted in the open software package R (R Core Team 2016). We first standardized each habitat factor by reach length (as defined by the length of bank per reach) for all habitat features except sinuosity which was already a measure per reach, and then plotted each of the environmental variables across river regions in order to ascertain whether there exist any clear differences among regions. For detailed information regarding the biological relevance of each of our environmental variables on juvenile salmon, please see the supplemental information section.

Table 2: A description of the source, extent and modifications to spatial habitat features along the Sacramento mainstem river. All spatial features had limitations in their applicability to out-migrating Chinook salmon, but are the best spatial representation of habitat we could produce at this time.

Habitat Feature and Metric	**Data source and modifications**
River area Defined the bankwidth of the Sacramento mainstem	Source: These data come from the "Mapping standard land use categories for the Central Valley Riparian Mapping Project," developed for the Central Valley Flood Protection Program System wide Planning Area. Prepared for: DWR by Geographical information center, Cal State Chico, and shared with permission. This layer was heads-up digitized based on National Agriculture Imagery Program (NAIP) 2009 imagery. Extent: This layer represents the mainstem Sacramento River from Keswick to the I-80 bridge. Only riverine habitats directly connected to the mainstem were included in this layer. Modifications: This layer was modified to match the bankwidth outlines from the DWR revetment layer for the Sacramento River-which may reflect slight changes to the banklines as a result of recent revetment actions. The parent datasets were DWR layers [Vegetation-Central Valley Riparian Vegetation and Land Use, 2011 (medium scale)] ds292 and ds723 (metadata)
Sinuosity Index of 0 to 1 calculated per reach	Source NHD high-resolution river line layer (edited to match NAIP 2009 imagery). Modifications: Sinuosity values were derived from the python Sinuosity toolbox in ArcGIS, using the NHD high resolution flowline depiction of our study reaches. Sinuosity is calculated as the distance the river travels between reaches compared to the Euclidean distance of that same reach.
Diversion density # of diversions per reach	Source: Field data were collected through a joint effort by the authors at the National Marine Fisheries Service (NMFS), Southwest Fisheries Science Center (Santa Cruz) and the State of California Department of Fish and Wildlife, Fish Screen Fish Passage Program (FSFPP). Field surveys involved verifying the position and condition of diversions from the Passage Assessment Database (ds069). PAD Extent Sacramento River from ACID diversion in Redding to the I-80 Bridge in Sacramento. NMFS covered the portion from ACID to the Meridian Bridge, Colusa and the state FSFPP collected data from the I-80 Bridge in Sacramento to Hamilton City (although in this study we only utilized state collected data below our Southern survey extent at the Meridian bridge) Data collection field data were collected by jet boat in the Spring of 2016 – the location of each diversion was recorded with a GPS device and the condition of diversion intakes examined. New diversions were added when encountered. Additionally, intake diameter measurements were measured either directly (FSFPP) or estimated visually (NMFS). Limitations: Diversion records inaccessible to boat (at least in the Northern, NMFS surveyed section) were omitted from analysis, as well as diversions that may still have been operational and accessible but were off the main channel. Abandoned records were removed. Also, there was no reliable method for obtaining information regarding the quantity or timing of water pumping.
Adjacent land use Mean area of adjacent land use type (within 120m of river) [m^2] per reach	Data source: Multi-Resolution Land Characteristics Consortium (MRLC), National Land Cover Database (NLCD) Metadata This is a raster layer with each 30x30 meter cell representing one of 16 land use classes. Extent We clipped this nation wide dataset to our study area (Jelly's Ferry to the I-80 bridge) Modifications: We reclassified land use from 16 classes to 3 ("natural", developed and agricultural) and clipped data to within a 120m buffer around our bankwidth river layer. We calculated land use area per reach by taking the mean land use data from 2006 and 2011. Limitations: The 30m grid size meant that there were some gaps and overlap between the river bankwidth layer and adjacent land use data.
Revetment Length of rip-rapped river bank	Data source: This data layer was provided upon request from the Department of Water Resources and is part of the joint revetment-bank-SRA layer. *This data was developed as part of the DWR Floodsafe CA initiative-specifically the development of the Conservation Strategy in support of the Central Valley Flood Protection Plan 2017 update*. Metadata Extent Red Bluff to I-80 bridge (this section of data was an update to data previously collected by DWR Northern Region). Colusa to Verona (updated data previously collected by US Army Corps (USACE)- Sacramento Bank Protection Project, 2007). Data collected

per reach [m]	in the fall of 2013 and spring of 2014 by DWR and synched to NAIP 2013 and overlaid on 2009 channel features. Modifications/Limitations: In order to extend the coverage from Red Bluff to Jelly's Ferry, this portion of the dataset was estimated by the authors via 2015 Google Earth imagery. Thus, the northern section is an approximation of riprap and does not necessarily reflect current conditions
Tributaries # of large tributaries per reach	Data source: The data used for this analysis come from NHDPlus Version 2 (http://www.horizon-systems.com/nhdplus/NHDPlusV2_data.php), which was released in 2012- but houses data from disparate times. In some cases this data did not match current hydrography conditions. Extent although there are many tributaries leading into the Sacramento River, we were only interested in large perennial tributaries, and assume that those smaller inputs are captured in the bankwidth layer which traced water body outlines using NAIP 2009 Modifications: We created a geometric network, joined the flowlines to the VAA attribute table and selected only those tributaries to the Sacramento River with stream order >3 (only the major tributaries). Canals and Sloughs were removed-although there are some sections of the tributaries, which may be canal features during part or most of their course. Limitations : This data set only includes large tributaries, and omits potentially valuable seasonal and small tributaries to the Sacramento River.
Shaded Riverine Aquatic Cover (SRA) Meters SRA per reach [m]	Data source: This layer contains information from the DWR revetment data as well as the DWR vegetation layers (ds723 and ds292) [Vegetation-Central Valley Riparian Vegetation and Land Use, 2011 (medium scale)]. We followed the DWR convention of defining SRA as: non-riprapped bank with adjacent natural woody vegetation, as adapted from (USFWS 1992) Extent This layer covers our study region from Jelly's Ferry to the I-80 bridge in Sacramento. Modifications: While the vegetation layer covered the full extent of our study region, the revetment layer, as mentioned previously, missed the Northernmost portion of the river from Red Bluff to Keswick, which was estimated by hand via Google Earth Imagery (with 2015 imagery). We then selected those areas of SRA using select by attributes in ArcMap, and divided per reach. Limitations: This is an estimation of overhanging cover and in-stream cover, but is an inferred proxy, not confirmed in the field. Thus, this is only an approximation of cover.
Off-channel habitat Area off-channel habitat [m^2] per reach	Data source: This data came from the DWR [Vegetation-Central Valley Riparian Vegetation and Land Use, 2011 (medium scale)] layer, which was digitized from NAIP 2009 aerial imagery. This data layer digitally traced all water bodies along the mainstem at the time of analysis (a snapshot of the area in 2009). Extent This layer covers our study region from Jelly's Ferry to the I-80 bridge Modifications: We selected all water bodies within 50 m of the mainstem while removing tributaries and canals. Limitations: This layer may contain off-channel water bodies that are inaccessible to out-migrating smolts (such as holding bays beyond diversions or pools not always connected to the mainstem) and would naturally vary depending on prevailing water conditions.

Acoustic telemetry data processing

The acoustic receivers automatically process all detection data and drop false detections or incomplete codes from the detection file. To ensure that no false detections due to pulse train collisions occurred in the dataset, we performed a number of quality control procedures. We first removed all detections that occurred prior to the release date and time of each tag. We then removed all detections from fish that had only a single detection throughout the study. Finally, we examined the detection history of each individual fish and removed any detection history that appeared out of the ordinary. For example, any upstream movements had to be validated by three or more detections at the same receiver. Furthermore, we examined travel time between receivers and removed any detections resulting from a fish traveling time greater than 10 km per hour that were not subsequently validated by more than three detections.

