

Fish predation on a landscape scale

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Abstract. Predator–prey dynamics can have landscape-level impacts on ecosystems, and yet, spatial patterns and environmental predictors of predator–prey dynamics are often investigated at discrete locations, limiting our understanding of the broader impacts. At these broader scales, landscapes often contain multiple complex and heterogeneous habitats, requiring a spatially representative sampling design. This challenge is especially pronounced in California’s Sacramento–San Joaquin River Delta, where managers require information on the landscape-scale impacts of non-native fish predators on multiple imperiled native prey fish populations. We quantified relative predation risk in the southern half of the Delta (South Delta) in 2017 using floating baited tethers that record the exact time and location of predation events. We selected 20 study sites using a generalized random tessellation stratified survey design, which allowed us to infer relationships between key environmental covariates and predation across a broader spatial scale than previous studies. Covariates included distance-to-nearest predators, water temperature, turbidity, depth, bottom slope, bottom roughness, water velocity, and distance-to-nearest riverbank and nearest aquatic vegetation bed. Model selection determined the covariates that best predicted relative predation risk: water temperature, time of day, mean predator distance, and river bottom roughness. Using this model, we estimated predation risk for the South Delta landscape at a 1-day and 1-km resolution. This effort identified hot spots of predation risk and allowed us to generate predicted survival for migrating fish transiting the South Delta. This methodology can be applied to other systems to evaluate spatio-temporal dynamics in predation risk, and their biotic and abiotic predictors.

Key words: landscape ecology; non-native species; predator–prey; research design; salmon; trophic interaction.

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INTRODUCTION

Ecological processes are difficult to effectively measure and predict on landscape scales. Evaluating multi-species ecological processes (e.g., predator–prey interactions) across a landscape is particularly challenging because species react uniquely as conditions progressively change. It is nonetheless critical to do so; ecological processes can have drastic population-level and ecosystem-

level impacts, and understanding these at a biologically relevant scale is crucial to avoid overlooking important trends and relationships (Levin 1992). The challenge is therefore to collect information on ecological processes at a logistically feasible observational scale that can be appropriately generalized to the larger process scale.

Predation has been shown to have not only significant impacts on prey populations, but also

impacts that can ripple throughout an ecosystem or nearby ecosystems (Estes and Palmisano 1974, Power 1990, Fortin et al. 2005). One well-studied example is the cross-ecosystem transfer of nutrients mediated through predation on salmon (Hilderbrand et al. 1999, Merz and Moyle 2006). Understanding the spatial and temporal dynamics in predation, as well as the biotic and abiotic drivers of these, is essential for managing predator and prey populations. This information is particularly valuable in managed ecosystems where humans can control conditions in order to influence predation dynamics. However, observing predation events in situ is often nearly impossible and, as a result, is often measured in laboratory settings. Predation events that are observed in situ are generally at extremely small spatial or temporal scales (e.g., Neuswanger et al. 2014), making landscape-scale predictions challenging (Hunsicker et al. 2011).

This challenge is especially pertinent in California's Sacramento–San Joaquin River Delta where non-native piscine predators are known to have substantial impacts on imperiled salmonid and other native fish populations, and yet, resource managers are lacking the landscape-scale predator–prey information they require to mitigate these impacts. Historically, the Delta was an important rearing area for some of the largest salmon runs in North America (Yoshiyama et al. 1998), but over the past century, all of these populations have declined drastically, with at least one population that is locally extinct and the remaining listed as endangered, threatened, or species of concern under the Endangered Species Act. Evidence from long-term tagging studies suggests that the survival of juvenile salmon during outmigration has a disproportionately large impact on juvenile-to-adult return ratios (Michel 2019). Furthermore, evidence from telemetry studies on juvenile salmonids suggests that low survival while transiting the Delta during outmigration may be one of the major contributors to the declines of these populations (Kjelson and Brandes 1989, Perry et al. 2010, Buchanan et al. 2013, Michel et al. 2015). While all of the mechanisms of this mortality are not known, studies indicate that predation by the large populations of non-native piscine predators present in the Delta is significant (Grossman et al. 2013, Grossman 2016). The Delta is part of

what is considered to be the most invaded estuary in the world (Cohen and Carlton 1998), and many of these invasions and introductions are predator fish species that are potentially negatively impacting native fish populations (Moyle and Williams 1990). Recent studies have used diet analyses to quantify the impact of non-native predators on salmonids migrating through the Delta (Sabal et al. 2016, Michel et al. 2018). However, these studies sampled few locations, making it difficult to extrapolate findings to a broader landscape scale.

While some studies have attempted to quantify the incidence of predators, prey, and piscivory on a landscape scale in the Delta (Nobriga and Feyrer 2007), no data exist on the environmental factors affecting predator–prey dynamics at this scale. Such data are critically needed to inform the numerous Delta-wide ecological models currently being developed and implemented for management purposes (Hendrix et al. 2014, CVPIA Science Integration Team 2019). A landscape-level approach to understanding predator–prey dynamics will allow for better predictions of the effectiveness and ecosystem-wide responses of management actions, including predator control, habitat alteration, and water management strategies. In addition, it is hypothesized that predation risk is spatially heterogeneous, resulting in key locations with relatively high predation risks compared to the surrounding area (Sabal et al. 2016). Such locations, referred to as predation hot spots (Grossman et al. 2013), are often identified anecdotally or as an ancillary product to a different project. However, a temporally and spatially explicit predation risk model may be able to objectively identify likely predation hot spots. Finally, predation risk estimates can also be compared to historical salmonid survival estimates to discern what proportion of mortality is due to predation.

Our goal of this project was to generate spatially and temporally robust estimates of relative predation risk for salmonids as a way to reveal plausible mechanisms for predation-related mortality. We measured the spatial and temporal dynamics using predation event recorders (PERs; Demetras et al. 2016), which are baited tethers that record the time and location of predation events, yielding relative (but not absolute) predation rates through space and time. We

concurrently collected habitat, water quality, and predator density data, and used model selection to identify the most plausible relationships between these variables and predation events. Using the most parsimonious model or suite of models, we then predicted fine-scale (1-km, daily) spatial and temporal patterns in predation risk during the 2017 juvenile salmonid outmigration season for the South Delta region. Using this model, we then objectively identified likely predation hot spots. Finally, we compile these fine-scale predictions to generate through-Delta cumulative survival estimates as experienced by migratory fishes transiting the Delta.

METHODS

Field site selection

The Sacramento–San Joaquin Delta is a complex and expansive body of water, with over 1100 km of waterways, making it difficult to comprehensively investigate the predator–prey relationships across the entire domain. Our study design allowed for sampling in such a way as to extrapolate to the larger region in an objective manner. We used generalized random tessellation stratified (GRTS) spatial sample selection (Stevens and Olson 2004) to identify study sites. This method is a spatially balanced random sampling technique that ensures that all regions of interest are adequately sampled.

