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Factors Affecting Spatiotemporal Variation in Survival of Endangered Winter-Run Chinook Salmon Out-migrating from the Sacramento River

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Abstract

    Among four extant and declining runs of Chinook Salmon *Oncorhynchus tshawytscha* in California's Central Valley, none has declined as precipitously as the Sacramento River winter run. Migratory winter-run Chinook Salmon employ a life history strategy to reside and feed in stopover habitats on their way from freshwaters to the ocean. Migratory winter run, on their way from freshwaters to the ocean, employ a life history strategy to reside and feed in stopover habitats that have been affected by anthropogenic disturbance. Using acoustic telemetry, we examined conditions that influenced reach-specific movement and survival of out-migrating juveniles during a prolonged, multi-year drought from 2013 to 2016, followed by one of the wettest years on record (2017). We modeled how time-varying individual riverine covariates and reach-specific habitat features influenced smolt survival. Model selection favored a model with mean annual flow, intra-annual deviations from the mean flow at the reach scale, reach-specific channel characteristics, and travel time. Mean annual flow had the strongest positive effect on survival. A negative interaction between mean annual flow and intra-annual reach flow indicated that within-year deviations at the reach scale from annual mean flow had larger effects on survival in low-flow years. These factors resulted in higher survival during years with pulse flows or high flows. Changes in movement behavior in response to small-scale changes in velocity were negatively associated with survival. Covariates of revetment and wooded bank habitat were positively associated with survival, but the effect of these fixed habitat features changed depending on whether they were situated in the upper or lower part of the river. Fish exhibited density-dependent stopover behavior, with slowed downstream migration in the upper river in the wet years and extending to the lower river in the most critically dry year. This paper contributes two key findings for natural resource managers interested in flow management and targeted habitat

restoration. The first is new insight into how the magnitude of pulse flows in dry and wet years affects survival of winter-run fish. The second is that density dependence influences where stopover habitat is used. Despite this, we identified an area of the river where fish consistently exhibited stopover behavior in all years.

Migration is a fundamentally important ecological process for animals that reproduce and forage in different places. Environmental decision making is challenging in application to migrating species because management approaches must span a vast range of distant and distinct habitats (Runge et al. 2014). Stopover behavior is an important component of migration for animals that must refuel along the migration path before continuing toward their ultimate destination. Studies of birds have found that migrants will select stopover habitats that allow refueling with maximum efficiency to remain on schedule (Alerstam and Lindström 1992). Loss of even a small amount of stopover habitat can have disproportionately large impacts on migratory populations (Iwamura et al. 2014). Effective management of migratory species therefore depends on accurate characterization of habitat use.

In diadromous fishes, migration can be long and complex (Thorstad et al. 2012), but little is known about how stopover habitats vary in quality and how they are used. The Chinook Salmon *Oncorhynchus tshawytscha* is a suitable species in which to examine this behavior because the juveniles migrate through entire watersheds from inland freshwater streams where they are born to productive coastal estuaries (Moore et al. 2016). Accordingly, rivers function as a migratory corridor during the smolt migration phase, which is considered one of the most vulnerable periods in their anadromous life history (Quinn 2005). Alternatively, juvenile salmon may stop over during transit to capitalize on foraging opportunities, seek refuge from predators, or simply rest. Quantifying how juvenile salmon allocate their time across the riverscape is foundational to understanding the relative importance of different riverine habitats (Thorpe 1994; Moore et al. 2016).

California's Central Valley represents the southern extent of the range for Chinook Salmon, where they are confronted with a number of stressors (Fisher 1994; Yoshiyama et al. 1998). Mild winters with a receding snowpack and dry summers frequently result in a hydrologic system where water availability and demand are mismatched (Berg and Hall 2017). Dams on the major rivers block access to historical habitat, and water storage and managed releases to meet human demands throughout the year result in a flattened hydrograph relative to natural flows (Kondolf and Batalla 2005). Muted peak flows in winter and increased summer flows can mask cues that salmon use to initiate migration (Bunn and Arthington 2002). Finally, climate change projections of rising temperatures in the Sacramento River (Cloern et al. 2011) show an increased likelihood and duration of drought conditions, which have been occurring in California with increasing frequency over the past two decades (Diffenbaugh et al. 2015).

All four populations of extant Chinook Salmon races in California's Central Valley have declined over the past decades and have experienced precipitous declines since the onset of the latest megadrought in the early 2000s (Johnson and Lindley 2016), which was the second-driest 20-year period since 800 CE (Williams et al. 2020). Sacramento River winter-run Chinook Salmon (hereafter, "winter run") are the most critically endangered of the four Chinook Salmon runs in the Central Valley. The spawning population crashed from 87,000 in the late 1960s to fewer than 200 in the early 1990s (Fisher 1994) and remains at risk of extinction (Lindley et al. 2009; Poytress et al. 2014).

Historically, the winter run adapted to California's dry and variable climate by holding in the coldest upper reaches of headwater tributaries of the Sacramento River during summer months, when temperatures in the Central Valley were unsuitable for spawning and rearing (Yoshiyama et al. 1998). Fry reared in thermal refuges of these tributaries throughout summer (5–10 months) and migrated as smolts during the first freshets of the following autumn (Williams 2006). For the past 75 years, access to historic spawning tributaries has been eliminated by construction of Shasta and Keswick dams, forcing three populations to mix and spawn as one in the main stem of the Sacramento River downstream of Keswick Dam (Williams 2006). In the post-dam era, otolith geochemistry provides some evidence that winter-run fish continue to rear in nonnatal tributaries extending as far downstream as the San Francisco estuary (Phillis et al. 2018).

Hatchery releases of juvenile winter-run "pre-smolts" into the river are timed to maximize survival and occur during storm events when high instream flows can facilitate rapid emigration. However, the mechanism for how survival per unit time is related to flows is not well understood. On one hand, high flows could move fish rapidly through hazardous habitat. Alternatively, if fish move in response to density-dependent habitat availability, high flows could reduce pressure to move by creating more stopover habitat. Furthermore, it is unknown whether flows affect survival the same way across all reaches. Understanding which mechanisms most influence survival and identifying the reaches in which juvenile salmon experience particularly high or low mortality can therefore help managers find ways to focus on specific, targeted actions to improve survival.

Without this information, the National Marine Fisheries Service has had to rely on out-migration information from larger, yearling hatchery late-fall-run fish as surrogates to

fill data gaps in their winter-run recovery plans (Johnson and Lindley 2016; Johnson et al. 2017). However, a growing body of scientific literature cautions against inferring too much from surrogates because they often do not respond in the same way as the targeted taxa to similar environmental conditions (Caro and O'Doherty 1999; Andelman and Fagan 2000). Even within a Chinook Salmon run, the responses of hatchery and wild fish to environmental conditions may differ, resulting in differences in mortality during out-migration (Buchanan et al. 2010).

Nevertheless, research using acoustic telemetry primarily on late-fall Chinook Salmon has yielded some important insights into some of the immediate challenges confronted by migrating salmon smolts in general, such as disorienting structures with magnetic fields that influence seaward orientation (Klimley et al. 2017), predation dynamics (Sabal et al. 2016, 2021), entrainment into the south Sacramento–San Joaquin Delta (hereafter, "Delta"; Perry et al. 2015), and loss of habitat and limited food resources (Donaldson et al. 2014). This study builds upon earlier work on flow-mediated survival relationships that are gaining prominence in the field. Flow-mediated survival during the out-migration phase of the life cycle has been shown to have a greater effect on smolt-to-adult returns than marine survival (Michel 2019). The magnitude of bidirectional, tidally influenced flows has also been recognized as an important determinant of migration routing and survival in the Delta (Perry et al. 2018; Singer et al. 2020), and intra- and interannual reach flow has a greater impact on late-fall-run survival than other riverine and predation-related covariates (Henderson et al. 2019).