Mark-recapture analysis

To estimate survival of out-migrating late-fall run Chinook salmon we fit a Cormack-Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) model 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 2016). 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. For species that express an obligate migratory behavior, a spatial form of the CJS model can be used, in which recaptures (i.e., tagged fish detected acoustically downstream from release) occur along a migratory corridor (Burnham 1987). Using this space for time substitution, we were able to estimate overall survival of an individual fish through a given reach, as the model uses individual fish capture histories to estimate the likelihood that a fish would survive and be detected at each receiver (Lebreton et al. 1992).

Although our analysis shares similarities with Michel et al. (2015), we did make some modifications in processing the data. We did not restrict our analysis to only those detections at the receivers separating the 19 reaches of interest. Instead, detections that occurred at any receivers within the reach of interest were included as detections for that reach. The 20 receiver locations that we used to delineate our reaches were consistently positioned in the same location throughout the five years of the study; however, there were additional receivers throughout the river that were either added, removed, or moved inter-annually. Further, we focused our modeling efforts on the Sacramento mainstem, and only utilized encounter history data collected within the delta and estuary (below our study site) to estimate apparent survival through these reaches, and did not include any spatial or spatial-temporal covariates. In the standard formulation of the CJS model, detection probabilities are estimated for a single resampling occasion (i) in time or space. For example, Michel et al. (2015) estimate the probability of detection at a given receiver location. We used detections at the receiver delineating the upstream boundary of the reach as well as detections at any receiver between the upstream boundary and the downstream boundary. Thus, the estimated detection parameter is a measure of the probability of detection from receiver (i) to receiver (i+1). We also made the assumption that any tag that was consistently detected at a receiver for more than 4 weeks was a mortality. These fish were censored and did not have any impact on the estimated survival or detection probabilities downstream from where the presumed mortality occurred.

We included a number of individual and spatial covariates in our analysis to identify the factors contributing to the mortality of out-migrating smolts. Fish size influences juvenile salmon survival (Zabel and Achord 2004), thus we included length and condition factor (Fulton's k) as individual covariates. We also included a binary individual covariate to distinguish fish released together with thousands of other hatchery fish and those released in small batches. Our a priori hypothesis was that large batches of fish could improve survival by saturating predators. The spatial covariates included in the model for each reach were: revetment area, shaded riverine aquatic area, tributary density, diversion density, off-channel habitat, and the proportion of the adjacent land use that was developed, natural, or agriculture.

Due to the importance of the environmental factors to salmon movement and survival (Michel et al 2010), we included individual spatial-temporal covariates. These covariates were flow, velocity, depth, water temperature, and individual swim speed. Including individual spatial-temporal covariates requires an estimate for every fish in each reach regardless of whether or not the fish was detected. To input data for locations where fish were not detected, we developed a mixed effects model to estimate individual swim speeds as a function of release year, release week, reach, and fish condition (Fulton's $K = \frac{W}{L^3} * 100$). We also included a random intercept for each individual fish to account for individual behavioral variability. The uncertainty in location based on the mixed effects model is inherently carried through the model by the way the

mark-recapture likelihood is built. The likelihood in all reaches, after the last time a fish was detected, account for the possibility that the fish died and the possibility that the fish survived and was not detected. The fate of fish that survive through a reach, in which case we knew when a fish was within that reach (and its actual, not predicted swim speed), are more influential in estimating the model likelihood than those whose fate (and in turn conditions) were unknown. However, we plan to test the impact of the swim speed predictions on survival estimates with an uncertainty analysis in a future iteration of this study. To verify that the mixed effects model did not violate any assumptions, we examined model diagnostics (QQplot and residuals) using the DHARMa package (Hartig 2016). We used the results from the mixed effects model to estimate swim speeds for all fish in all reaches. This also provided an estimate of the dates and times undetected fish were within each reach.

We then used environmental covariate data derived from the RAFT model (Pike et al 2013) to approximate the physical conditions experienced by each fish in each reach. We extracted all estimated values for the physical variables (temperature, flow, velocity and depth) for each fish in each reach and then calculated the mean for that variable, which we used as the environmental covariate in the CJS model.

We fit a series of different CJS models to determine which covariates had the greatest impact on out-migrating smolt survival. Prior to fitting the CJS models, all continuous covariates, including the individual and spatial covariates, were normalized by subtracting the mean and dividing by the standard deviation. We also conducted pairwise comparisons of all continuous individual, spatial, and spatial-temporal covariates to determine if any covariates were collinear (Table 3). We did not include covariates that had correlation coefficients greater than 0.7 in the same model. Likewise, we did not include models that had both fish length and fish condition since they are both measures of individual fish health. We then fit three different groups of models: 1) a model that included year and reach as factors, which we refer to as our “full model” 2), models that excluded year but included reach as a factor, as well as the various individual and spatial-temporal covariates, referred to as our “temporal-covariates” models and 3) models that excluded year and reach as covariates, but included the various individual, spatial-temporal and spatial covariates, referred to as our “spatio-temporal-covariates” models. The reason for fitting the different groups of models was to better understand how the covariates that we included in our model affected salmon survival, while accounting for the inherent differences between different covariate types. Because it is impossible to measure, or estimate, all potential factors that influence salmon survival, we hypothesized that the model that included year and reach as factors would have the best fit to the data and provide us with the best available estimates of reach survival by year. Conceptually, year and reach can be considered all-encompassing factors that account for a large portion of the spatial and temporal variability in survival, when in actuality it is likely the variability in the individual and environmental covariates that are driving these changes. Therefore, by fitting models that exclude both year and reach we can partition that variation between the covariates we have included in the model and thus, gain a better understanding of the mortality mechanisms. However, we emphasize that the factors included in our best models are based on correlations, so any potential mechanism must be inferred.

For each model set, we fit models with all possible combinations of covariates and selected the most appropriate model using Akaike’s information criterion (AIC). Due to the large number of potential models, and the long execution times required for models with spatial temporal 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 to RMark, the marked package fits models based on the hierarchical likelihood construction described by Pledger et al. (2003). Although we were able to successfully fit models and estimate AICc criterion using the marked package, we were unable to estimate standard errors for all model parameters due to indefinite Hessian matrices. However, the models converged when we ran them without estimating the hessian matrix, and we used those models in the model selection

process. Thus, we used the marked package to conduct model selection and then refit the top models using RMark to calculate the final parameter estimates and confidence intervals.

Covariate plots

Once the relative importance of covariates had been determined from the model selection exercise, we extracted the β parameter coefficients for these covariates from the top model in which they occurred. The β parameter coefficients were then used to simulate what survival would be given a chosen covariate value, while keeping other covariates constant at their mean value. We selected regularly spaced covariate values ranging from the minimum to the maximum recorded values for that covariate, then simulated survival at each of these covariate values. The results from these simulations were then plotted, giving us a graphical representation of the relationship of flow and fish condition on survival dynamics across a reasonable range of flow and fish condition values.

Table 3: At left: covariates included in our survivorship model sets. Middle: those covariates that were not included in our analysis (excluded covariate) and at right: covariates that those excluded covariates were correlated with. Note that diversion density was collinear to depth, riprap, developed area, agricultural area and natural area.

Covariates (included)	***Excluded covariate:***	***Collinear with:***
Sinuosity	*Velocity*	*Flow*
Shaded riverine aquatic cover	*Depth*	*Flow + Diversion density*
Diversion density	*Riprap*	*Diversion density*
Off-channel habitat	*Developed area*	*Diversion density*
Fish length	*Agricultural area*	*Shaded riverine aquatic cover + Diversion density*
Fish Condition	*Natural area*	*Diversion density*
Flow		
Temperature		
Swim speed		
Released with other hatchery fish		

Results

Riverine habitat was spatially heterogeneous across the ~300 kilometers of Sacramento River that defined our study area. Although there were no major channel changes during our study period, 2011 was considered a "wet" water year, while 2007-2010 were considered "dry" years. There was a general North to South gradient in habitat features associated with human influence, with lower reaches exhibiting elevated levels of human modification concomitant to decreases in natural area (see figure 2). We compared diversion density, amount of riprapped bank, and land use area among our three river regions (upper, middle and lower) and found a general increase in the number of diversions and developed land area from the upper to lower reaches. Amount of riprapped bank also increases in the lower portions of the river compared to the upper and middle reaches. Finally, the total adjacent natural land use area decreased from the upper to lower reaches, with approximately a three-fold decrease in the total natural area in the lower reaches compared to the upper reaches (figures 2 and 3).