Our study focused on the lower San Joaquin River and South Delta, a region of extremely low survival for outmigrating salmonids from the San Joaquin River drainage (Buchanan et al. 2013). This region is represented by low-gradient, tidally forced rivers and sloughs that are largely channelized and leveed. We delimited this area into 7 regions that share similar characteristics (Fig. 1). The San Joaquin River was split into an Upper (from Mossdale to Stockton), a Middle (from Stockton to Turner Cut), and a Lower (Turner Cut to Antioch) region. We delimited Old River (a major tributary channel of the South Delta) into an Upper (Head of Old River to State Water Project) and a Lower (State Water Project to confluence with the lower San Joaquin River) region. Middle River was not considered in our site selection protocol because few salmonids use this waterway (Buchanan et al. 2013). Franks Tract was delimited as a region; however,

the open water portions of this region were not sampled due to logistical constraints. Finally, we sampled in one additional region that consisted of areas found between San Joaquin River and Old River that are geographically distinct from these two: Mildred Island, Turner Cut and Columbia Cut. All regions are freshwater but experience tidal influence, and during most years, flow in the upstream direction is observed during flood tides.

The GRTS sample site selection method draws sites randomly while balancing between regions and assigns them a draw number. For pairs of sites that were less than three river kilometers (kilometers by way of the river) away from each other, we dropped one site and replaced it with a new site from an oversample list that maintained spatial balance. We selected 20 sample sites (Fig. 1), three of which were visited every week (repeat sites) and 17 of which were visited only once. The three repeat sites (Sites 1, 25, and 28) were included in order to assess overall temporal trends in predation across the six-week sampling season that should not be attributed to spatial patterns. The repeat sites were selected to be spatially balanced across the entire region of interest in order to best capture temporal trends throughout the South Delta. One sampling site was visited on each day, and sampling was conducted from 3 April through 13 May 2017 to overlap with the primary outmigration season of San Joaquin River salmonid populations (exact sampling dates are shown in Appendix S1: Table S1).

We note that 2017 was an extremely wet year in California, and this may have affected predator abundances, distribution, and behavior. The 2017 water year had the highest annual precipitation index for the Northern Sierras and the second highest index for the San Joaquin River Basin since 1964 (CDWR 2018). We describe the potential impacts of this anomalous water year on our results in Discussion.

Predation event recorders

We developed predation event recorders (PERs) to measure the relative predation rates on juvenile salmon swimming through our study reaches. PERs—described in detail in Demetras et al. (2016)—are drifting buoys with a live juvenile hatchery Chinook salmon *Oncorhynchus tshawytscha* tethered as bait (Fig. 2). The drifting

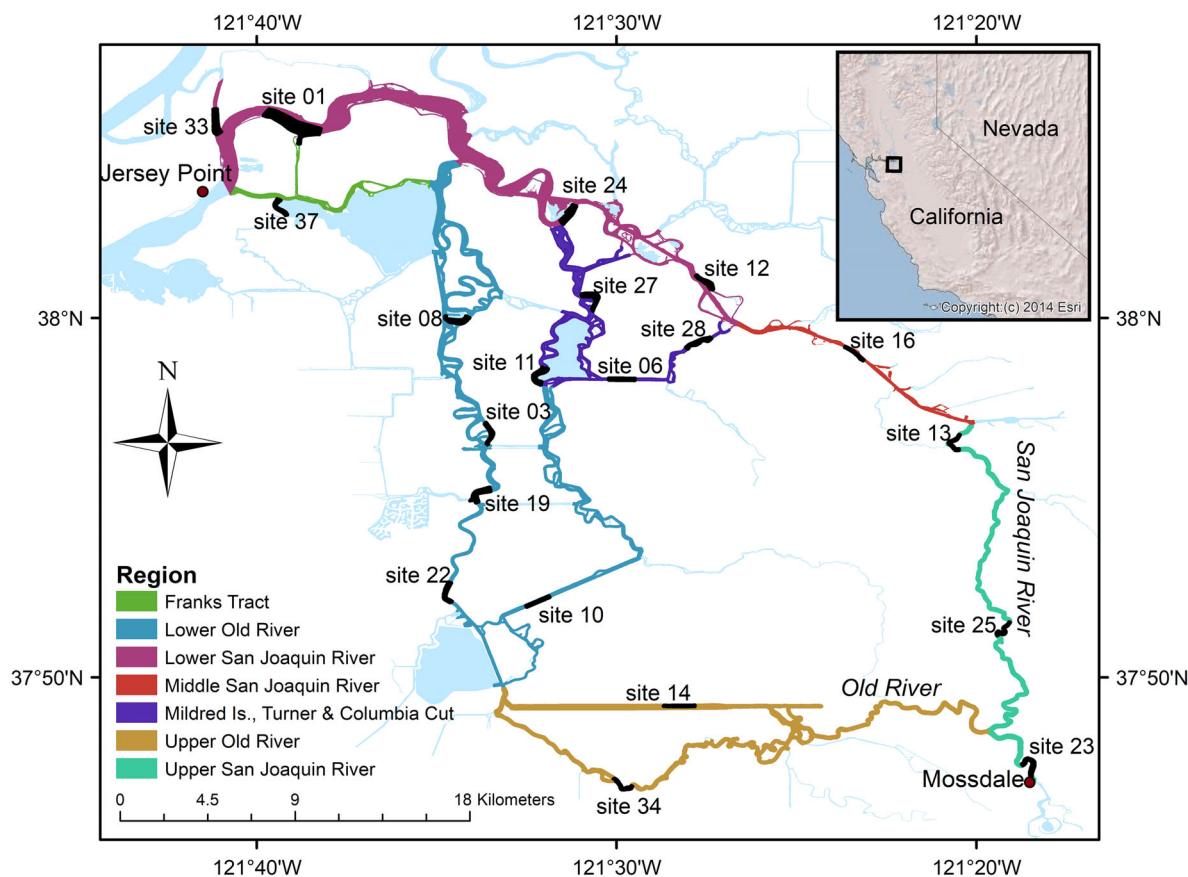


Fig. 1. A map of the regions selected for the GRTS site selection protocol, as well as the final sampling sites selected.

PERs were outfitted with a GPS tracker and predation-triggered timer that allowed us to determine the exact time and location of predation events. PERs were additionally outfitted with cameras in order to determine whether a triggered timer was due to predation or other circumstances, as well as ensure the salmon was alive and swimming for the duration of the PER deployment. Mean fork length of the Chinook salmon used for baiting the PERs was 68.0 mm (SD 5.4).