This study was designed to evaluate the effects of flow on winter-run survival at multiple scales and in the presence of other habitat covariates by directly evaluating the survival of hatchery-origin winter-run out-migrants using the Juvenile Salmon Acoustic Telemetry System (JSATS). Due to their scarcity, it was not feasible to obtain natural-origin winter-run fish (i.e., offspring of adults spawned in the river); therefore, extrapolation of our findings to natural-origin fish should be considered with caution (Buchanan et al. 2010). Furthermore, because our study used smolt-sized fish released in the upper river, our understanding of movement rates will be skewed to fish that would have reared in natal habitat and then initiated their smolt out-migration rather than rearing downstream. Evidence of downstream rearing is therefore likely to be conservative.

Within this framework, we developed a suite of mark–recapture models following the approach developed for the late-fall run by Henderson et al. (2019). We examined how individual features of the fish themselves (i.e., fish size); temporal, reach-constant riparian habitat features; and spatial, time-varying hydrologic conditions affected survival of out-migrating, hatchery-origin, winter-run juveniles. The study was carried out during a 5-year period under extremely variable climate conditions: a prolonged, multi-year drought (2013–2016) followed by one of the wettest years on record (2017). Although only one wet year was represented in our study, it allowed us to contrast movement behavior and survival outside of the drought conditions that characterized all other years in this study. To quantify relationships between covariates and survival, we used mark–recapture models and information-theoretic model selection criteria to rank alternative models. Our goals were to (1) examine spatial and temporal patterns in out-migration movement and survival in the river and (2) identify which combination of environmental covariates had the greatest influence on survival.

METHODS

Study site.— The Sacramento River is the largest river in California, flowing south from Mount Shasta for 410 km before reaching the Delta. Mean daily discharge from the Sacramento River in 1955–2019 was 656 m³/s (California Department of Water Resources, Dayflow database), draining about 68,635 km² of the Central Valley. Keswick Dam (river kilometer [rkm] 557 from the Golden Gate Bridge [rkm 0]) is the upper limit to anadromy on the Sacramento River. For this study, we focused on movement and survival in the Sacramento River, ending 387 rkm downstream at the city of Sacramento, prior to entering the branching Delta and tidal estuary (Figure 1).

Acoustic-tagged fish.— The acoustic tags used with the JSATS in this study were manufactured by Advanced Telemetry Systems (ATS, Isanti, Minnesota). The model used in 2013 weighed 430 mg, with dimensions of $11.9 \times 5.3 \times 3.8$ mm and a pulse rate interval (PRI) of 7 s, while the model used in 2014–2017 weighed 310 mg, with dimensions of $10.8 \times 5.3 \times 3.0$ mm and a PRI of 10 s. Each year, 5% of tags were randomly sampled and used to verify tag life, which ranged from 43 to 90 d, with an average of 70 d. This satisfied the assumption of closure in the mark–recapture models because the longest duration travel times occurred early in the upper to middle river and did not exceed this value over the course of migrating through the study area.

At Livingston Stone National Fish Hatchery (U.S. Fish and Wildlife Service, Shasta Lake, California), fish that were selected for acoustic tagging were taken from tanks that contained the largest fish (one to eight tanks depending on the year) to keep individual tag burden below 5.9% (Brown et al. 2010). Prior to tag implantation, each fish was anesthetized to stage IV (i.e., fish were observed to have lost equilibrium and exhibited minimal response to touch; average time to stage IV was 141 s). Anesthetized fish were weighed to the nearest 0.1 g, and FL was measured to the nearest millimeter. Fish were placed ventral side up on a V-shaped, foam surgery cradle. Anesthesia was maintained
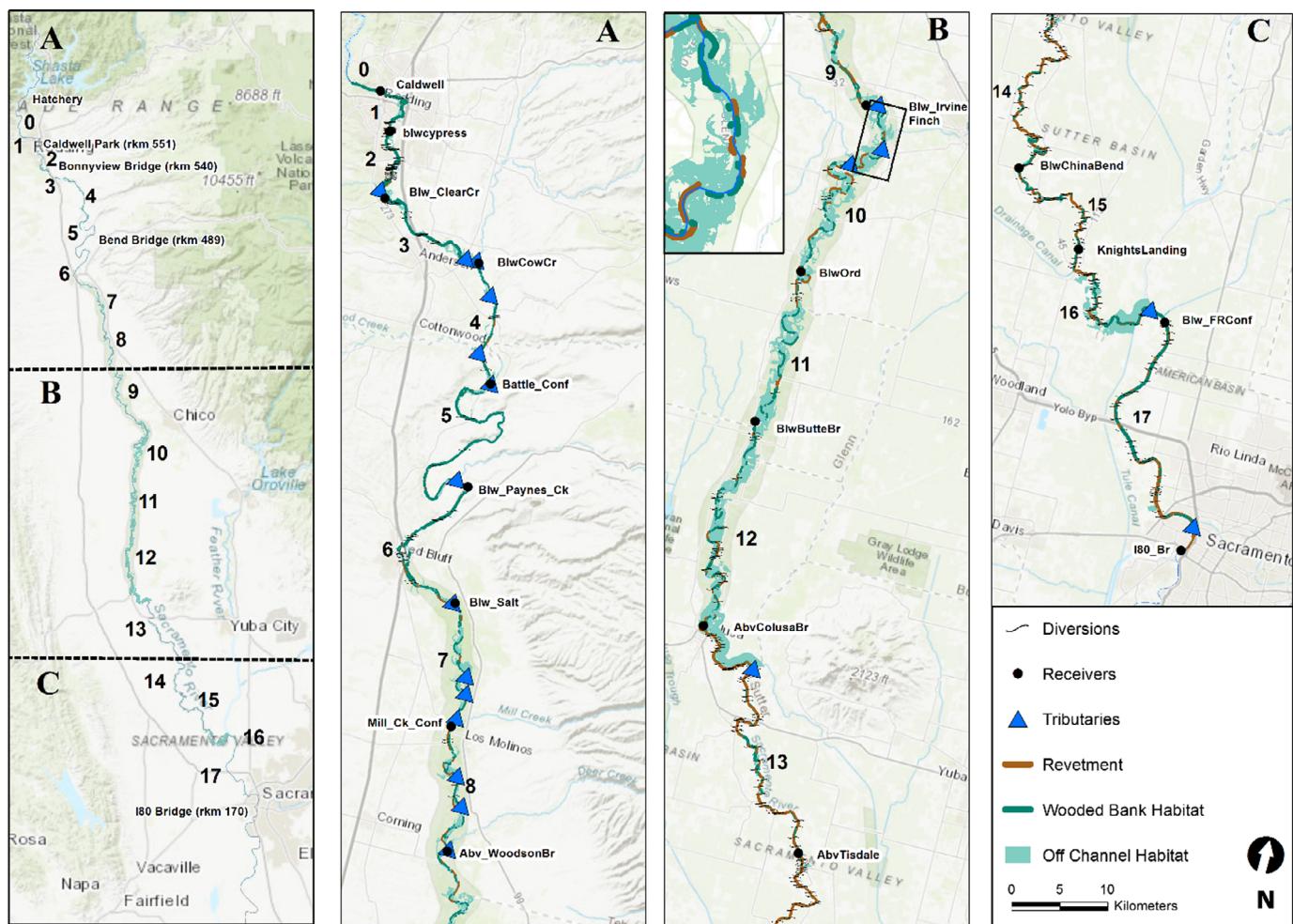
FIGURE 1. Extent of the study area from Redding to Sacramento (left panel). River reaches are numbered between acoustic receiver sites. Time-constant habitat features are mapped over the study area for the (**A**) upper, (**B**) middle, and (**C**) lower sections of the river. The inset map magnifies wooded bank habitat, revetment, and off-channel habitat that was connected within 1 km of the main-stem Sacramento River in the wet year. World topographic base map source: Esri, DeLorme, TomTom, Intermap, GeoTechnologies, General Bathymetric Chart of the Oceans, U.S. Geological Survey, Food and Agriculture Organization of the United Nations, National Park Service, Natural Resources Canada, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, Ministry of Economy, Trade and Industry (Japan), Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

during surgery with dilute anesthetic solution pumped through a small plastic tube leading into the mouth. An incision about 7 mm long was made between the pelvic and pectoral fins approximately 3 mm off the ventral midline using a 3-mm scalpel (Sharpoint 15° stab knife). A disinfected acoustic tag was inserted battery first into the coelom through the incision, and the incision was closed with one or two sutures of absorbable monofilament (6/0 Monoswift). Surgery time averaged 142 s. Fish were observed to resume normal swimming behavior after an average of 236 s. Mean tag burden (tag weight expressed as a percentage of fish weight) by year ranged from 3.2% to 4.3%.