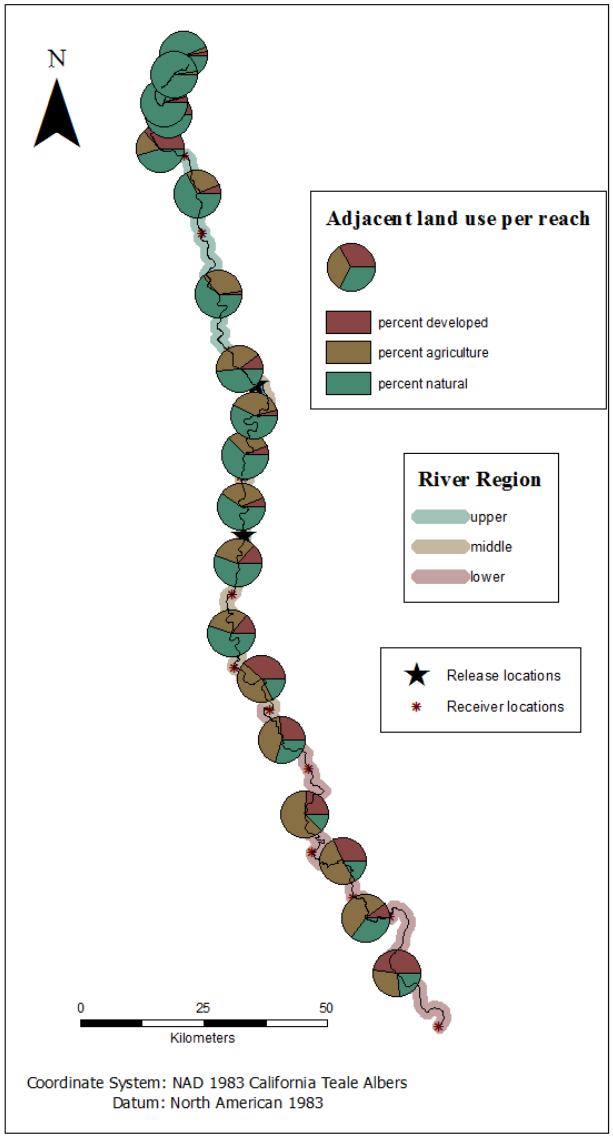

Figure 2: Map depicting the percent adjacent land-use type for each of our 19 reaches along the mainstem Sacramento River. Adjacent land is defined as land within 120 meters of the mainstem Sacramento River. The categories of land use we were interested in were "natural, developed and agricultural, because adjacent land use may impact juvenile salmonid outmigration conditions. Land use data were obtained from the National Land Cover Database (NLCD) and we calculated the mean land use cover between the years 2006 and 2011.

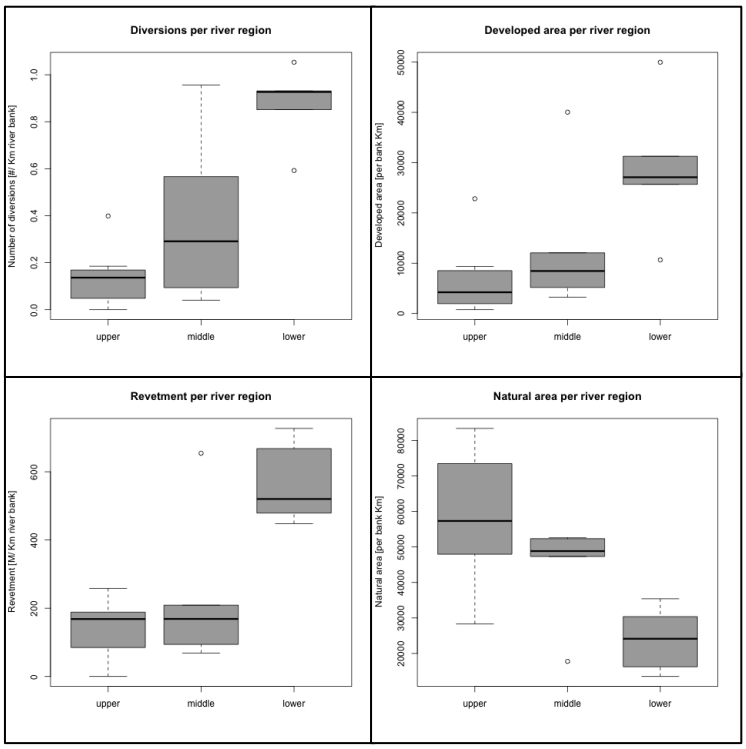

Figure 3: Upper left: mean diversion density increased from the upper reaches to the lower reaches, with a lot of variability for those reaches in the middle river region. Upper right: mean area of developed land per river region increased in the lower region. Lower left: length of riprapped bank per region, which had a clear increase in the lower reaches of the Sacramento. Bottom right: mean natural area declines from the upper to lower reaches, although the upper reaches are variable. All values were standardized by kilometers of river bank per reach.

Mark-recapture analysis- Full survival model and mortality zones

The full CJS survival model, a reach, year, interaction model, had the greatest support of all our model sets according to Akaike Information Criterion (AICc) values. We thus utilized the full model: φ (~reach * year) ρ(~reach *year) to estimate per-reach smolt survival (per 10km). Survival per reach varied spatially and temporally. Between years, cumulative survival estimates, calculated as the product of reach specific survival rates (per 10km) within the Sacramento mainstem for the five years of our study (2007-2011) were 44%, 42%, 50%, 47% and 60%, respectively.

There was a general trend of decreased per-reach survival in the upper and middle reaches of the Sacramento mainstem, compared to the lower reaches (figure 4). For 2008, 2009 and 2010, reaches exhibiting the greatest estimated mortality (defined as reaches with estimated survival rates lower than 1.5 standard deviation from mean per-reach survival for that year), were not spatially consistent between years. Survival above Red Bluff Diversion Dam was inconsistent, but tended to be relatively high, while survival between Colusa and the I-80 Bridge was consistently high. In 2008, the reach adjacent to Ord Bend had the lowest survival (87% per 10 km ± 3.8 SE), while survival was lowest in the reach above the Red Bluff Diversion Dam in 2009 (89% per 10 km ± 3.6 SE) and near Butte City in 2010 (87% per 10 km ± 2.1 SE), while the mean within reach survival for each of these years was ~96%. Thus, while there is a general trend of relatively higher survival in the lower portion of our study area, and relatively lower survival in the upper and middle reaches, the specific location with the greatest mortality risk appeared to vary between years. We were unable to generate comparable reach-specific survival estimates for

2007 due to incongruent receiver positions (6 of the 20 receiver positions were absent) and in 2011, high flows negatively impacted our detection efficiencies, rendering 12 receivers without reliable detection data (although the receivers in the lower portions of our study still produced reliable data, and thus allowed us to accurately estimate out-migration survival overall). The 2007 and 2011 years were included in the model sets that included individual and environmental covariates.