Our daily sampling period was from approximately 3 h before to 1.5 h after sunset, during which we made multiple deployments of each PER. Previous studies have shown that predation risk is highest at sunset when compared to sunrise, midday, and midnight (Demetras et al. 2016, C. J. Michel, *unpublished data*); we therefore chose this focused period to develop more robust

relationships between predation risk, habitat, and environmental variables. While some potential predators are known to be nocturnal and were therefore likely not significantly influencing predation rates in this study, we also chose the period of highest probable predation so as to serve as a representation of the maximum daily predation rate. Boat-based crews would begin deploying drifting PERs, 15 in total, scattered across the cross section at the upstream end of each 1-km study reach (as determined by the direction of current during that tide cycle). PERs were redeployed at the upstream end of the reach once they reached the end of the 1-km reach (typically every hour) until 1.5 h after sunset, which would typically result in approximately 45 individual PER drifts per night. Every time a PER was removed from the water, the status of the predation-triggered timer and Chinook

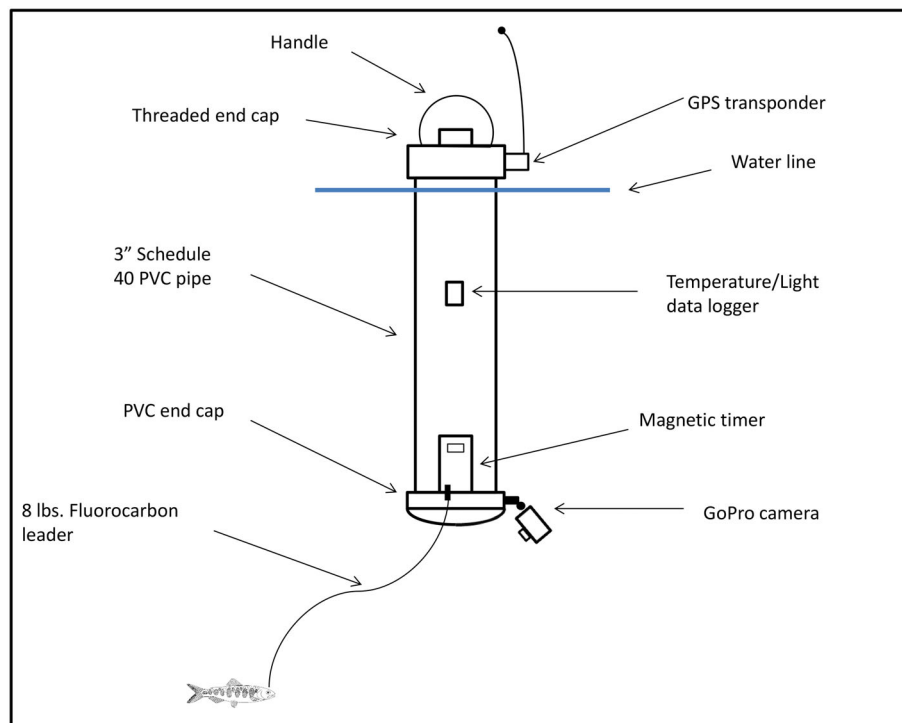


Fig. 2. A schematic of the PER, taken from Demetras et al. (2016).

salmon bait was recorded, the timer was reset, and the bait was replaced before redeployment if necessary.

Predation risk model

We analyzed the PERs data with a Cox proportional hazard model (Cox 1972, Therneau and Grambsch 2000) to estimate relative predation risk at each sample site. The Cox model is a time-to-event model that estimates the instantaneous rate of an event, in this case, predation, as a function of predictor variables. The response variables for a Cox model are the right-censored time interval length and whether an event (predation) occurred during that interval. The Cox model is therefore temporally explicit, which allowed us to associate spatial and temporal environmental conditions at 1-min intervals for each unique PER drift, and estimate predation risk as a function of these covariates. We employed a mixed-effect Cox model in order to include study site as a random effect to account for inherent differences in site-specific predation risk not captured by the predictor variables. Because each

sampling week balanced 3 sampling days at repeat sites (same 3 sites visited weekly), with 3 sampling days of visiting new sites, the model was effectively able to identify the effect of seasonal trends (e.g., changing water temperatures) on predation risk and the effect of spatial and temporal trends occurring within a single sampling day (e.g., time to sunset). The resulting relationships determined by model selection therefore represent a blend of the most important relationships acting on these different, equally important, scales.

The exponentiated parameter coefficient in a Cox model represents the hazard ratio, an easily interpretable metric of effect size. Hazard ratios between 0 and 1 mean that the risk is decreased over mean conditions; that is, a predation hazard ratio of 0.7 means that predation risk will be reduced by 30% over mean conditions. A hazard ratio of 1 means risk remains unchanged over mean conditions. A hazard ratio above 1 means that risk is increased; that is, a predation hazard ratio of 1.3 means that predation risk will be increased by 30% over mean conditions.

Estimating weekly predation rates

In order to elucidate seasonal trends in predation risk, we constructed an initial mixed-effect Cox model using only PER data from the repeat sites. Predation risk was modeled as a function of week, with study site as a random effect. We then predicted the predation rate per week given the PER data, except with no random effect. To generate 95% confidence intervals, we employed nonparametric bootstrapping with 100 simulations and estimated the 2.5% and 97.5% quantiles for these predicted predation rates per week.

Influence of habitat features and environmental variables on predation rates

The distribution, behavior, and abundance of both predator and prey fish species are variable in response to environmental variables and the availability of suitable physical habitat features. In turn, predation rates likely vary in response to the heterogeneous nature of the surrounding physical environment. In order to examine relative predation rates upon juvenile Chinook salmon across the diverse spatial landscape of the Southern Delta, we measured environmental variables and quantified habitat metrics for each of our twenty study sites and incorporated these covariates into a predation risk model. We associated temporal environmental variables with the PER data at one-minute intervals, and similarly associated spatial habitat variables at the location of one-minute intervals along with each PER drift. We then used model selection with the mixed-effect Cox proportional hazard model structure to determine fine-scale spatial and temporal relationships between habitat and water quality variables and predation risk.

We selected environmental variables and habitat features known to exert influence over the relative abundance, energetic demands, behavior, and efficacy of predatory freshwater species present in the Southern Delta. They included submerged aquatic vegetation (SAV; Nobriga et al. 2005, Conrad et al. 2016, Hestir et al. 2016), depth, habitat complexity (as measured by bottom slope and bottom roughness), distance from shore (Michel et al. 2018), flow velocity (Čada et al. 1997), turbidity and time to sunset (Helfman 1986, Gregory and Levings 1998, Sweka and Hartman 2003), water temperature (Rice et al. 1983, Hartman and Brandt 1995, Callihan et al.

2014), and predator density. Time to sunset was expected a priori to have a nonlinear relationship with predation risk, and therefore, a spline function was utilized to allow for a nonlinear relationship during model fitting. Environmental variables were collected using a water quality sonde recording at one-minute intervals (deployed in each study site for the duration of sampling). We quantified habitat features for each of our study sites using a combination of field-collected and remote-sensed data.

We quantified the distribution and extent of SAV for each of our study sites utilizing 455 kHz side-scan sonar images with a low-cost side-scan fish finder sonar (Kaesler and Litts 2010, Kaesler et al. 2013). Only SAV patches >5 m along the longest axis were digitized within ArcGIS (ESRI version 10.4.1). We used an inverse distance weighted distance-to-nearest SAV patch as the predictor variable in the model, based on the assumption that increasingly distant SAV patches would have less influence on predation. We extracted water depths for our study sites from a San Francisco Bay-Delta digital elevation model developed by USGS (Fregoso et al. 2017), a 10 × 10 m bathymetry layer covering the extent of our study area. To quantify habitat complexity, we estimated both bottom slope (degrees from horizontal) and bottom roughness (coefficient of variation across all depths of a site) from the USGS bathymetry layer. Unlike most other habitat variables, bottom roughness was estimated across each of the 1-km study sites, and associated with the PER data at this scale. In essence, bottom slope was included to represent the instantaneous habitat complexity, while bottom roughness was included to represent the habitat complexity throughout the site. Finally, we used PER speed over ground as a surrogate for flow velocity since PERs drift with the surface current and are negligibly affected by other forces (such as wind).