Following surgery, tagged fish were returned to tanks and held for 1–3 d until the hatchery production fish were loaded into transport trucks. Acoustic-tagged fish were transferred into portable PVC/mesh holding pens and

placed within the tank of a transport truck. Transport time from the hatchery to release into the Sacramento River at Caldwell Park (Redding) was approximately 45 min; in 2016, fish were released at Bonnyview Bridge (Redding), and transport time for those fish was approximately 60 min. Acoustic-tagged fish were released simultaneously with the other hatchery-origin fish, which were released after sunset. In 2015, when hatchery fish were released over three consecutive days, acoustic-tagged fish were released on the first and third days. The number of acoustic-tagged individuals and the number of hatchery fish released varied substantially among the 5 years of this study; in particular, hatchery releases were much higher in 2014 and 2015 to compensate for anticipated severe losses of naturally produced fish due to drought, with elevated river temperatures and associated critically dry conditions (Table 1).

Acoustic receivers.— As part of the California Fish Tracking Consortium, we tracked fish by using an array of acoustic receivers beginning 3 km below the release location in Redding; extending down the Sacramento River, Delta, and San Francisco Bay; and ending at a dual line of receivers at the Golden Gate Bridge. However, for this study we were interested in examining riverine survival using outputs from the River Assessment for Forecasting Temperature (RAFT) model, which terminates at the tidal Delta, so we restricted this analysis to only receiver locations in the Sacramento River, ending at the city of Sacramento, to estimate survival and movement over 379 km (Figure 1). Receivers positioned downstream in the Delta to the point of ocean entry at the Golden Gate Bridge were therefore pooled into a single site and used to improve estimates of detection probability and survival for all reaches upstream of the final line.

Three different types of JSATS receivers were used in this study: ATS Model SR3000; Lotek Wireless (Newmarket, Ontario, Canada) Model WHS4000; and Teknologic Engineering (Edmonds, Washington) Model LER. Detection range varied from 50 to 300 m depending on river conditions (A. J. Ammann, unpublished data), with an 85% probability of recording at least four valid transmissions from a distance of 135 m (Ammann 2020). We deployed 40 receivers at 18 locations demarcating 17 river reaches (Figure 1). At most of the receiver locations, two receivers were deployed across the river to improve cross-sectional detection coverage. Receivers were held in position with a bottom anchor that was either attached to a shore cable or suspended from a bridge structure.

Postprocessing.— All receiver files contain some amount of invalid or false positive detections. These must be distinguished from true detections and removed to prevent biased interpretation of fish movement and survival (Beeman and Perry 2012). Therefore, each raw receiver file was processed using a set of algorithms to remove false

detections (Deng et al. 2017) and to add location information and a unique fish identifier. The filtering algorithm was customized for each of the three receiver models. Briefly, the filtering algorithm used criteria that included the following constraints: (1) the detection code had to match that of a released fish; (2) detection time had to occur after the release time and before the tag was expected to expire; (3) detections that occurred less than 0.3 s after the previous detection (multipath) were removed; and (4) detections had to have occurred within a time window and within the tag's PRI that was specified depending on receiver make. Lotek receivers required a minimum of four detections within 16.6 times the PRI, and the observed PRIs among these detections had to be within 20% of the nominal PRI. Additionally, the SD of these PRIs had to be less than 0.025. Teknologic receivers required at least two detections within four times the PRI, the observed PRI had to be within 10% of the nominal PRI, and the difference in frequency of the two detections had to be less than 55 kHz. The ATS receivers required at least two detections within four times the PRI, the observed PRI had to be within 10% of the nominal PRI, frequencies of the two detections had to be between 416.30 and 418.75 kHz, and the difference in frequency of the two detections had to be less than 0.505 kHz. Separate receiver files were then compiled into a single table. Plots of the time of detection versus rkm were created for each fish and visually inspected for detections that were not spatially and temporally congruent with the remaining detections. We considered any upstream movements as those of predators having ingested a tagged fish. Where predation was inferred, we ended the fish's detection history at the furthest downstream detection.

Mark–recapture analysis.— We used a Cormack–Jolly–Seber survival model (Cormack 1964; Jolly 1965; Seber 1965) to analyze capture histories and estimate the effects of covariates on survival (ϕ) and detection (p). The

TABLE 1. Number and size (mean $\pm$ SD) of acoustic-tagged winter-run Chinook Salmon juveniles released each year. Fish were reared at Livingston Stone National Fish Hatchery and released at Caldwell Park (Redding, California; rkm 551) except in 2016, when the release location was Bonnyview Bridge (Redding; rkm 540). Tag burden was calculated as 100 $\times$ (tag weight/fish weight). Flow at Bend Bridge was calculated from the date of release to the date on which the last fish was detected at Tower Bridge in Sacramento.

Release date	Number of fish acoustic tagged	Weight (g)	FL (mm)	Tag burden (%; mean, range)	Hatchery winter-run fish released	Flow (m³/s) at Bend Bridge[a] (mean, range)
Feb 7, 2013	148	10.3 ± 1.7	98 ± 5.0	4.3 (2.5–5.4)	166,967	168 (127–289)
Feb 14, 2014	358	9.4 ± 2.4	95 ± 7.7	3.9 (2.0–5.8)	190,905	187 (108–790)
Feb 4 and 6, 2015	249; 318	10.5 ± 2.0	100 ± 6.1	3.2 (2.0–5.9)	590,623	197 (105–1,453)
Feb 17 and 18, 2016	285; 285	9.3 ± 1.6	96 ± 5.1	3.6 (2.3–5.3)	415,865	432 (151–1,603)
Feb 2, 2017	569	9.1 ± 2.4	93 ± 7.5	3.7 (1.7–5.7)	141,388	1,315 (385–2,832)

[a]U.S. Geological Survey/U.S. Bureau of Reclamation (Bend Bridge hydrologic station [40.28849°, −122.186661°; rkm 489.4]; https://dashboard.waterdata.usgs.gov/api/gwis/2.0/service/site?agencyCode=USGS&siteNumber=11377100&open=15630).

Cormack–Jolly–Seber model was adapted from its original intended function to estimate survival over time into a spatial form of the model that could be used for animals that migrate unidirectionally (Burham et al. 1987) and could be "recaptured" in the form of acoustic detections along the migratory corridor. River reaches were bounded by receivers positioned at approximately 7–38-km intervals along the Sacramento River to the beginning of the Delta at the I-80/I-50 Bridge. In three locations where receiver positions were adjusted slightly among years (Butte City, Knights Landing, and Tower Bridge), the receivers were moved 6, 2, and 2 rkm from their original locations, respectively. For this analysis, these sites were assigned the rkm of the upstream-most receiver at each location. A capture history for each fish was created by assigning a "1" (detected) or a "0" (not detected) at each receiver location.