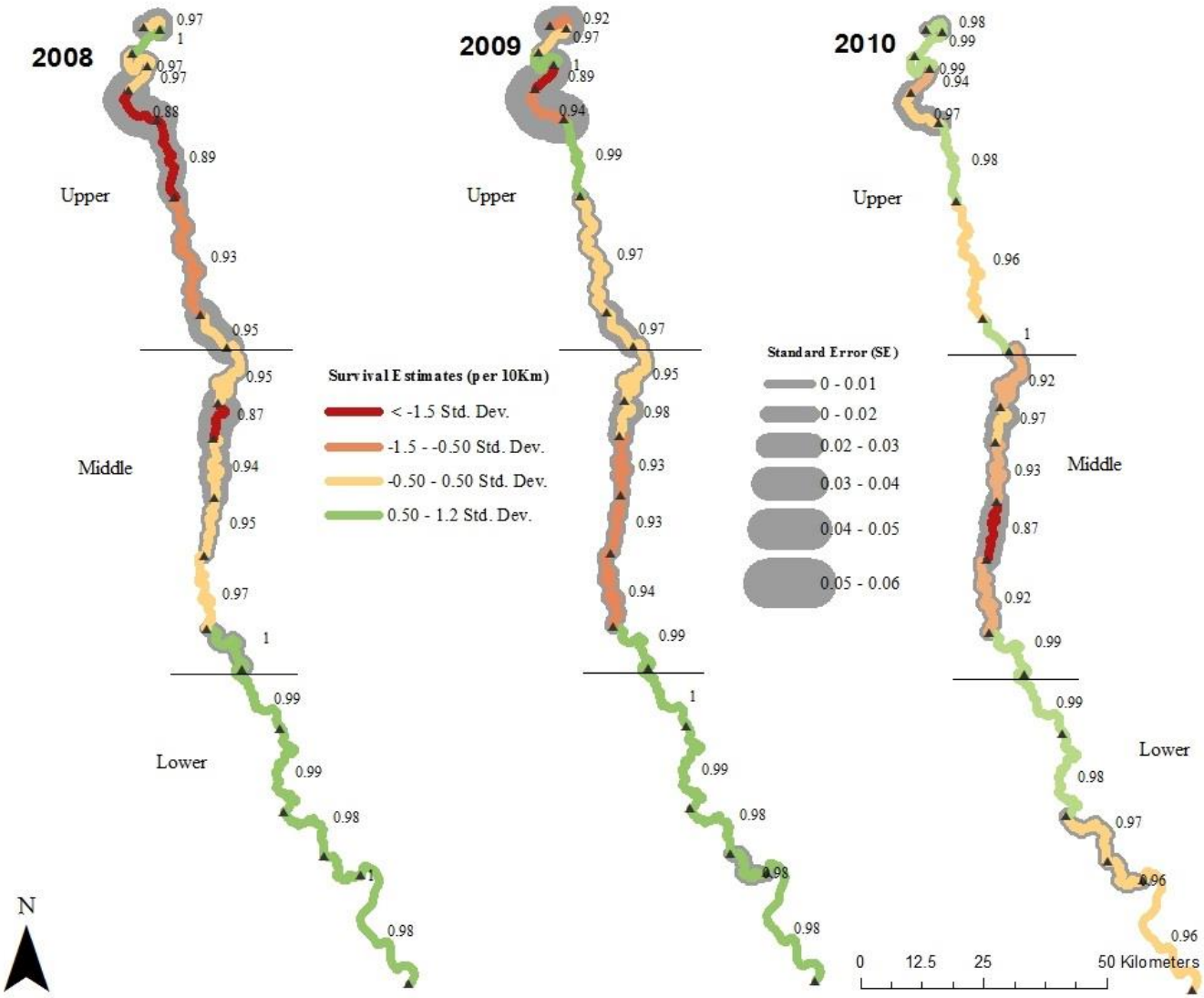

Figure 4: The following map depicts reach-specific survival estimates (per 10km) for each of our study years colored to represent per reach survival risk. Standard error is represented in this map as the grey buffer surrounding each reach. The values adjacent to each reach represent the survival estimate for a given reach (per 10 km) from our full survival model. Note that the spatial distribution of mortality zones (those areas with lower estimated survival compared to mean survival for that year) varied between reaches and years, with mortality zones occurring in the upper and middle reaches of the river. In 2010, the reach with the greatest amount of mortality (near Butte) was greater than 2 standard deviations from the mean survival of that year.

Temporal- covariates survival models

The second model set, which included reach but did not include year as a factor, did not have as much support in the data as our full model (AICc of 16239.88 compared to AICc of ~16161.47). However, we were still interested in the outcome of the temporal-covariates survival models because unlike the full model, these results allow us to investigate mechanistic hypotheses regarding the influence of the individual, habitat and environmental covariates on smolt survival. Within the temporal-covariates model set, the top model, based on ΔAIC scores, included flow, reach, fish condition, swim speed and batch release, indicating these factors were most correlated with survival (Table 4). Ten models had a ΔAIC value of four or less, when compared to the top model, indicating that all of these models had similar levels of support to the top model. Using the most parsimonious model φ (~reach + condition + flow + speed + batch release) ρ(~reach * release year), we were then able to generate β parameter estimates. Because covariate values were standardized prior to fitting, their coefficient values (β estimates) provide an indication of the relative importance of a given covariate compared to others. Standardized β coefficients can be interpreted as the estimated change in survival predicted from one standard deviation increase in the covariate value. Flow (0.53), hatchery release (0.33), fish condition (0.08) and swim speed (0.05) had an impact on smolt survival (Table 5). Flow had the greatest β estimate value, indicating that this factor had the strongest correlation with outmigration success of juvenile late-fall run yearlings. Hatchery release, specifically whether or not an individual tagged smolt was released concurrently with other hatchery fish, had the second strongest correlation with survival, followed by fish condition and swim speed. Plotting the covariates of flow and condition as a function of estimated survival (figures 5 and 6) revealed the strength of the relationships between survival and both flow and fish condition.

Spatial- temporal- covariates survival models

The final model set, which removed reach and year as covariates, did not fit the data as well as our previous model sets (AICc ~16355.62 for the spatial-temporal-covariates top model compared to a AICc of ~16239.88 for the temporal-covariates models and AICc of ~16161.47 for the full model). However, just as in our temporal-covariates model exercise; we were specifically interested in the comparative contribution of the individual, habitat and environmental covariates contained within our models to smolt outmigration survival. Including reach in the previous section allowed us to capture some of the spatial variability in survival that we were unable to explain with our habitat covariates. Modeling survival without a reach factor allowed us to explore the relationship between smolt survival spatial dynamics and spatial environmental covariates that would be otherwise explained by the reach factor. While it was beyond the scope of this study to directly test mechanistic relationships, the output of these statistical models reveals consistencies with mechanistic explanations.

The covariates of flow, hatchery release, fish condition and swim speed appeared consistently in the most parsimonious models (with ΔAICc<4). In addition to these covariates, which were also important in our temporal-covariates model set, reach length, diversion density, area of off-channel habitat and sinuosity further improved the models. The existence of multiple models with similar ΔAICc<4 indicated that several of these models support the data similarly well, and did not necessarily support the selection of only one top model. Conversely, shaded riverine aquatic cover (SRA) and temperature did not appear as consistently in those models best explaining the observed variation in smolt survival. Standardized β coefficients for the covariates occurring most frequently in our top models (φ (reach length+ sinuosity+ diversions+ off channel+ condition + flow + speed + batch release) ρ(~reach * release year)) revealed reach length to be the most important determinant of survival dynamics in this modeling exercise, with survival decreasing as reach length increased (Table 7). Flow was once again the most important environmental covariate in predicting outmigration success, with increased levels of flow correlating with increasing smolt survival. Sinuosity had a negative relationship to survival.

While there was a positive relationship between diversion structures and survival, with the higher density of diversions corresponding to increased survival estimates. Finally, we compared delta AIC values for models with and without the most explanatory covariates to give a sense for how important specific covariates, especially flow, is relative to these unexplained reach-specific differences in survival (figure 7).

Model comparison

We compared the results between the temporal covariate model and the spatial-temporal covariate model in order to visualize regions where our spatial-temporal-covariates model either over or under estimated survival when compared to the temporal-covariates models (figure 8). We assume that the better fitting temporal-covariates model (based on ΔAIC values**)** is the more accurate representation of the survival process. Thus, the comparison between these models provides some indication of where additional processes, beyond the covariates included in the spatial-temporal covariate model, had a significant impact on survival. Negative index values imply that the spatial-temporal-covariates model is over-estimating survival and additional mortality processes are occurring. We primarily observed these survival overestimates in the lower reaches of the river. Specifically in the reach between Butte and Colusa and the reach between Knights landing and the confluence with the Feather River.