Predator densities at each site were estimated concurrently to PER sampling using DIDSON acoustic cameras (Loomis 2019). A separate boat and crew conducted DIDSON surveys to collect information on the distribution, abundance, and density of predators. Within each 1-km survey reach, DIDSON surveys ensonified the upper water column following longitudinal transects both along the shoreline and in the channel.

DIDSON survey footage was then manually reviewed, and all fish larger than approximately 15 cm were measured in multiple video frames. Finally, any fish larger than 20 cm was deemed to be a potential piscivore, counted, and georeferenced. Loomis (2019) was able to further refine the DIDSON predator counts by distinguishing known predators (e.g., striped bass and largemouth bass) from the common carp (*Cyprinus carpio*), the most abundant large-bodied non-predator species in the Delta, with a 98% classification accuracy.

In order to provide an index of predator abundance with sufficiently high spatial and temporal resolution for association with PER data, we used a nearest neighbor analysis with a time-scaled distance measure between all observed predators and each 1-min interval PER location within a sample reach. A time-scaled distance (D_{ij}) between two points i and j was calculated following the same practice used in t-LoCoH home-range construction (Lyons et al. 2013) summarized in the equation below:

$$D_{ij} = \sqrt{\Delta x_{ij}^2 + \Delta y_{ij}^2 + (s \times y_{\max} \times \Delta t_{ij})^2} \quad (1)$$

where s is a dimensionless scalar to control the effect of time, and y_{\max} is the maximum velocity of a predator fish. For this analysis, we set y_{\max} equal to the maximum swimming velocity of a striped bass, 0.83 m/s (Freadman 1979). s was set to a value of 0.03 so as to produce nearest neighbor sets composed of approximately 50% time-selected predators, ensuring that the final metric incorporated predators that were known to exist near a PER both in time and in space. For each 1-min interval PER location, we calculated the time-scaled distance from the PER location to all observed predators in a sample reach. We used the mean of the distance to the nearest 10 predators as the final index of local predator abundance.

Prior to fitting the Cox models, we performed pairwise comparisons of continuous variables to determine whether any variables were collinear. All variables had pairwise correlation coefficients of <0.7 and were therefore deemed sufficiently non-collinear and kept (Dormann et al. 2013). We standardized covariate values such that the resulting standardized beta coefficients could be interpreted as the predicted change in the hazard

ratio given a one standard deviation increase in the covariate value.

To determine the best predictive predation risk model, we performed model selection on 100 simulations of 10-fold cross-validation resampling. We used Akaike's information criterion corrected for small sample size (AIC_c) to select the most parsimonious model based on both the random- and fixed-effects structure (Akaike 1974). For each simulation, we randomly selected 90% of the data, then performed model selection (utilizing AIC_c) for a suite of Cox proportional hazard models with all possible combinations of the linear predictor variables. All models included site as a random effect. We assumed models with $\Delta AIC_c < 2$ had equal support (Burnham and Anderson 2002); thus, if multiple models had a $\Delta AIC_c < 2$, we selected the model with the fewest degrees of freedom, that is, the most parsimonious model. We then tested for the discriminatory power of the best model by making predictions using the remaining 10% of the data, and estimating the Gonen and Heller's Concordance Index (GHCI; Gonen and Heller 2005). The GHCI is equivalent to the area under the receiver operating characteristic curve and, in this application, is the probability that a randomly chosen PER deployment that was preyed upon had a higher hazard ratio than a PER that was not preyed upon. All analyses were performed in program R (v. 3.5.1; R Core Team 2018). Model selection was performed using the dredge function from the MuMIn package (v. 1.42.1; Barton 2018) and run using the Surv and coxme functions from the survival (v. 2.38; Therneau 2015) and coxme (v. 2.2-10; Therneau 2018) packages. GHCI was estimated using the GHCI function from the survAUC (v. 1.0-5; Potapov et al. 2012) package.

Based on how frequently a particular predation model appeared as the most parsimonious model in the cross-validation exercise, an overall top model was selected. This top model was then run with the entirety of the dataset to obtain parameter estimates for the ensuing analyses. We then generated response plots for the predictor variables included in the top model by making hazard ratio predictions for the range of observed values of each predictor variable, while holding all other predictor variables at their mean. To generate 95% confidence intervals for

the response plots, we employed nonparametric bootstrapping with 100 simulations and estimated the 2.5% and 97.5% quantiles for every prediction point along the response curve.

South Delta-wide extrapolation of predation risk model

Future applications of this and similar projects will likely be focused on extrapolating the statistical relationships found here to spatial and temporal scales more relevant to the management of prey species. As such, we extrapolated our top predation risk model to the entire South Delta, from Mossdale to Jersey Point on the lower San Joaquin River including all major sloughs and waterways adjoining the lower San Joaquin River on its river-left side. Because the statistical relationships in the predation risk model are based off data collected in rivers and sloughs only, we did not attempt to extrapolate predation risk to large open bodies of water in the South Delta, such as Franks Tract and Mildred Island.

The extrapolation was performed by first dividing the sloughs and rivers of the South Delta into approximately 1 km long segments along the centerline of those waterways, resulting in a total of 303 1-km segments. We collected and summarized the habitat variables that occurred in the top predation risk model per 1-km segment. We also selected the temporally fluctuating variables from the top model and simulated data values along their ranges of observed values within our study sites. We then used these habitat and temporal variables to predict Predation Hazard Ratios for each 1-km segment given the parameter estimates in the top model. Finally, we also collected information on the temporally fluctuating variables for all 1-km segments in order to make day-step predictions of predation risk for the spring of 2017.

For the purposes of demonstrating additional value of the predation risk model, we can estimate the overall impacts of predicted predations risks on migrating salmonids, by considering the cumulative effects of multiple 1-km segments along a migration route. We attempted this exercise by predicting the survival rate of a PER at the end of a 20-min residence time in all 1-km segments and for all day-step predictions. We then estimated the daily product of all survival rates for all 1-km segments (i.e., through-Delta

survival) along the two primary migration routes: San Joaquin River and Old River, 68 and 83 1-km segments, respectively. This geographic area was defined as starting at Mossdale, California, USA, on the upstream end and ending at Jersey point, California, on the downstream end (Fig. 1). We should note that the estimated daily cumulative survival estimates are not exactly representative to the survival experienced by salmonids: Firstly, sampling occurred near sunset and likely represents higher-than-average predation rates; secondly, salmonids attached to a PER cannot evade predators; and thirdly, we assume a 20-min residence time per 1-km reach, when in reality, residence times of salmonids vary widely and are themselves dependent on many factors, including location within the Delta, time of day, season, and local conditions. Nonetheless, this analysis can effectively demonstrate the day-step dynamics of predation risk on survival through the outmigration season.