Survival was modeled in program MARK (White and Burnham 1999) through the RMark package (Laake 2013) within R (R Core Team 2020). By substituting space for time, we modeled reach-specific survival (S) as a logistic function using a linear structure,

$$\text{logit}\big(S_{i,j}\big) = \sum_{k=0}^{K} \beta_{j,k} x_{i,j,k}, \tag{1}$$

where logit() is the logit link function, $S_{i,j}$ is the survival probability for the ith individual in the jth reach, and $\beta_{j,k}$ is the slope coefficient of the kth covariate, $x_{i,j,k}$.

This model structure allowed for a mixture of spatially and time-varying covariates (e.g., water temperature), spatially and time-constant individual covariates (e.g., FL), spatially varying but time-constant covariates (e.g., reach length), and time-varying but spatially constant covariates (e.g., mean annual river flow). Each of the covariates we included in the analysis had an a priori hypothesized effect on smolt survival (Table 2). Fish size, as measured by FL, was the only covariate that was unique to each individual but constant across reaches and time. The time-varying, reach-constant covariate was annual mean flow at Bend Bridge, confined to the period spanning from the date of fish release to the date on which the last fish was detected in the river. Bend Bridge was chosen because it was upstream of major tributaries and diversions and therefore representative of flow in the Sacramento River watershed.

For each of the reaches, we derived spatially varying, time-constant covariates to define habitat features, many of which did not change between years and represented the best available approximation of reach-specific physical habitat for the Sacramento River (Figure 1). Each of the habitat features was mapped using ArcGIS version 10.4.1 (Esri, Redlands, California). River area and off-channel habitat were calculated as area per reach. Off-channel habitat was summarized as an annual mean from Landsat scenes corresponding to January–April, when fish were in the river. Median travel time was calculated from all observed travel times on a per-reach basis for each year. All other habitat features did not vary temporally across the study period. Shaded riverine aquatic cover (wooded bank) was defined as the nearshore aquatic area at the interface of the river and adjacent woody riparian habitat. This measure does not quantify instream cover. Specifically, to be designated as shaded riverine cover, the adjacent bank had to be composed of natural, eroding substrates supporting riparian vegetation that overhung or protruded into the water, with the water containing variable amounts of woody debris, such as leaves, logs, branches, and roots. Wooded bank and revetment were summarized as percentages of the length of the riverbank per reach. Remaining riverbank that was not classified as revetment or shaded was designated as bare bank. Other reach-specific covariates included the number of diversions, number of tributaries, and river sinuosity (Table 2).

A time-varying individual covariate was defined as the mean of the daily covariate (e.g., water flow, velocity, or temperature) over an individual's travel time through a reach. For the purposes of defining covariate values for each fish, individuals that were undetected at a given receiver location but subsequently detected at a location further downstream had that missing arrival time imputed by using the observed arrival time at the upstream location, the observed arrival time at the next downstream location, the distance between these two locations, and the reach length between the upstream location and the missed location,

$$A_{(missed)} = A_{(upstream)} + \frac{\text{RL}_{(upstream \to missed)} \times \big[A_{(downstream)} - A_{(upstream)} \big]}{\text{RL}_{(upstream \to downstream)}}, \tag{2}$$

where A is arrival time and RL is reach length (km) between locations.

There were many more reaches defined by acoustic receivers than there were flow stations in the river. Therefore, to more closely match fish presence with environmental covariates, we used the RAFT model (Pike et al. 2013), which is a one-dimensional physical hydrodynamic model that estimates laterally and vertically averaged channel water temperature, flow, depth, and velocity every 10 min at a 2-km spatial resolution. We included temperature because metabolic rates and predation rates increase at higher temperatures (Vigg et al. 1991; Killen et al. 2010).

We considered flow at the reach scale and at the watershed scale because flow dynamics have been shown to be important for survival (Michel 2018; Perry et al. 2018;

TABLE 2. Hypothesized effects of covariates on winter-run Chinook Salmon survival for covariates included in the top mark–recapture survival model.

Category	Covariate	Definition	Prediction	Hypothesis
Individual	Length[a]	FL	Positive	Larger fish have higher survival due to improved predator avoidance and gape limitation
Temporal	Annual flow[b]	Mean flow at Bend Bridge (Jan–Apr)	Positive	Higher flows produce more habitat, facilitate downstream migration, and increase turbidity, which reduces predator exposure
Spatial	Reach length	Distance between upstream and downstream receivers	Negative	Longer migration distance increases exposure to predators
	Off-channel habitat[c]	Connected wetted area per reach within 1 km of river edge	Positive	Increased off-channel habitat produces more refuge and forage habitat
	Travel time	Median travel time	Negative	Longer travel time will decrease survival because of increased exposure to predators
	Sinuosity[d]	Deviation of reach length from shortest path	Positive	Increased sinuosity creates more instream habitat
	Revetment[e]	Percent revetment	Negative	Increased revetment reduces habitat refugia
	Diversions[f]	Number of diversions per kilometer for each reach	Negative	Increased habitat structure for predators
	Tributaries[g]	Number of tributaries per kilometer exceeding a Strahler stream order of 3	Positive	Increased access to nonnatal habitat
	Wooded bank habitat[h]	Percentage of nonriprapped bank with adjacent woody vegetation	Positive	Increased cover produces more refuge habitat
	Width:depth ratio[i]	Mean ratio of wetted channel width to depth	Positive	Wider, shallow channels increase refuge habitat
	Slope[j]	Mean elevation gradient of a reach	Positive	Steeper gradients will decrease travel time

TABLE 2. Continued.

Category	Covariate	Definition	Prediction	Hypothesis
Time-varying individual[i]	Temperature	Mean river temperature per reach	Negative	Increased temperature increases predator activity and reduces aerobic scope, potentially impacting locomotion
	Depth	Mean river depth per reach	Positive	Favors avoidance of bottom-oriented predators (catfish) and surface-oriented predators (birds)
	Interannual reach flow	Mean river flow per reach	Positive	Higher flows within a reach produce more habitat in that reach
	Intra-annual reach flow	Mean river flow per reach and year	Positive	Higher flows will be associated with increased turbidity and refugia
	Reach velocity	Mean river velocity per reach	Positive	Higher velocities will shorten travel time and reduce predator exposure

[a]Measured at tagging.
[b]U.S. Geological Survey data inventory page for site 11377100–Sacramento River above Bend Bridge, near Red Bluff, California: U.S. Geological Survey Web page, accessed January 20, 2022, at https://dashboard.waterdata.usgs.gov/api/gwis/2.0/service/site?agencyCode=USGS&siteNumber=11377100&open=15630.
[c]Normalized difference water index using 2-week conglomerates in Landsat (https://landsatlook.usgs.gov; April 9–23, 2013; February 21–March 18, 2014; February 24–March 5, 2015; March 23–30, 2016; and February 22–March 1, 2017).
[d]Sinuosity toolbox in ArcGIS.
[e]California Department of Water Resources.
[f]California Department of Fish and Wildlife (Passage Assessment Database) and the National Oceanic and Atmospheric Administration Southwest Fisheries Science Center.
[g]National Hydrography Dataset Plus (U.S. Environmental Protection Agency) with a Strahler stream order of 3.
[h]California Department of Water Resources and Google Earth imagery.
[i]Produced by the authors using the River Assessment for Forecasting Temperature (RAFT) model (Pike et al. 2013).