Table 4: Model output for temporal-covariates CJS models. Note that a model that is more than 4 AIC points lower than another is generally considered to be substatially more supported than the latter (Burnham and Anderson 2002). If **Δ**AIC is less than 4, support of one model over another is equivocal . Lower AIC scores indicate greater relative model parsimony.

Model	**num # cov**	**AICc**	ΔAIC	**Weight**
φ (~reach + condition + flow + speed + batch release) ρ(~reach * release year)	4	16234.38	0	0.1622064
φ (~reach + condition + flow + temp + speed+ batch release) ρ(~reach * release year)	5	16235.66	1.28	0.08553018
φ (~reach + sinuosity+ condition + flow + speed + batch release) ρ(~reach * release year)	5	16236.36	1.98	0.0602721
φ (~reach + diversion+ condition + flow+ temp+ batch release) ρ(~reach * release year)	5	16236.38	2	0.05967238
φ (~reach + diversion+ off channel + condition+ flow + batch release) ρ(~reach * release year)	5	16236.38	2	0.05967238
φ (~reach + sinuosity+ diversion+ condition + flow + batch release) ρ(~reach * release year)	5	16236.38	2	0.05967238
φ (~reach + sinuosity+ condition + flow + temp+ speed+ batch release) ρ(~reach * release year)	6	16236.7	2.32	0.05084945
φ (~reach + sra+ condition+ flow + temp+ speed+ batch release) ρ(~reach * release year)	6	16236.7	2.32	0.05084945
φ (~reach + sra+ condition+ flow + temp+ batch release) ρ(~reach * release year)	5	16237.32	2.94	0.03729538
φ (~reach + diversion+ sra+ condition+ flow + speed+ batch release) ρ(~reach * release year)	6	16237.68	3.3	0.03115172

Table 5: β coefficient estimates for those covariates occurring in the top model from our temporal-covariates model set. These standardized β values indicate relative importance as well as the direction of that relationship to survival. Flow, with a positive β value of 0.532 was the most correlated value to smolt outmigration survival.

Covariate and β coefficient
Flow (0.532)
Hatchery release (0.333)
Fish condition (0.084)
Swim speed (0.047)

Table 6: Model output for spatial-temporal-covariates CJS model. These 7 models have similar levels of support to the top model (as indicated by **Δ**AIC values). The most common covariates included in these top models were flow, hatchery relesae, fish condition, swim speed (as in our temporal-covariates output), as well as the habitat variables: diversion density, off channel habitat area and sinuosity).

Model	**npar**	**AICc**	ΔAIC	**weight**
φ (reachL+ sinuosity+ sra+ diversions+ off channel+ condition + flow + speed + batch release) ρ(~reach * release year)	123	16350.62	0	0.19938523
φ (reachL+ sinuosity+ diversions+ off channel+ condition + flow + speed + batch release) ρ(~reach * release year)	122	16350.86	0.24	0.17683884
φ (reachL+ sinuosity+ sra+ diversions+ off channel+ condition + flow + temp+ speed + batch release) ρ(~reach * release year)	124	16352.52	1.9	0.07711045
φ (reachL+ diversions+ off channel+ condition + flow + speed + batch release) ρ(~reach * release year)	120	16353	2.38	0.06065723
φ (reachL+ sinuosity+ diversions+ off channel+ condition + flow + speed + batch release) ρ(~reach * release year)	121	16353.16	2.54	0.05599368
φ (reachL+ sinuosity+ diversions+ off channel+ flow + speed + batch release) ρ(~reach * release year)	121	16353.94	3.32	0.0379109
φ (reachL+ sinuosity+ diversions+ off channel+ condition+ flow + temp+ speed + batch release) ρ(~reach * release year)	123	16354.02	3.4	0.0364244

Covariate and β coefficient
Reach length (-0.566)
Flow (0.482)
Hatchery release (0.3928)
Diversion density (0.3245)
Off-channel habitat (0.1306)
Swim speed (0.0999)
Sinuosity (-0.0974)
Fish Condition (0.0721)

Table 7: Spatial-temporal-covariates model β estimates for those covariates occurring in the most parsimonious models. β values are standardized, thus allowing for comparison of relative influence on outmigration survival. Reach length had the strongest, negative correlation to outmigration survival, while flow had a positive relationship to survival (with more flow corresponding to greater survival estimates).

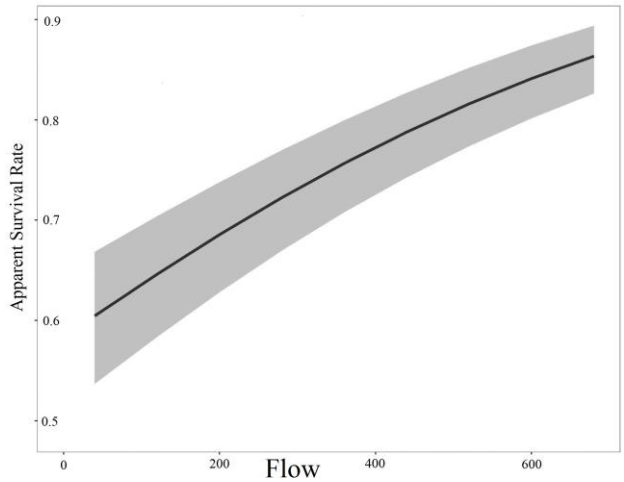

Figure 5: A plot depicting simulated survival as a function of flow (cubic meters per second) in the Sacramento River. As flow increases, apparent survival increases. Dark line indicates survival estimate, and grey area represents 95% confidence intervals.

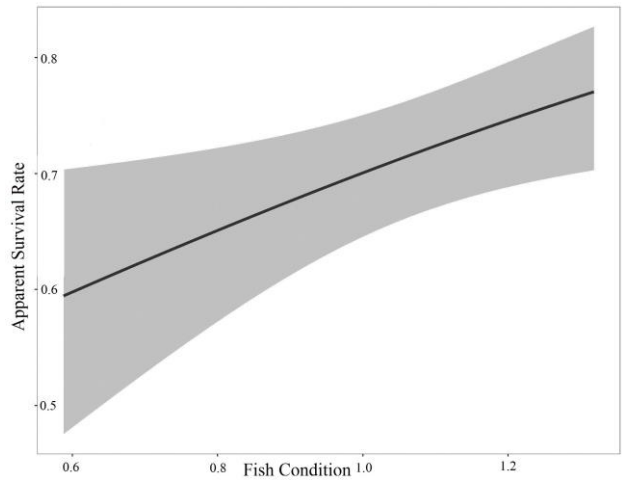

Figure 6: A plot depicting simulated survival as a function of fish condition (Fulton's K). As fish condition (an indication of fish health, calculated as a length to weight ratio) increases, so does apparent survival. Dark line indicates survival estimate, and grey area represents 95% confidence intervals.

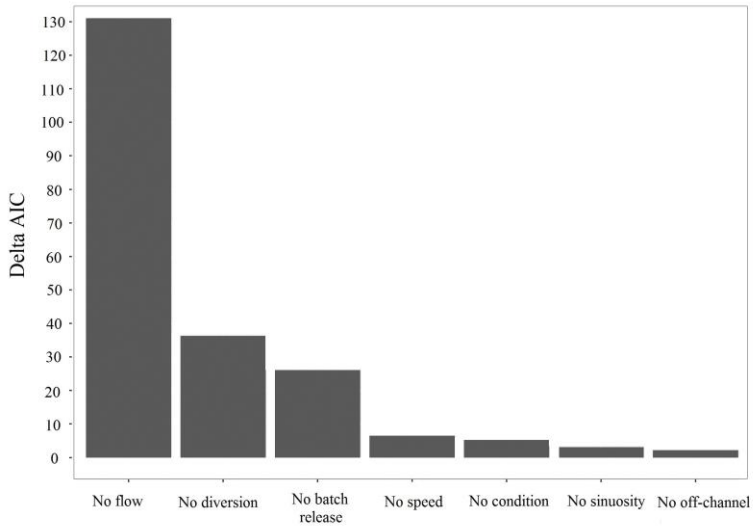

Figure 7: A plot comparing ΔAIC values for the models where only a single variable is removed. This plot demonstrates the comparative importance of flow as a correlate to apparent survival compared to the other covariates in our models.