RESULTS

Percent of preyed-upon PERs varied through time and between sites, ranging from 0% to 37% (Fig. 3, Appendix S1: Table S1). In total, we deployed 1,670 PERs during the spring of 2017, of which 15.7% were preyed upon. Overall, there was an increasing trend in percent of preyed-upon PERs as the season progressed (Fig. 3). Weekly predation rates at the repeat sites as estimated from the weekly Cox model indicated significantly higher predation rates in weeks 5 and 6 compared to weeks 1 through 4 ($p < 0.01$; Fig. 3).

The environmental Cox proportional hazard model that consistently ranked the highest, appearing as the most parsimonious model in 82 of the 100 10-fold cross-validation simulations, included temperature, bottom roughness, mean predator distance, and time to sunset (Table 1). The mean GHCI for this top model was 0.75, suggesting that for 75% of randomly chosen pairs of PER deployments, the model would have correctly predicted the higher risk PER deployment. These four variables also appear in all other models (with the exception of 1 cross-validation simulation with a best model that did not include mean predator distance). In addition to the four variables that were included in the top model,

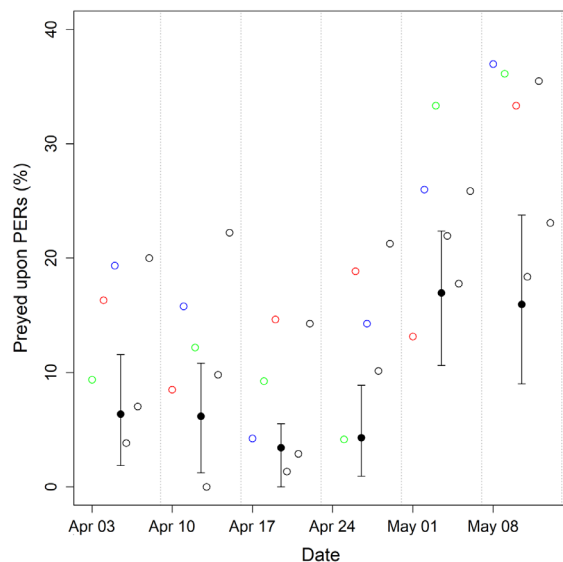


Fig. 3. Percent of preyed-upon PERs through time during the 2017 field season. Black hollow points depict sites visited only once, and colored hollow points depict repeat sites (site 1 in red, site 25 in blue, and site 28 in green). Solid black points depict percent of preyed-upon PERs as predicted by the weekly predation Cox model using data from repeat sites only (with 95% confidence intervals). Vertical gray lines depict the delineation between sampling weeks.

the next most frequently occurring covariate (appearing in 14% of models) was distance-to-nearest SAV. Finally, distance to shore also appeared in 9% of models. Temperature and bottom roughness had a positive relationship with relative predation risk, while mean predator distance had a negative relationship with relative predation risk. For the models including distance-to-nearest SAV, the parameter coefficient was negative, but due to being inverse distance weighted, this indicated that predation risk was lowest in close proximity to SAV. For the few models including distance to shore, that coefficient was negative, indicating a higher relative predation risk when closer to shore.

Using the top model with the full dataset, predicted cumulative PER survival proportion through time decreased to approximately 0.85 (or 0.15 PER mortality) over the span of 5000 seconds (83.3 min). The parameter coefficients for temperature, mean predator distance, and bottom roughness were 0.72, -0.35 , and 0.30,

respectively, and their hazard ratios (exponentiated coefficients) were 2.05 (1.61–2.60, 95% C.I.), 0.70 (0.56–0.88), and 1.35 (1.01–1.80), respectively. The hazard ratio is interpreted as the factor increase in predation risk based on a one standard deviation increase in the factor; for example, for temperature, 1 standard deviation increase leads to a doubling in predation risk. Due to the spline, time to sunset had several coefficients, making it difficult to interpret; nonetheless, it was a strong predictor of predation risk. Both time to sunset and water temperature had an approximate threefold increase in predation risk at its maximum compared to mean conditions (Fig. 4).

South Delta-wide extrapolation of predation risk model

We then predicted predation hazard ratio estimates throughout the South Delta at a 1-km resolution for the spring of 2017 using the top model. For this, covariates in the top model needed to be estimated for the entire South Delta. For mean predator distance, we used predator densities as predicted by the most parsimonious predator density model (Loomis 2019) as a proxy. This sub-model included sinuosity, bottom roughness, and number of SAV patches as predictor variables. Additional information on how predator densities were predicted and utilized in the extrapolation exercise can be found in Appendix S2.

Because temperature was the only temporally varying environmental covariate in the top predation risk model, we first predicted what the predation hazard ratio would be throughout the South Delta given different fixed temperature scenarios. We ran a scenario at the minimum, mean, and maximum temperatures recorded (13° , 16° , and 19°C) in the lower San Joaquin during the project. The per 1-km predation hazard ratios estimated for the 13°C scenario were almost all below 1, indicating lower predation risk throughout almost the entire South Delta, relative to mean conditions experienced during spring of 2017 (Fig. 5). The predation hazard ratios for the 16°C scenario ranged from 0.5 to 4.2 (with one outlier at 22.0), indicating an increase or decrease predation risk depending on the site. The predation hazard ratios for the 19°C scenario ranged from 1.7 to 14.8 (with one outlier at 77.2), indicating increased predation risk over

Table 1. Top predation risk models from 10-fold cross-validation model selection exercise.

Mean predator distance	Bottom roughness	Distance to shore	Temperature	Distance to SAV (inverse distance weighted)	Flow velocity	Turbidity	Time to sunset	Percentage of simulations as top model	Mean GHCI
−0.36	0.30	...	0.71	+	82	0.75
−0.35	0.29	...	0.68	−0.22	+	7	0.76
−0.34	0.26	−0.31	0.73	−0.30	+	6	0.75
−0.33	0.29	−0.23	0.73	+	2	0.75
−0.47	0.26	...	0.73	...	0.26	...	+	1	0.77
−0.26	0.25	...	0.71	0.21	+	1	0.76
...	0.33	−0.28	0.71	−0.35	+	1	0.75

Notes: Each row represents one unique model, and the rows are sorted by how frequently they are the top model from the 100 simulations (decreasing order). The eight left columns depict the mean standardized parameter coefficients (i.e., logged hazard ratios) for the covariates that appear in at least one of the top models. Row cells with ellipses signify that the model did not include that variable. Factors that did not appear in any top models were not included in the table. Due to the spline function applied to the time-to-sunset covariate, that covariate had multiple parameter coefficients; we only present here if the covariate was included in each model with a +.

mean conditions throughout the South Delta, with a 77-fold increase in one site (Head of Old River, HOR).

In order to estimate predation risk for the entire 303 1-km segments of the South Delta at a day time-step for the spring of 2017, water temperature was estimated at this same resolution (Appendix S2). The resulting predation risk extrapolations indicated that there were important regional differences in predation risk within the daily time-step results across the South Delta. Although the overall highest risk site was in the southern (upstream) part of the Delta (at Head of Old River site) in the relatively warmer late spring of 2017, the more northern (downstream) sites of the South Delta tended to have higher water temperatures and therefore higher predation during this period (Fig. 6).