Henderson et al. 2019). In addition to mean annual flow at Bend Bridge, we included flow variables that measured variation from each reach's mean flow and variation relative to the mean flow in each year. We refer to these covariates as "interannual reach flow" and "intra-annual reach flow," respectively, following the methods of Henderson et al. (2019). Interannual reach flow was calculated by standardizing flow to each reach's mean flow:

$$z_{\mathrm{inter},d,y,k} = \frac{Q_{d,y,k} - \mu_k}{\sigma_k}, \tag{3}$$

whereas intra-annual flow was calculated by standardizing daily flow within each reach and year:

$$z_{\mathrm{intra},d,y,k} = \frac{Q_{d,y,k} - \mu_{y,k}}{\sigma_{y,k}}, \tag{4}$$

where $z_{\mathrm{inter},d,y,k}$ and $z_{\mathrm{intra},d,y,k}$ are the inter- and intra-annual reach flows on day d in year y and reach k; $Q_{d,y,k}$ is discharge; μ_k and $\mu_{y,k}$ are the means of $Q_{d,y,k}$ for each reach and each reach and year, respectively; and σ_k and $\sigma_{y,k}$ are the SDs of $Q_{d,y,k}$ for each reach and each reach and year. Including intra-annual reach flow allowed us to examine whether large freshet events within a reach would increase survival relative to the mean flow for that year (Cavallo et al. 2013; Courter et al. 2016). We included intra-annual reach flow in models with mean annual flow at Bend Bridge because scaling intra-annual flow by both year and reach removes the effect of annual differences in intra-annual reach flow, thus eliminating correlation between these variables. We also included an interaction term between mean annual flow and intra-annual reach flow, which tests whether within-year deviations from the mean annual flow had a different effect in high- and low-flow years.

Before fitting mark–recapture models, we conducted pairwise comparisons of all covariates to evaluate collinearity. If the correlation coefficients between any two variables exceeded 0.70 (Dormann et al. 2012) or if the variance inflation factor exceeded 10 (Kutner et al. 2004), we retained only the covariate with a greater hypothesized effect on survival (Supplementary Material available in the online version of this article). All continuous variables were standardized to zero mean and unit SD so that changes in survival could be predicted by a 1-SD change in each covariate value.

Model selection. — We used Akaike's information criterion (AIC) to rank alternative models based on the best trade-off between improved fit and model complexity (Burnham and Anderson 2002). Models with lower AIC values are considered better-fitting models in the model set. Our model selection process consisted of first

identifying the best-fitting model for detection probability, then assessing goodness of fit, and finally fitting alternative survival models using the best-fitting detection model. We evaluated goodness of fit by estimating the degree of overdispersion using two different parameters in program MARK: the median-$\hat{c}$ procedure and the bootstrap goodness-of-fit procedure. Goodness of fit was evaluated using a model that allowed both survival and detection to vary independently among reaches and years (i.e., a reach $\times$ year interaction). Estimates of $\hat{c}$ less than or equal to 4 indicate that variability in the data was greater than expected given the multinomial likelihood structure of the mark–recapture model. Values of $\hat{c}$ greater than 1 indicate overdispersion, with more variability in the data than expected given the multinomial structure of the mark–recapture model, while values much greater than 1 (e.g., $\hat{c} > 4$) indicate a fundamental lack of fit, whereby the model structure poorly describes variation in the data (Burnham and Anderson 2002). We estimated $\hat{c}$ to be 1.54, indicating that our model structure was appropriate but that our data were slightly overdispersed. We therefore used the quasi-AIC (QAIC$_c$), which adjusts the AIC value based on $\hat{c}$, to select the model that was most supported by the data and ranked with the lowest QAIC$_c$ score. In addition, $\hat{c}$ was used to inflate the SEs of parameter estimates in the model selected for inference.

The relative importance of covariates in the selected model (lowest QAIC$_c$ score) was evaluated graphically and by examining point estimates of β coefficients with 95% CIs. Covariates having β coefficients with large absolute values were interpreted to have a larger effect on survival. Covariates having β coefficients with 95% CIs that overlapped zero were interpreted as not being significantly different from zero (i.e., no detectable effect). Covariates that did not contribute significantly to explaining the data were still retained in the selected model because they were chosen a priori to be important for their potential effect on survival (Burnham et al. 2011).

To identify the most parsimonious detection model, we fitted a series of models with increasing complexity while holding the survival model structure fixed using the reach $\times$ year interaction model. Like survival, we modeled the effect of covariates on detection as linear on the logit scale (equation 1). The simplest model included only sampling occasion (i.e., receiver site) as a main effect on detection probability (Supplementary Material). Next, we added year as a categorical factor to the reach model. The third model added an interaction between year and receiver site because the number of receivers and/or receiver model used at each location varied among years. Finally, the mean reach-specific velocity for each individual was added to each of the three models above for a total of six models

in the model set. We hypothesized that river velocity and the ambient noise associated with velocity impact the attenuation of acoustic signals in water, thereby affecting detection probability. For all models, detection probabilities were set to zero when receivers were not deployed below Paynes Creek (location 6) and at the Mill Creek confluence (location 8) in 2013, below Cypress (location 2) when fish were released downstream of this location in 2016, and below China Bend (location 15) in 2017. We found that the model with water velocity and a site × year interaction had the lowest $QAIC_c$, which was considerably lower than that of the second-best model, which included only a site × year interaction ($\Delta QAIC_c = 2,069$; Supplementary Material). Therefore, the model including water velocity and the site × year interaction was used for all survival models.

Using an approach similar to that described above for the detection models, we fitted a set of eight survival models (Table 3) of increasing complexity and we used the $QAIC_c$ model selection criterion to rank each model. Subsets of the more parameterized models were evaluated using the same model selection criteria. As a basis of comparison with more parameterized covariate models, the models with the fewest variables only estimated survival separately for each reach or for each reach and year. From there, we included a model to test the effect of reach length (i.e., travel distance) and travel time on survival, with an intercept offset for each year. This model tested whether reaches with longer travel times and reach lengths, which increase exposure to predators (Anderson et al. 2005), could better explain variation in survival among reaches and years. Third, we added the RAFT model's flow variables (e.g., flow and velocity) to models that included reach length and travel time to test whether river flows affected survival after accounting for effects of travel time and reach length. Fourth, we evaluated models that only included time-constant habitat covariates (e.g., wooded bank habitat, number of tributaries, etc.; see Table 2 for the full list) or time-varying covariates (e.g., temperature and depth) that excluded flow variables. Finally, the most complex models combined all covariates from the preceding models, fitting one full model with interannual reach flow and another with intra-annual reach flow.

RESULTS

Spatiotemporal Conditions

Water temperatures ranged from 8°C to 16°C throughout the study period and varied among years but always had an increasing trend from February to April, as measured at Bend Bridge (Figure 2). Drought years 2014 and 2015 had the warmest mean February–March whole-river temperatures (12.2°C and 13.6°C, respectively). Peak flows

in the Sacramento River varied temporally between years in response to storm events: no pulses in 2013, a few weak pulses in 2014, a single large pulse in 2015, two moderate pulses in 2016, and many large pulses on top of extremely high sustained flows in 2017 (Figure 2).

Riparian channel features varied spatially across the study area, with a greater number of tributaries upstream and greater percentage of revetment, greater number of diversions, and a smaller width : depth ratio downstream (Figure 1). Bank type characteristics were distributed in distinct sections of the Sacramento River (Figure 3). The upper section (reaches 1–6) contained mostly wooded bank, with some bare bank and lesser amounts of revetment. The middle section (reaches 7–12) was predominantly bare bank, with some wooded bank and lesser amounts of revetment. The area with the highest proportion of bare bank was associated with off-channel habitat (Figure 1) in drought years ($r = 0.80$). The lower river section (reaches 13–17) was predominantly revetment, with some wooded bank and a lesser amount of bare bank.