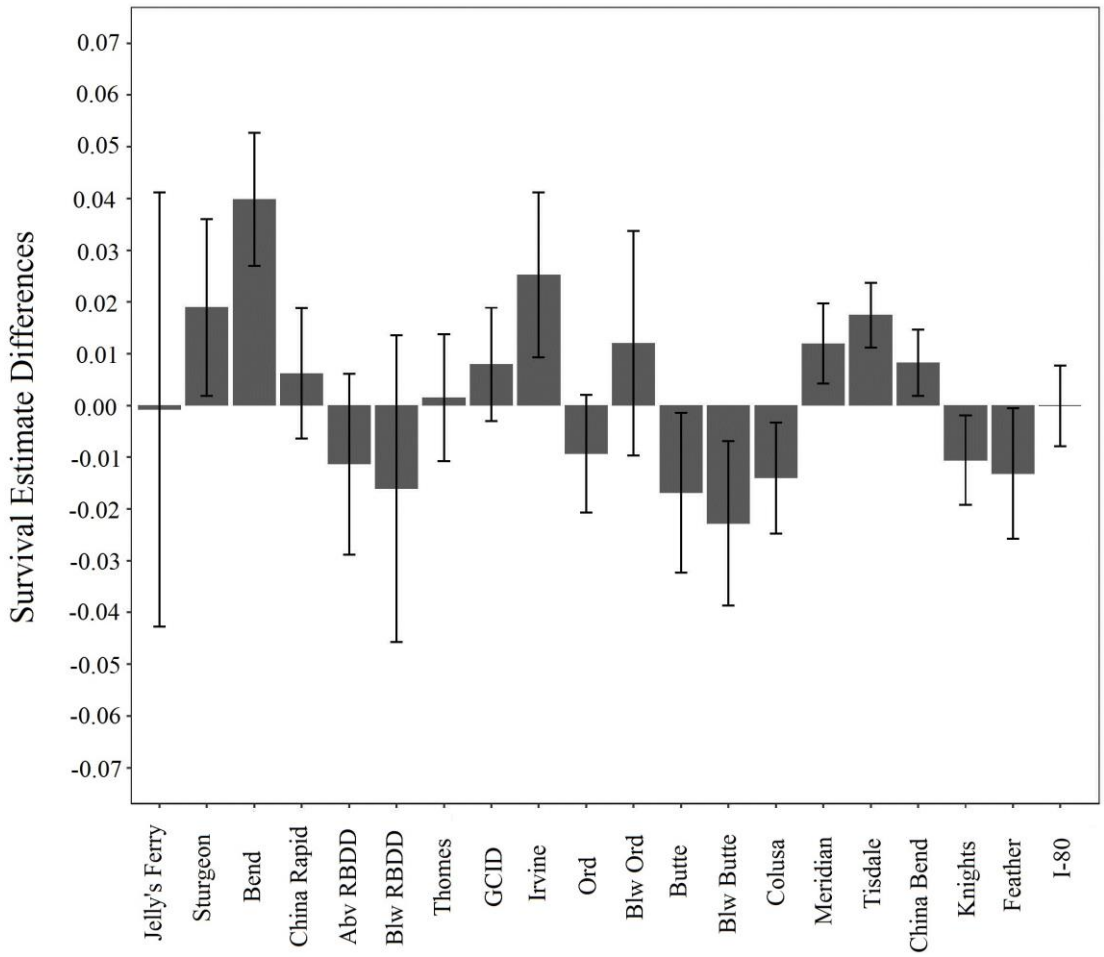

Figure 8: A plot of the differences in standardized survival estimates for the spatial-temporal-covariates model and the temporal-covariates model. We used the delta method to estimate the variance for these differences. Negative values indicate reaches where our spatial-temporal-covariates model underestimated survival. There is a slight spatial trend in the data whereby reaches in close proximity tend to be either over or under estimated with similar magnitude. This suggests that there may be some spatial correlations in mortality operating at a scale slightly larger than the reaches used in our analysis.

Fish summary

Of the 1,536 fish that entered the Sacramento River (this removed those fish released at Battle Creek that were never detected within our study area), only ~584 fish were detected at the end of our study area or beyond. Of those 584 fish that were detected at or below the southern edge of our study area, mean annual fish condition closely mirrored those values from the tagged fish population within a given year (table 8).

Finally, the majority of outmigration movement occurred at night, with most smolts leaving and arriving at night (see figure 9). We determined outmigration timing by grouping the times that fish were detected at receivers for the first and last time, and assumed that these detections were indicative of fish moving downstream. If we standardize detections by the number of hours per time of day however, and compare the number of detections per hour, night

still has the greatest percentage of departures, but the effect is muted, and the largest percentage of arrivals occur at dawn (46.7%) and dusk (38.9%) (table 9).

Release Year	# Tagged fish	# detected survivors	Mean fish condition (survivors)	Mean fish condition- all
2007	130	18	1.024 (SE±0.012)	1.033 (SE±0.004)
2008	304	126	1.072 (SE±0.005)	1.072 (SE± 0.003)
2009	300	129	1.098 (SE±0.006)	1.093 (SE± 0.004)
2010	408	130	1.085 (SE±0.007)	1.088 (SE± 0.003)
2011	394	181	1.081 (SE±0.004)	1.080 (SE± 0.003)

Table 8: The total number of fish tagged and released into our study area (Jelly's Ferry to the I-80 bridge in Sacramento) and the number that were detected at the end of our study area or beyond. Mean fish condition for those fish that survived through our study area is contrasted to the mean condition for all tagged fish.

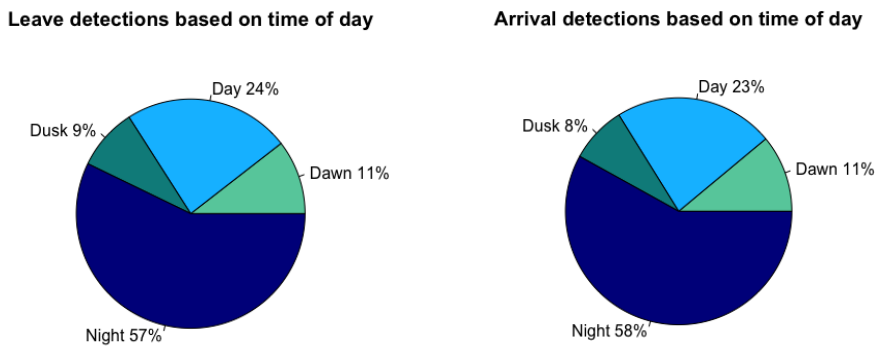

Figure 9: Out of a total of 8,967 detections for leave time and 8,860 detections for arrival time, these pie charts represent the percent of detections occurring at these specific times of day. Day represents 9am-5pm, dusk (5pm-9pm), night (9pm- 5am) and dawn (5am- 9am), both pie charts show the majority of arrival and leave times occur at night, indicating that fish out-migrate at night.

Table 9: When we standardize the number of detections by the number of hours within that time of day, night still has the greatest proportion of leave detections, but not by as great of a margin as Figure 9, and the greatest percent of arrivals occur at dawn.

Time of day	Percent of detections (per hour/time of day) **leaving**	Percent of detections (per hour/time of day) **arriving**
Dawn	29.7	46.7
Day	13.3	4.19
Dusk	24.7	38.9
Night	32.3	10.2

DISCUSSION

Conservation of beleaguered salmonid populations is currently hindered by a disparity of scale- with research commonly occurring in distinct time frames and locations, and management acting on broader scales of human disturbance (Fausch et al. 2002). In our study, we bridge this gap by examining mortality factors associated with low survival at multiple spatial scales. Examining the landscape of mortality revealed zones of elevated mortality that occurred in different locations in different years. While we could not include all possible sources of mortality in our analysis, we ascertain that even when reach-specific habitat features and individual covariates are included, flow remains the single most influential factor for determining survival of late-fall run salmon smolts.