Despite the additional 15 km along the Old River route, the predicted daily through-Delta survival along the two routes was almost identical from late March to early May (Fig. 7). During the month of May, survival in the San Joaquin route improved relative to the Old River route, likely due to the increased water temperatures in the Old River during this period, although both routes have drastically lower survival than the early spring. If HOR survival is removed from the San Joaquin route, survival is higher throughout the season, but marginally so during May due to the near-zero survival. To contextualize the real-world ramifications of these predictions, we estimated weekly juvenile Chinook salmon catch per unit effort during our study period

from a near-daily Kodiak trawl operated at the upstream end of the South Delta (Mossdale, California, USA) by the U.S. Fish and Wildlife Service and the California Department of Fish and Wildlife (https://www.fws.gov/lodi/juvenile_fish_monitoring_program/jfmp_index.htm). This effort indicated that the large majority of juvenile Chinook salmon entered the South Delta during the period of lowest predicted survival (Fig. 7).

DISCUSSION

We developed a spatially explicit statistical model of predation risk for outmigrating juvenile salmonids for the southern portion of the Sacramento–San Joaquin Delta. In the spring of 2017, predation risk for salmonids and other similar prey species in the South Delta were strongly influenced by water temperature, time of day, predator density, and bottom roughness. The direction and form of all discovered relationships between these variables and predation risk are congruent with our a priori expectations. We used the model to generate out-of-sample predictions based exclusively on environmental conditions, which allowed us to identify several locations that are predicted to have consistently high predation risk throughout the season (i.e., predation hot spots). This included the Head of Old River, which has been identified by previous telemetry studies as an area of abnormally high predation rates (Vogel 2010, CDWR 2015). We also identified a strong seasonal trend in predicted migration success through the South

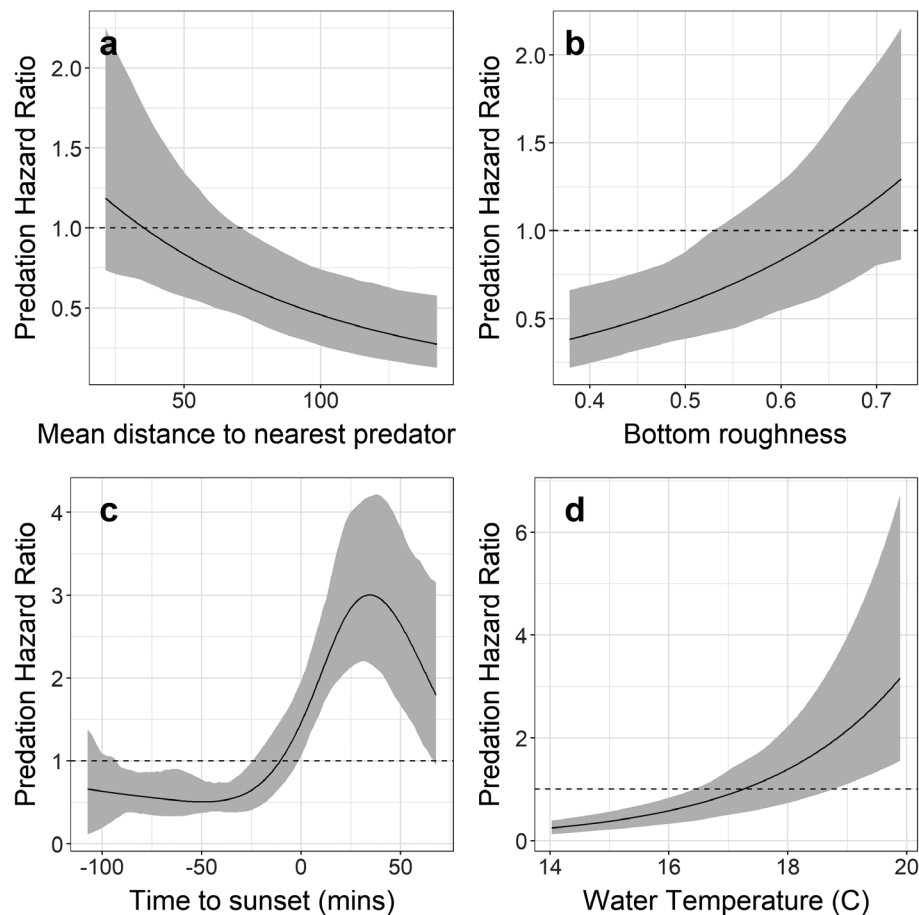


Fig. 4. Predicted predation hazard ratio given the range of observed values for (a) mean predator distance (m), (b) bottom roughness, (c) time to sunset (minutes), and (d) temperature (Celsius) from the top Cox proportional hazard model. Predictions for each plot are simulated while holding the other variables constant at their mean value. Bold black line depicts the estimate, and gray ribbon depicts the 95% confidence intervals as estimated by nonparametric bootstrapping. Dashed horizontal black line depicts a predation hazard ratio of 1, that is, unchanged predation hazard ratio over mean conditions. Time to sunset is a continuous variable, with sunset being at zero, and minutes before sunset are negative numbers leading up to zero, and minutes after sunset are positive numbers increasing from zero.

Delta, and found strong evidence that the majority of Chinook salmon migrants in the South Delta in the spring of 2017 likely experienced relatively high predation risk. The elucidation of these important spatial and temporal trends in predation risk is critical to resource managers tasked with restoring these imperiled populations, and clearly demonstrates the value of the landscape-level approach to understanding predator–prey dynamics.

Temperature is well recognized as a potential driver of predation risk, likely by impacting

bioenergetic demands of exothermic predators (Rice et al. 1983, Hartman and Brandt 1995). Temperature can also influence predator behavior and distribution in response to their thermal preferences (Diaz et al. 2007, Callihan et al. 2014). The upper limit of temperatures measured during sampling in the spring of 2017 (20°C) is approximately the lower end of the thermal preference of striped bass (Coutant 1986), which is the primary salmonid predator in the South Delta (Michel et al. 2018). It is possible that the highly migratory striped bass were not found in