Travel Time

The time it took fish to travel downstream varied by reach and across years with different flow, velocity, and temperature profiles (Figure 4). Fish slowed down through the upper and middle reaches of the river during the high-flow year, through the middle reaches during all years, and in the lower reaches during the most critically dry year (2013; Figure 5). Travel times were the longest in the wettest and driest years. In the wettest year (2017), median travel time in the upper Sacramento River (Figure 1) was 24 d, ranging up to 70 d, while in the critically dry year (2013), median travel time in the middle Sacramento River was 33 d, ranging up to 54 d (Table 4). The most consistent slow travel times occurred in the middle Sacramento River, within a 55-km stretch of the river between Woodson Bridge and Tisdale (reaches 9–13; Figures 1, 5). This part of the river coincides with the greatest extent of connected off-channel habitat that was visible during the wet year between Red Bluff and Colusa (Figure 1).

Reach-Specific Patterns in Survival

Reach-specific survival scaled by distance and time (per 10 km per day) was consistently high (98–100%) in the upper reaches (1–4) and lower reaches (13–17) of the Sacramento River (Figure 6A). Reach-specific survival was lowest (96%) at reach 7 and intermediate (97–98%) through reaches 8–12 between Red Bluff and Colusa.

Factors that Affect Survival

Survival models with flow and habitat covariates received more support than the models that included only reach or reach and year, indicating that we had identified features that were important for juvenile salmon survival. The top-ranked survival model based on $QAIC_c$ was the full intra-

TABLE 3. Covariates included in each of the candidate mark–recapture survival models.

| Covariate name	Reach	Distance–travel time	Interannual flow	Habitat	Intra-annual flow	Reach and year	Full interannual	Full intra-annual
Reach distance		x	x	x	x		x	x
Fish FL				x			x	x
Proportion of revetment				x			x	x
River sinuosity				x			x	x
Diversions per kilometer				x			x	x
Proportion of shaded riparian area				x			x	x
Tributaries per kilometer				x			x	x
Channel width : depth ratio				x			x	x
Mean slope of reach				x			x	x
Median travel time per reach		x	x	x	x		x	x
Reach	x							
Calendar year		x	x		x	x		
Reach × year interaction			x			x		
Flow standardized by reach			x			x	x	
Mean water temperature per reach							x	x
Mean water depth per reach							x	x
Mean water velocity per reach							x	x
Off-channel habitat per kilometer							x	x
Flow standardized by reach and year					x			x
Annual flow at Bend Bridge					x		x	x
Yearly reach flow × annual flow interaction								x
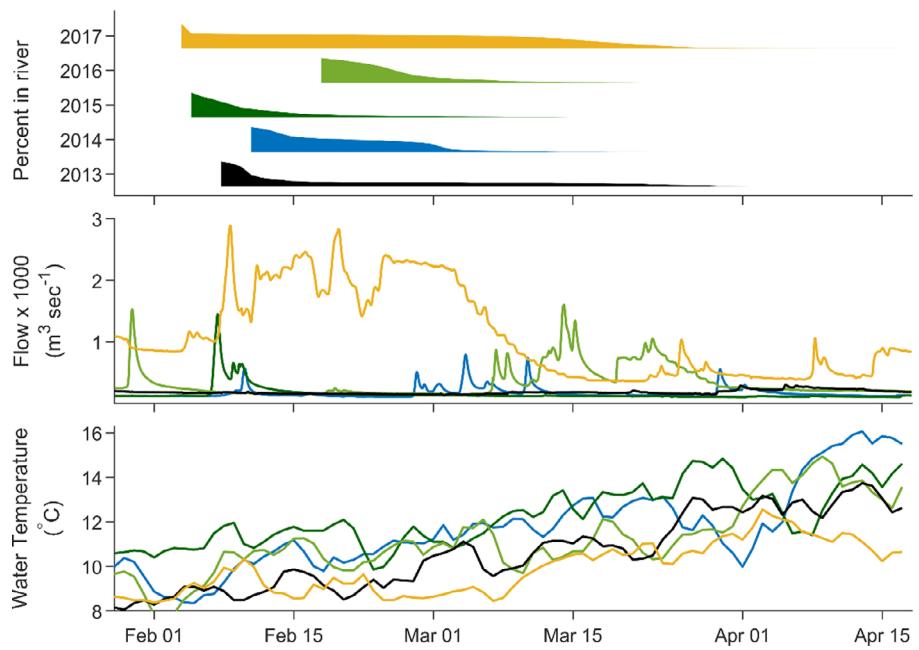
FIGURE 2. Percentage of acoustic-tagged winter-run Chinook Salmon juveniles in the Sacramento River from the date of release to the date on which the last fish was detected at Tower Bridge in the city of Sacramento for each year (upper panel). Flow (middle panel) and water temperature (lower panel) at Bend Bridge are also presented for each year (U.S. Geological Survey/U.S. Bureau of Reclamation hydrologic station [40.28849°, −122.186661°; rkm 489.4]; https://dashboard.waterdata.usgs.gov/api/gwis/2.0/service/site?agencyCode=USGS&siteNumber=11377100&open=15630).
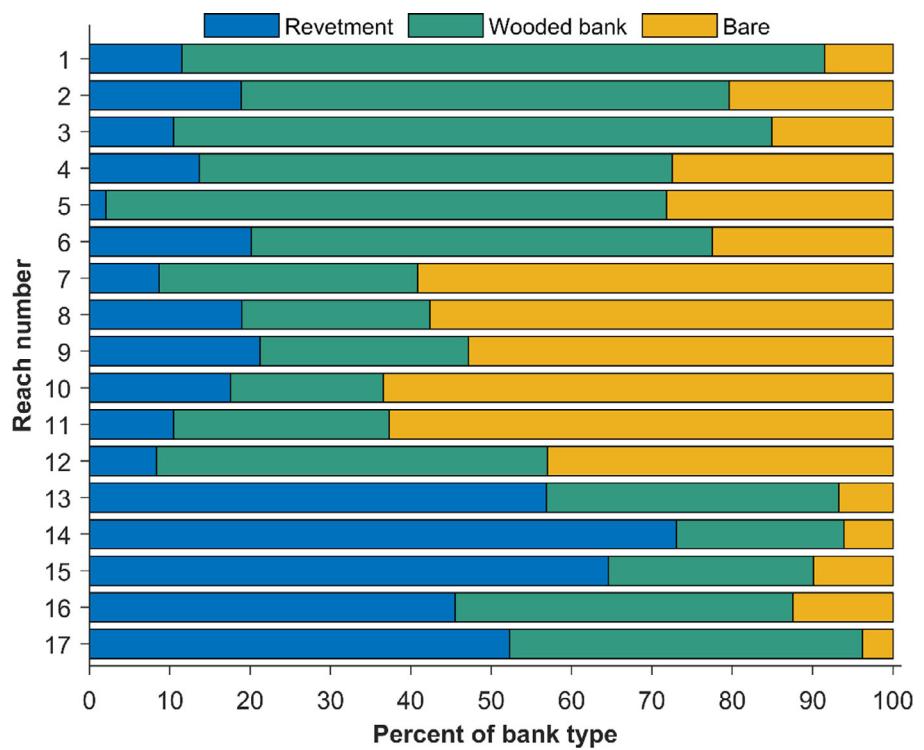
FIGURE 3. Percentages of revetment, wooded bank, and bare bank shoreline habitat types from upstream (reach 1) to downstream (reach 17) reaches of the Sacramento River. The area with the highest proportion of bare bank is associated with off-channel habitat (Figure 1) during drought years ($r = 0.80$).