Spatial heterogeneity of survival

Our results indicate that mortality during outmigration is spatially heterogeneous; with certain reaches exhibiting elevated levels of mortality. The severity of mortality in each reach varied between years, and is likely a result of the dynamic nature of the Sacramento system. However, our reach designations (mortality zones) were composed of large swaths of river, and it is difficult to draw conclusions about what features, specific to a given reach, may contribute to smolt mortality from survival estimates alone. Further, because survival estimates were standardized by reach length, it is possible that the larger length reaches included mortality hotspots, but the effect of these were attenuated by areas of higher survival within the same reach. Overall, we can conclude from our reach-specific survival estimates that mortality zones occurred most frequently in the upper and middle regions of the Sacramento River, while survival increased through the lower reaches, specifically below Colusa to the I-80 Bridge. One possible explanation for this is that in the upper regions, sick or weak fish which survived in hatchery conditions were picked off soon after release and only the strongest fish survived to the later reaches, at which point they had higher chances of survival. The observation that fish condition was positively correlated with survival suggests that this kind of effect is possible. Overall we can conclude that mortality risk is not evenly distributed across the outmigration corridor, and some zones may pose a greater risk to out-migrating smolts. Future work would benefit from exploring mortality zones at a finer spatial resolution, as well as investigating potential mechanisms responsible for observed decreases in survival within these zones, especially the upper regions, through time.

Environmental covariates

Based on model selection criteria, the full model had the greatest level of support, but did little to elucidate the role of environmental and individual covariates in survival. As our main priority in this study was to compare the relative role of individual, habitat and environmental covariates on outmigration success, it was imperative to examine model results without the all-encompassing factors of reach and year. Both model sets revealed flow, hatchery release strategy, fish condition and swim speed to be important factors influencing survival. Flow exerted the greatest overall effect on outmigration success, with increased flow correlated to increased smolt survival. Flow has been significantly reduced and homogenized in the Sacramento River system from historic levels (Buer et al. 1989). Flow determines the amount of habitat available for juvenile salmon (USFWS 2005), and in some cases, may be an important outmigration timing cue (Young et al. 2011). Flow has repeatedly been the most important factor affecting overall survival of Chinook salmon in the Central Valley (Kjelson and Brandes 1989, Zeug et al. 2014, Michel et al. 2015), likely as a result of concurrent temperature, velocity and turbidity conditions that influence the ability of smolts to evade predation while staying within their physiological tolerances. Further, because we included both flow and swim speed as covariates in our models,

we were able to separate the effect of flow from swim speed, suggesting that there are features inherent to flow itself, not just its effect on travel time, that correlate to survival. Finally, while we did not include turbidity as a factor in this analysis due to the current paucity of data, it is also hypothesized that higher flows increase turbidity, which in turn decreases smolt susceptibility to predation (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. Future research would benefit from controlled-release studies concomitant to tagged-release investigations in the Central Valley, in order to establish possible threshold values.

Individual covariates

Our results indicate that the batch release of smolts is correlated to increased smolt outmigration survival. One rationale for why this release strategy may improve overall survival is the theory of "predator swamping;" whereby predators, inundated by prey, pose less of an individual threat for smolts. This effect has already been demonstrated for Chinook salmon in the Yakima River (Fritts and Pearsons 2008) and juvenile sockeye salmon in British Columbia (Furey et al. 2016). Furey et al. (2016) posit that outmigration timing, whereby smolts hold during the day and travel by night, may have evolved as a strategy to encourage predator swamping. One thing we were not able to account for is whether this effect persists for the whole riverine system, or is just observed within the initial reaches.

Another individual covariate that correlated strongly to improved survival rates for out-migrating smolts was fish condition. Calculated as Fulton's k factor, which describes the relationship of weight to length for an individual fish, fish condition can be used to infer overall health of an individual fish. According to Davidsen et al. (2009), survival of post-smolt Atlantic salmon was dependent on fish size (fork length), and in the San Joaquin Basin, downstream survival during outmigration was influenced by size (and life stage) (Sturrock et al. 2015). The yearlings utilized in our study were large (only those smolts 140mm or larger were tagged due to concerns of tag burden), and may only represent the upper limit in size frequencies within natural populations. Fish condition may be of even greater importance for naturally occurring populations of Chinook salmon, who exhibit a wide range of sizes during out-migration, and could be subject to size selective mortality. There are many unknowns regarding the size and timing of outmigration of naturally occurring Chinook salmon populations in the Central Valley, and future studies should focus on the comparative outmigration success of different life-history strategies under different environmental conditions.

Predicted swim speeds were an important factor describing out-migrant survival data, with increasing swim speeds correlating to increased survival. For out-migrating yearling smolts, it is likely that swim-speed in the context of our study is a proxy for duration of exposure to mortality factors. In the Columbia River system, yearling smolt outmigration rates were not correlated with river discharge, temperature, release date or fish size (Giorgi et al. 1997), indicating that yearlings are not passive particles during outmigration, and can control their speed through the system. However, Michel et al. (2013) found that Sacramento River smolt migration rates were related to river width to depth ratio, flow, turbidity and water velocity, so the degree to which environmental factors influence the amount of time spent traversing the outmigration corridor warrants further research, especially if the duration of exposure to mortality factors during outmigration is important in overall survival during this phase. Finally, the swim speed of out-migrants may vary based on whether fish are hatchery or natural origin, at least according to Friesen et al. (2007), who found a significant difference in the outmigration rate between hatchery and natural Chinook salmon in the Willamette River. Thus, natural populations may be traveling slower and in turn exposed to a greater mortality risk based on increased duration of exposure. While the full model revealed the spatial heterogeneity of survival, and the temporal-covariates model elucidated the environmental and individual covariates most associated with mortality, it is

the outcome of the spatial-temporal-covariates model that allows us to examine a relative comparison of which habitat features are influencing these observed patterns of survival.

Physical habitat features

As revealed by the trend in the location of mortality zones, there is a general trend of relatively higher survival in the lower reaches of the Sacramento mainstem compared to the upper and middle reaches. Model selection results revealed reach length, diversion density, off-channel habitat and sinuosity to be correlated with survival. Sinuosity may have occurred in our model results as a result of its negative association with the channelized, riprapped reaches characteristic of the lower reaches. Thus, when we consider the role of finer-scale habitat features in shaping survival success, it is in the context of this larger trend of better survival towards the more modified lower reaches. It is important to note that while late-fall run yearlings tend to have lower survival in general in the upper reaches of our study area, we do not mean to imply that these habitats are not of critical importance to other life-stages and runs of Chinook salmon. Studies have shown that Chinook salmon fry, for example, have higher survival in the upper Sacramento River (Brandes and McLain 2001), suggesting that this area may provide critical habitat to other runs and life-stages. The lower reaches are highly channelized, with little available habitat. Diversions are more prevalent in this area due to greater agricultural land use, and were highly correlated to other habitat variables typical of agricultural zones; namely depth, riprapped banks and agricultural and developed land use. Because we did not wish to obfuscate the results of our analysis, we withdrew these factors from our modeling efforts because of their colliniarity, but the role of "diversions" on survival could be equally viewed as the role of depth, agriculture and developed land and riprap as well.