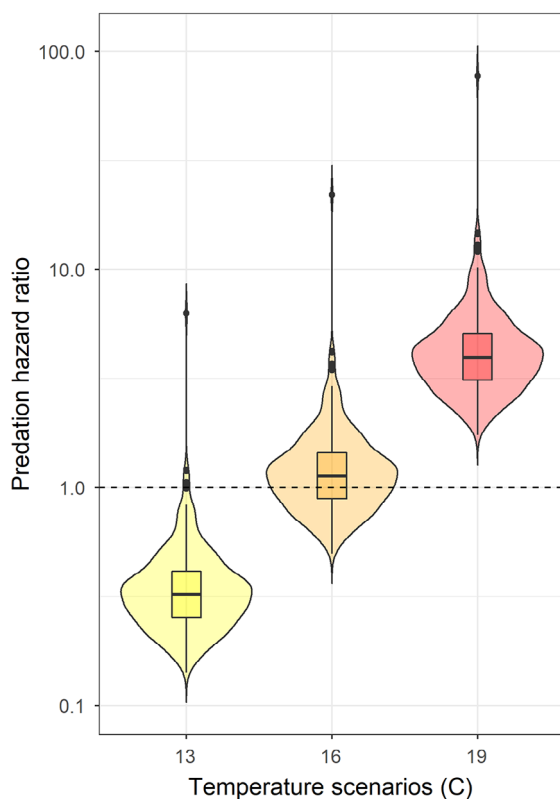


Fig. 5. Violin plots, with boxplots imbedded within, of predicted predation hazard ratios (log-scale) per 1-km site (303 in total) per temperature scenario (13°, 16°, and 19°C). Dashed horizontal black line depicts a predation hazard ratio of 1, that is, unchanged predation hazard ratio over mean conditions. Bold horizontal lines within boxplot boxes represent median values; lower and upper horizontal lines of the box represent 25th and 75th percentile values; upper and lower vertical lines beyond the boxes represent the 75th and 25th percentiles ± 1.5 times the interquartile range (distance from 25th to 75th percentile); values beyond these are considered outliers and are represented with solid points.

large numbers in sampling sites with water temperatures below this threshold.

Our study also found a strong influence of habitat features on predation risk, which managers may be able to manipulate through restoration actions. There was a positive relationship between bottom roughness and predation risk. This was likely mediated through the complex habitat that heterogeneous landscapes create, which likely increases predator densities (as

corroborated by the fact that bottom roughness was also a factor in the predator density sub-model) and predator ambush habitat. Distance to shore also had moderate support despite not appearing in the top model, with higher predation risk in the nearshore area. This could also be driven by the abundant predators commonly found in the shallow-water, SAV-abundant nearshore area.

Furthermore, our study also found a strong influence of predator densities on predation risk, indicating that predation risk is not solely mediated through habitat and environmental conditions. This suggests that if habitats could be modified to support smaller populations of predators, this would also impart survival benefits to imperiled prey populations. At the 1-km scale, the number of patches of an invasive SAV was one of the covariates that had the largest influence on predator density and could also be manipulated by managers (Appendix S2; Loomis 2019). This corroborates previous studies that have found significant relationships between SAV and both predators and predation risk in the Delta (Ferrari et al. 2014, Conrad et al. 2016). Loomis (2019) suggested that rather than attempting to modify the entire South Delta, one option would be to modify a consistent migration route (e.g., the mainstem San Joaquin River) to provide a corridor that had reduced predation risk for emigrating juvenile salmonids.

The top model correctly predicted a known predation hot spot in the South Delta at the Head of Old River. Other predation hot spots are known to exist throughout the Delta, and their impacts on population-level survival of salmonids (and other imperiled native species) are unknown. What is clear from this analysis is that predation risk during certain periods of their out-migration season can be sufficiently high throughout the South Delta that attempting to mitigate discrete hot spots may ultimately lead to negligible impacts on population-level survival. This is corroborated by a study that was unable to detect an increase in survival or a decrease in predation following an effort to remove predators from the Head of Old River site (Michel et al. 2020).

Some limitations of this study warrant discussion. Firstly, tethered prey cannot avoid predators and may behave differently than free-

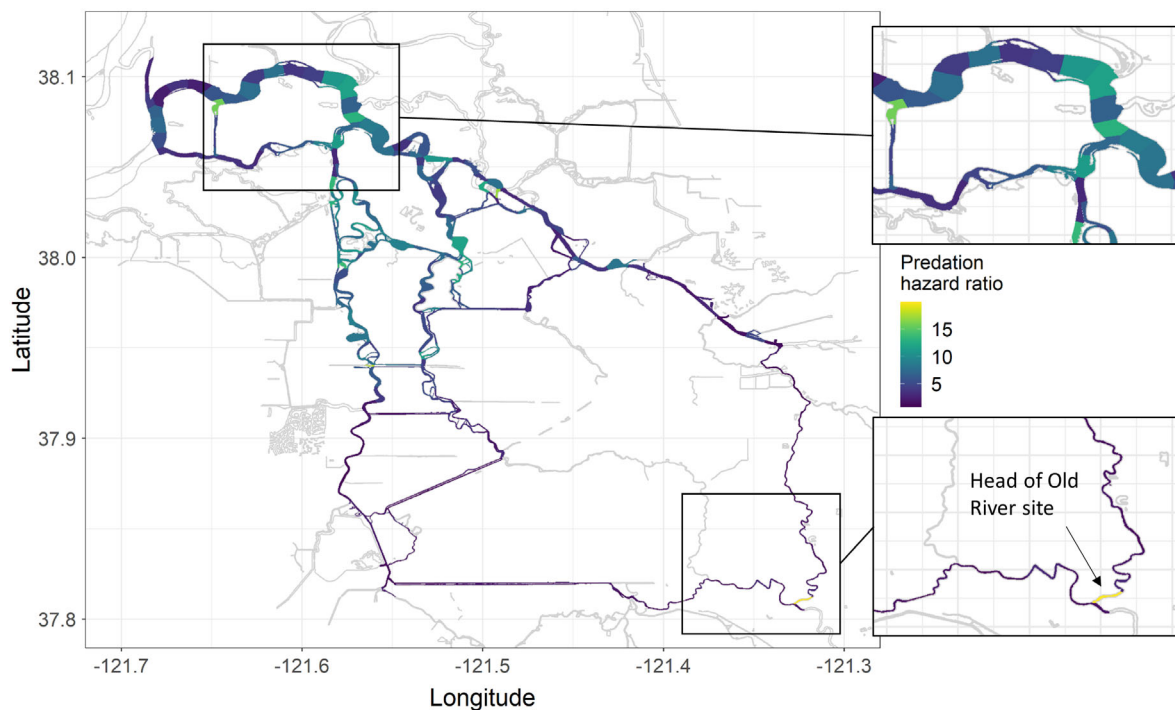


Fig. 6. Predicted predation hazard ratios for 1-km segments of the South Delta for 31 May 2019 (as an example), based on the top predation risk model. The left plot depicts the entire South Delta, set to the same scale as Fig. 1, while two insets (right) show the finer resolution of the 1-km hazard ratio predictions. The Head of Old River site is highlighted in the lower right inset.

swimming prey, and therefore, it is likely they are subject to higher-than-normal predation rates. Hence, these estimates, while useful in a relative sense, are only correlated with true predation intensity and not an exact measure of it. Similarly, when considering the relationships between environmental covariates and predation risk presented here, consider they are being mediated through the metabolic demands and behaviors of the predators only. This is only half of the equation: We did not investigate how environmental covariates may have also influenced juvenile salmonid distribution, health, and overall vulnerability to predation during our study. These prey-side responses are known to also be important determinants of predation risk (Marine and Cech 2004, Miller et al. 2014, Lehman et al. 2017). Future efforts should attempt to pair with studies to discern salmonid distribution and condition on a landscape scale. Secondly, predation risk estimates as measured by PERs are not representative of the entire cross section

of a waterway because they only sample the upper 1.5 m of the water column and do not effectively sample the extreme margins of the waterway channel. Nonetheless, actively migrating Chinook salmon are known to occupy the center channel of rivers (Sandstrom et al. 2013), and are largely found in the upper water column (Smith 1974).