annual reach flow and habitat model (Tables 3, 5), characterized by an interaction between mean annual flow and intra-annual reach flow and a combination of time-constant, reach-specific habitat features, reach water velocity, travel time, and fish length (Table 3). Among covariates with significant coefficients, as judged by 95% CIs that did not overlap zero, variation in annual flow had the strongest positive association with survival. These findings indicate that a 1-SD change in annual flow had a stronger effect on survival than a 1-SD change in any of the other covariates in the top-ranked model. However, the effect of annual flow was dampened by the negative effect of an intra-annual reach
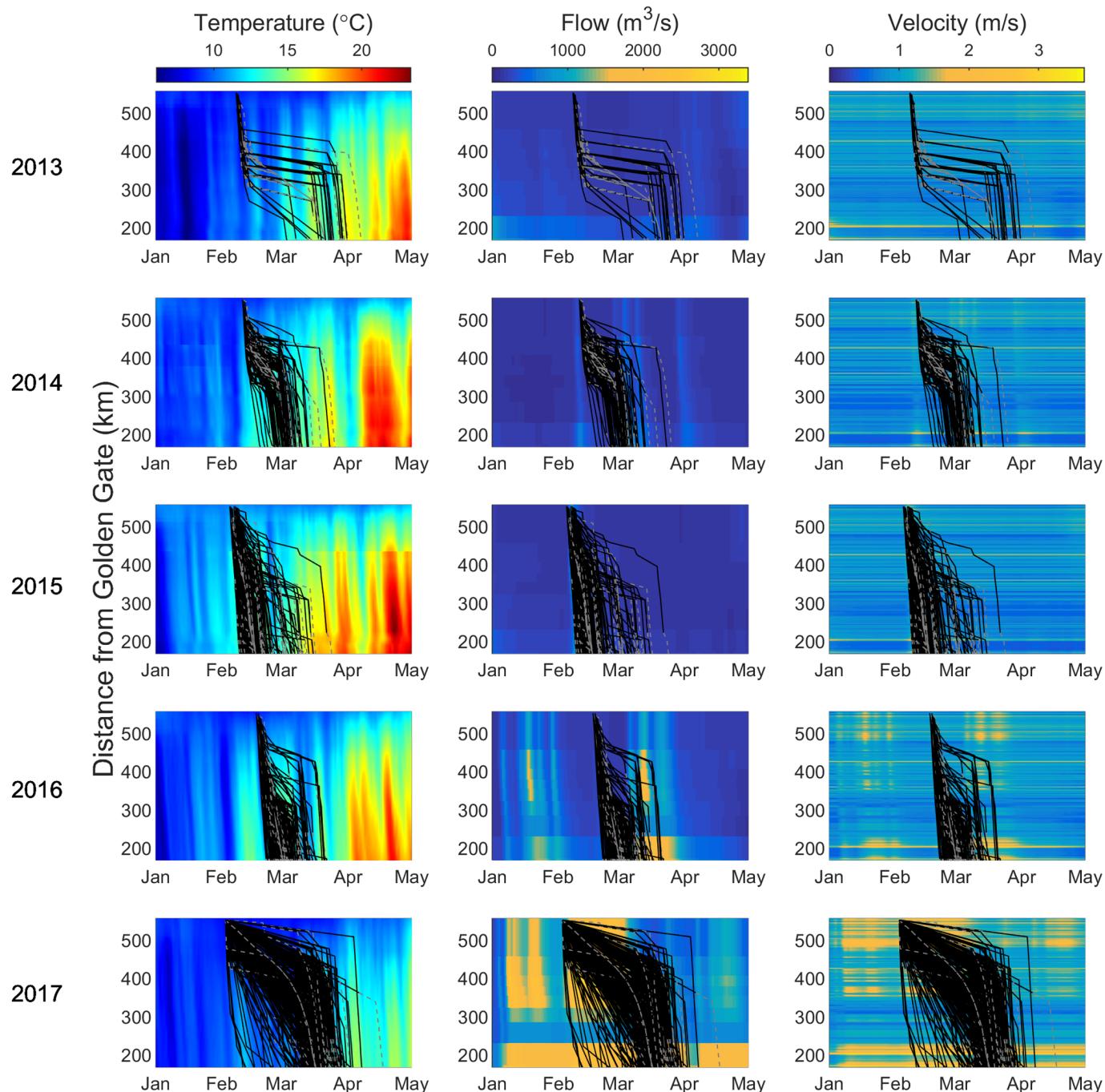
FIGURE 4. Downstream detections of juvenile winter-run Chinook Salmon (black lines) and interpolated tracks (gray dashed lines) in the Sacramento River from Redding to Sacramento, California. Detections overlay River Assessment for Forecasting Temperature (RAFT) model outputs for temperature (left column), flow (middle column), and velocity (right column) in water years 2013 (top row) to 2017 (bottom row).
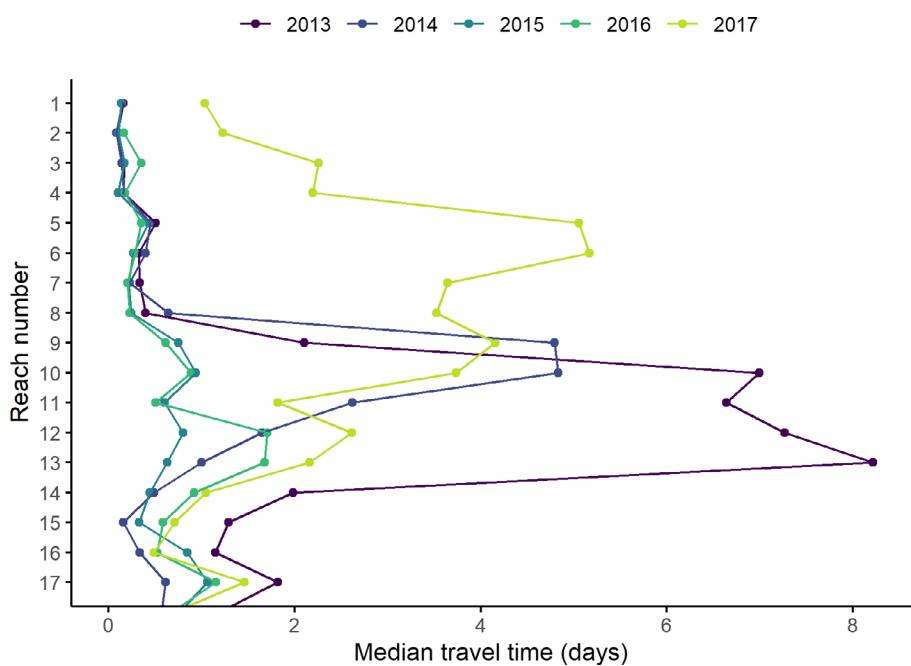
FIGURE 5. Travel time (d) by reach for juvenile winter-run Chinook Salmon migrating down the Sacramento River in each year. Each point represents the median number of days it took tagged fish to transit through a reach bounded upstream and downstream by acoustic receivers.

TABLE 4. Yearly variation in median travel time (d) of juvenile winter-run Chinook Salmon (Count) moving down the Sacramento River, with minimum (Min) and maximum (Max) values for the upper, middle, and lower sections (Figure 1) of the river.

Year	Section	Count	Median	Min	Max
2013	Upper	118	3	1	44
	Middle	23	33	4	54
	Lower	22	14	2	35
2014	Upper	288	3	1	36
	Middle	146	17	2	36
	Lower	135	3	2	13
2015	Upper	446	2	1	31
	Middle	310	5	1	36
	Lower	233	3	1	32
2016	Upper	531	2	1	28
	Middle	362	6	2	28
	Lower	285	5	1	28
2017	Upper	335	24	1	70
	Middle	293	18	2	44
	Lower	234	6	2	39

flow × annual flow interaction term. Other covariates with a significant positive effect on survival (i.e., 95% CIs that did not overlap zero) included percentages of revetment and wooded bank, fish length, and reach-specific intra-annual flow (Figure 7). Channel width : depth ratio, reach-specific velocity, depth, and reach length all had negative associations with survival, along with travel time, river temperature, and the intra-annual reach flow × annual flow interaction term. River sinuosity, diversion density, off-channel habitat, slope, and number of tributaries had negligible effects on survival, indicating that the covariates included in the selected model sufficiently explained differences in survival among years and reaches. Time-constant covariates, including river sinuosity, slope, and percent wooded bank, acted to increase estimates of survival in the upper reaches but decreased estimates of survival in the lower reaches relative to mean covariate values (Figure 6B). In contrast, the width : depth ratio decreased estimates of survival through the middle river (reaches 7 and 8) and increased estimates of survival relative to mean covariate values from reach 13 downstream, where the river becomes more channelized with revetment along the bank.