Diversions in our study are considered only for their structural value, as water pumping is presumed to be at a minimum during the winter outmigration periods of our study (fish released in Dec-Jan 2007-2011), thus limiting entrainment risk. The inclusion of diversions in our study was mainly to test the hypothesis that diversion structures, often large, prominent features of the riverscape, were increasing mortality risk through associated predation assemblages (Sabal et al. 2016). However, the positive association of diversions to smolt survival may be a result of a size refuge in which the late-fall run yearlings used in our study evaded predation, due to their larger size. Additionally, it is possible that these structures were not concentrating predators, which target late-fall run smolts. If late-fall yearlings in our study were exempt from predation pressure at these features, it is possible that due to the lack of natural habitat in the vicinity, diversion structures provided the only available cover for holding. Friesen et al. (2007) noted that yearling smolts in the Willamette River appeared to have an affinity for pilings during outmigration, so it is not unreasonable to assume out-migrants may utilize whatever cover is available in the absence of natural habitat. Conversely, it is possible that the lack of available shallow, natural habitat in the lower reaches of the Sacramento River reduced the available predator-aggregating habitat and thus decreases overall predation.

Off-channel habitat area was the final covariate correlated to survival. Our estimate of "off-channel" habitat comes with many limitations, as it was digitized from a static DWR vegetation and land use layer and only contained permanently wetted areas within 50 meters of the mainstem; in turn omitting those ephemerally inundated areas that have been demonstrated to be important habitat for juvenile salmonids, such as floodplain (Sommer et al. 2001, Limm and Marchetti 2003, Jeffres et al. 2008, Limm and Marchetti 2009). Given the rapidity with which smolts transited our study area, it is unlikely that the availability of off-channel habitat areas dramatically improved survival. However, if smolts were indeed transiting the system via a pattern of holding during the day and moving at night (Chapman et al. 2013), it is possible that small features of off-channel area may be providing a break from the prevailing currents or enhanced feeding opportunities while holding.

The importance of side-channel habitat for juvenile salmonids has been highlighted in other locations (Decker 2002, Morley et al. 2005), and Johnson et al. (2015) note that yearling Chinook salmon utilize off-channel areas in the Colombia River, prompting the author to suggest that management efforts should prioritize the restoration of shallow off-channel areas. Blackwell et al. (1999) suggest that it is the quantity more than the quality of these habitats that will influence the number of out-migrants. At the same time, yearling Chinook salmon have been documented distributed evenly across the river channel compared to sub-yearling fish, which tend to associate closely with shoreline habitat (Friesen et al 2007 and Dauble et al 1989), so in general it is unclear how yearling smolts utilize the 2 dimensional structure of the river and whether the availability of off-channel habitat would affect survival. While habitat does not account for considerable variability in the survival of late-fall run hatchery fish, smaller juveniles may rely more on these habitat features than the large late-fall run smolts used in our study. Thus, while habitat does not account for considerable variability in the survival of the late-fall run in this study, it likely constitutes essential habitat for natural populations and other salmon life-stages.

Modeling limitations

Models are only approximations of what is actually occurring *in situ*, and there are "no true models in life (Anderson 2008)." For a complex ecosystem such as the Sacramento River mainstem, there are many limitations to the conclusions we can draw regarding the interaction of out-migrating smolts and their environment, and there is always a risk of spurious results when including numerous factors. However, each of the covariates we included were chosen *a priori* and accompanied with a hypothesized biological mechanism, although mechanisms were not directly tested in this study. While we utilized a broad range of factors, there were some very important variables for which we did not have adequate data to include in our analysis. These factors are nonetheless likely indispensable for explaining survival variability. Among others, the three factors that likely would have improved our explanatory power are: turbidity, predator densities/ predation rates and the availability of large woody debris. Turbidity can affect predator avoidance behavior of Chinook salmon (Gregory 1993), and decrease predator foraging efficiency (Sweka and Hartman 2003). Predators have been identified as a major cause of mortality for out-migrating salmonids in other systems such as the Columbia River (Schreck et al. 2006) and Beamesderfer et al. (1996) estimated that Northern pikeminnow alone consume up to 8% of migrants in the Colombia and Snake River system. In the Central Valley, the density of predators can affect the survival of acoustically tagged Chinook salmon smolts (but is also related to flow) (Cavallo et al. 2013). In a study in the Stanislaus River, an estimated 70% of tagged smolts were eaten by predators (Demko et al. 1998). Predation hotspots have been documented within the delta (Grossman et al. 2013), and it is possible that some of the heterogeneity of survival is caused by the accumulation of high predator densities in certain regions. Currently, little information exists regarding the spatial heterogeneity of predator abundance and future outmigration studies should concurrently sample predator densities and predator affects on outmigration success. If predators do play an important role in smolt outmigration survival, as is suggested by the existing literature, we must also consider that all correlations between environmental variables and smolt survival could also be occurring through the pathway of those variables influence on predator movements and densities, and ultimately the probability of smolt/predator encounters. Finally, large woody debris is routinely shown to provide vital habitat for juvenile salmon, yet available data mapping the abundance and distribution of large woody debris in the Sacramento River is currently unavailable. While SRA was used as an approximation for in-water cover in our study, it was not directly measured in the field, and likely does not serve as an appropriate proxy for large woody debris specifically. Juvenile Chinook salmon utilize areas of submerged terrestrial vegetation and woody debris, as well as undercut banks, for protection during high-flow events and as cover from predators (Jackson 1992,

Hampton 1998). Additionally, large woody debris, which has declined significantly as a result of logging and removal to prevent flooding, is important for creating pools, and providing substrate for invertebrate production (Williams 2006). The inclusion of these factors of known importance to juvenile salmon could improve our model fit to survival data, as well as better explain biological mechanisms causing mortality during outmigration.

The residuals from our model comparison plot give us an idea of what the spatial-temporal-covariates model was either over or under estimating. A negative index value implies that the spatial-temporal-covariates models are over-estimating survival. The potential spatial trend in our reaches, whereby adjacent reaches similarly over or under estimate survival, suggests that there may additionally spatial correlations in mortality operating on a slightly larger spatial scale than the reaches delimited in our analysis. The over and under estimations of survival suggest there is another source of mortality in these reaches that we have not accounted for with the covariates we included in this study. This appears to happen more downstream, in the stretch from Ord to Colusa and from China Bend to the Feather River. Thus, while our models allow inferences regarding the relative importance of the environmental covariates we included, as recounted above, we are still missing additional covariates that would explain a greater amount of the variability in survival.

Finally, any discussion regarding the survival of out-migrating Chinook salmon smolts in the Central Valley would be remiss without the context that irrevocable transformations- wrought by hydraulic mining, channelization and the construction of the state and federal water projects- fundamentally altered the natural functioning of the Central Valley ecosystem. Our results, while important for understanding the current habitat realities and requirements of Chinook salmon smolts, should be viewed within the context of severe reductions of historic flow, the elimination of access to spawning grounds and the removal of vast expanses of rearing habitat. Further, our study utilized hatchery-origin Chinook salmon, which may differ from natural-origin smolts in their behavior and vulnerabilities.

Conclusion:

Flow, smolt condition, swim speed and release strategy had the strongest correlation to survival of out-migrating, hatchery origin, late-fall run Chinook during the 2007-2011 water years. The riverine portion of the outmigration corridor receives less attention than the lower delta, and estuary regions. However, for years with high flow, gains in in-river survival can lead to a three-fold 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. Reductions of bank erosion, channelization of river banks and massive reductions of flow resulting from land use changes (Buer et al. 1984) portend an uncertain future for Chinook salmon in the Central Valley. Here, we emphasize the importance of flow for outmigration survival of late-fall run, hatchery origin smolts in the Sacramento River. Individual covariates, specifically batch releases, fish condition and swim speed may additionally improve outmigration success. Certain habitat features, specifically off-channel areas, diversion structures and sinuosity were associated with survival, although to a lesser extent than flow and individual covariates. Although our study utilized hatchery fish, which have limitations as wild fish surrogates, and while the mechanisms through which environmental features affect the ability of Chinook salmon to rear and out-migrate successfully are largely unknown, we emphasize the importance of examining mortality factors on multiple spatial scales and in a holistic context. An individual fish experiences outmigration at a very fine scale, but both reach-specific habitat variables, and those spatio-temporal factors affecting survival on the large basin-scale, are each important considerations in maintaining Chinook salmon populations in the Central Valley.

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