The predation relationships from our study may only be representative of conditions during exceptionally wet years (as seen in 2017), and certain environmental covariates did not vary across their typical range as seen in more typical hydrologic years, and may have otherwise been an important predictor of predation risk. The water conditions may have also affected predator distributions: Anecdotal information from fishing guides suggested that striped bass densities in the Delta were low during the spring 2017, and that striped bass were drawn into the major river systems, upstream of the Delta, in larger numbers than usual due to the large river flows.

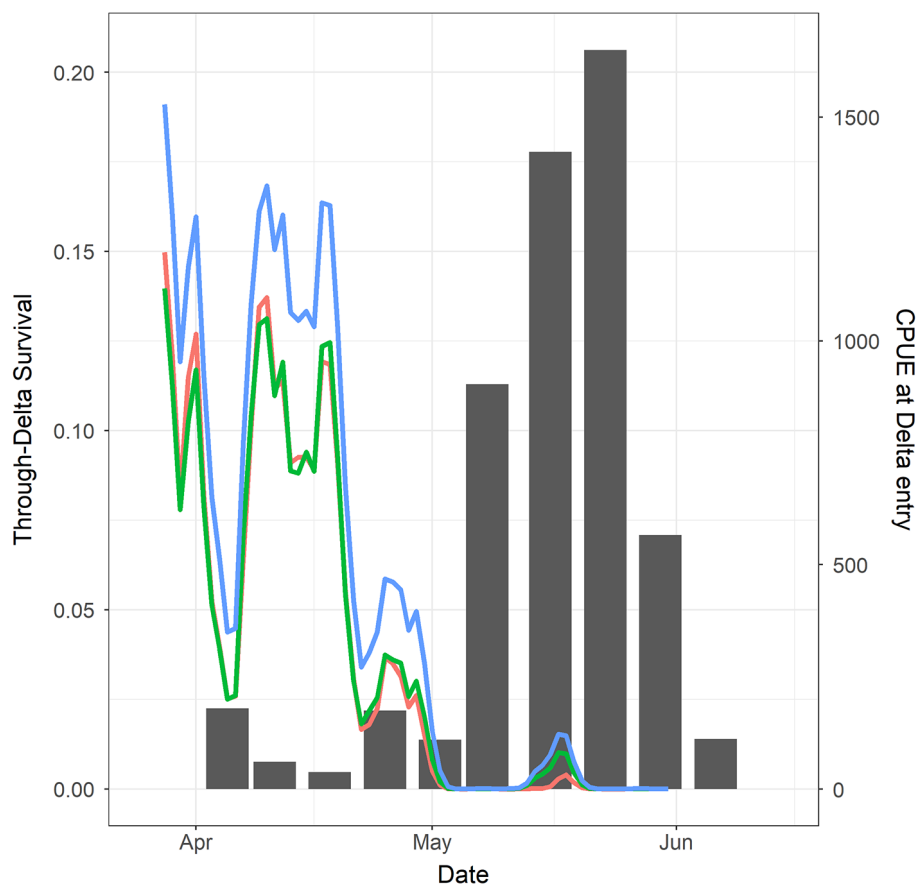


Fig. 7. Daily predicted through-Delta survival (given daily local conditions) along either the Old River migration route (green), the San Joaquin River migration route (red), or the San Joaquin River route without the HOR site (blue). Associated barplot represents weekly catch per unit effort of Chinook salmon from a near-daily Kodiak trawl survey on the San Joaquin River at the upstream entrance to the South Delta, starting the first week of April (Mossdale, California, USA).

Thus, one of the major predator species may have been lower in density than usual during this study. Taken together, such evidence implies that any extrapolation from the relationships described here should be done with caution unless the goal is to predict predation risk in extremely wet years.

Our study provides a repeatable methodology for quantitatively exploring the role of environmental conditions on predation dynamics in many different habitat types and water years. We set our spatial extent to the South Delta, but future work could easily extend such work to the entire Delta or beyond. Similarly, a follow-up study spanning several years of various water conditions would likely improve our models and

increase their applicability. This methodology can also be employed in other freshwater, estuarine, or marine systems where information on landscape-scale predation is critically lacking.

The management of water and ecological resources in the Delta is a contentious issue, involving multiple resource agencies, stakeholders, and academic institutions. Increasingly, management actions are being thoroughly evaluated before implementation using physical and ecological models. Many of these models, particularly those concerning the impacts of water and habitat management on imperiled native fish populations, attempt to incorporate the role of fluctuating environmental and habitat variables on the susceptibility of these populations to

predation. However, the mechanisms and relationships needed to make these evaluations are largely unknown, and are currently being informed by data from few, small-scale case studies. Our study is a first step in providing these models with predation data on the landscape scale, further improving their ability to predict the ecological ramifications of significant management decisions. The spatially and temporally explicit predation risk predictions generated by this model should also be incorporated into Chinook salmon survival models used by the many acoustic tagging studies conducted in the Delta (Perry et al. 2010, Buchanan et al. 2013, Michel et al. 2015). This will allow managers to tease apart what proportion of juvenile Chinook salmon mortality may be directly attributable to predation, a statistic that as of now is largely unknown.

Besides providing other physical and ecological models information they need on predation risk, this study has already yielded potentially powerful guidance to resource managers in the Delta. Firstly, our study provides strong evidence that managers could substantially increase the survival of juvenile salmonids in the South Delta if they were able to decrease water temperatures during the outmigration window. Secondly, we objectively identified predation hot spots where habitat characteristics are predicted to be particularly hostile to prey survival and therefore assist managers in prioritizing where habitat restoration may be most warranted. Finally, we developed a through-Delta survival metric that could be used by managers to promote migration of wild fish, as well as release hatchery fish, at times when through-Delta survival is forecasted to be high. A poignant example of this can also be seen in the spring of 2017, when the vast majority of outmigrating Chinook salmon entered the Delta during a period of relatively high predation risk (Fig. 7). A large proportion of these fish were hatchery-origin and could have avoided these conditions had they been released mere weeks earlier.

This issue of predation in the Delta resides at the intersection of industrial-scale resource management and extraction, a severely degraded estuary, ESA-listed native fish populations, non-native fish predators, and the needs of over 27 million Californians and 3 million acres of farmland. In the Sacramento–San Joaquin Delta, predation by non-native fish species on native

imperiled fish populations is a major management concern. The Delta provides water for a large portion of the agricultural and municipal needs of the state of California, but water diversions are often blamed for the poor state of native fish populations. At the same time, and likely exacerbated by these water diversions, non-native fish predator populations have recently increased leading to the further decline in native fishes. This has made recovery of these native fish populations, and therefore mitigation of predation risk, a legal and moral prerequisite for future water extractions. Although there is now a rush to manage the Delta to mitigate predation risk, the available information has only been collected at limited spatial and temporal scales. Our study is one of the first to provide managers with the information and tools to bridge this gap.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3168/full>