Mean annual flow, intra-annual reach flow, and their interaction had contrasting effects on predicted survival (Figure 8). Predicted survival per 10 km per day increased as a function of mean annual flow, with intra-annual reach flow and all other covariates set to mean values (Figure 8A). Due to the negative interaction between annual and intra-annual reach flow, the slope coefficient for intra-annual reach flow declined with annual flow such that reach effects were more positively associated with survival in low-flow years (Figure 8B). The combined effect of mean annual flow and intra-annual reach flow led to a positive relationship in low-flow years but a flat relationship in the high-flow year (Figure 8C). These findings
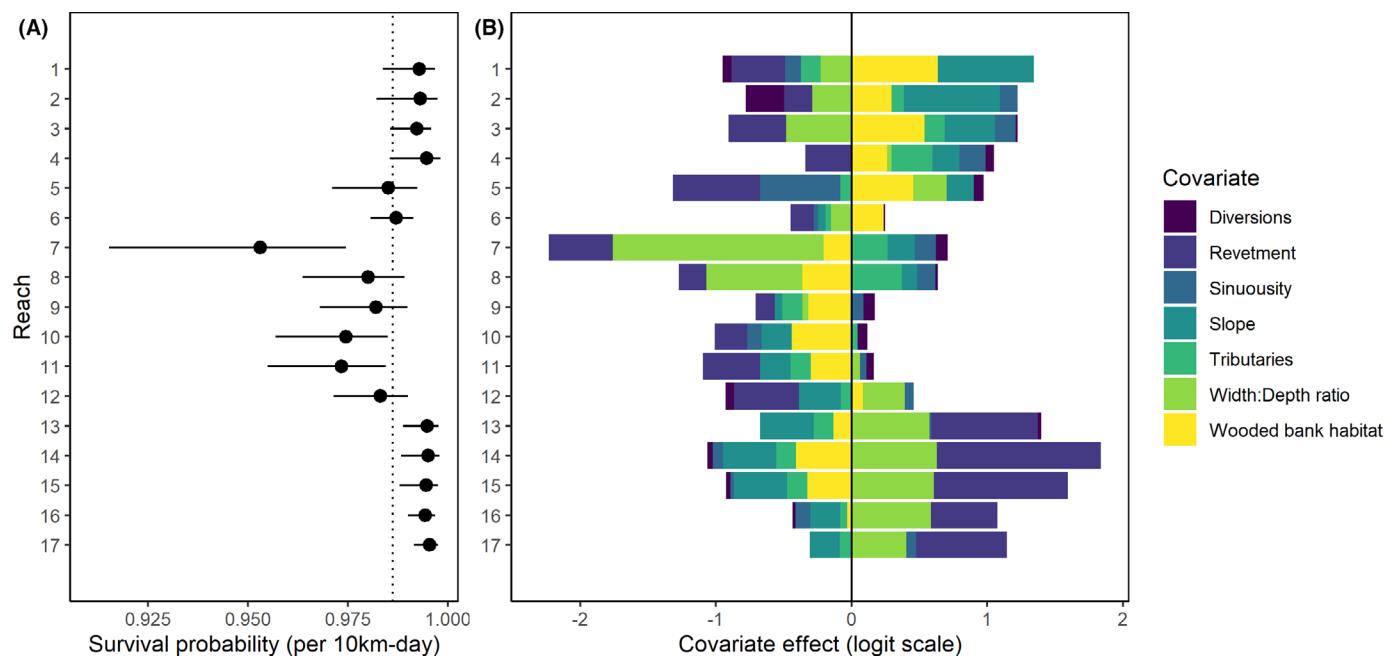
FIGURE 6. Effect of time-constant, reach-specific covariates on survival of juvenile winter-run Chinook Salmon: **(A)** predicted survival per 10 km per day (with 95% CIs) when all covariates are set to mean values except the reach-specific covariates shown in panel B (dashed line shows the mean survival over all reaches); and **(B)** the effect of each reach-specific covariate on the linear predictor (see equation 1). Covariate effects (represented as stacked bars) were calculated as the product of the standardized covariate and its corresponding slope coefficient (i.e., β). Habitat features associated with the riverbank also varied across the migration corridor (see Figure 3).

suggest that variation in daily reach-specific flows affect survival more in years when mean annual flow is low than in high-flow years.

DISCUSSION

The Sacramento River is the main source of California's water conveyance system and acts as a key migration corridor for anadromous fish moving from freshwater to ocean environments. Therefore, the management of reservoir releases directly affects the conditions encountered by juvenile salmon as they migrate to the ocean as smolts. Because of their small size, smolts are vulnerable to how these conditions affect exposure to predators during the downstream emigration phase of their life history (Sabal et al. 2021). Additionally, they may be vulnerable to delayed mortality in the ocean from associated migration duress (Michel 2018).

The decline of the winter run, as the most critically imperiled Chinook Salmon run, remains one of the most important issues confronting water management in the Sacramento River. In this study, we observed that mean annual flow over the time during which fish were in the river had the most positive effect on their survival out of all the modeled covariates. Moreover, we observed that higher flow at the reach scale had a more positive effect on survival in dry years with low flow than it did in wet

years with high flow. Although the interaction between annual flow and intra-annual reach flow occurs with one high-flow year observed in 2017 (Figure 5), similar observations have been made in previous work on late-fall-run Chinook Salmon (Courter et al. 2016; Perry et al. 2018; Henderson et al. 2019). Anomalous wet years like 2017 are important to consider because California remains in a state of extended drought, and obtaining data for years like this is likely to be difficult given their importance for fish survival. It has long been known that freshwater flow is connected to variation in survival of juvenile salmon migrating to the sea (Kjelson and Brandes 1989; Newman and Rice 2002; Michel 2018; Notch et al. 2020); however, our findings suggest that although it may not be possible to create wet-year flow conditions like those in 2017, increasing flow through managed flow pulses can benefit salmon survival. Our results also improve current understanding of how annual changes in flow can affect survival rates and spatially varying changes in habitat features known to be important for rearing (Zeug et al. 2019; Zeug and Winemiller 2008) with time-varying features of the river (i.e., reach flow, temperature, and depth; Henderson et al. 2019). Considering these factors together in a novel framework that scales survival by the amount of time fish are spending in a given part of the river provides a clearer way to examine spatial variation in migration survival.

TABLE 5. Survival (ϕ) model selection based on quasi-Akaike's information criterion (QAIC$_c$) ranks with a $\hat{c}$ of 1.54. Models are shown with the number of parameters (npar), the calculated value of QAIC$_c$, the difference in QAIC$_c$ value between the given model and the top model (ΔQAIC$_c$), and the deviance value (QDeviance).

Survival model	npar	QAIC$_c$	ΔQAIC$_c$	QDeviance
Full intra-annual	108	13,320.53	0.00	13,103.37
Full interannual	106	13,415.67	95.15	13,202.56
Separate survival for reach and year	175	13,438.75	118.23	13,085.71
Intra-annual reach flow	100	13,488.73	168.20	13,287.73
Habitat	102	13,508.79	188.26	13,303.76
Interannual reach flow	98	13,544.11	223.58	13,347.15
Distance–travel time model	97	13,547.31	226.78	13,352.37
Reach	107	13,576.39	255.86	13,361.25
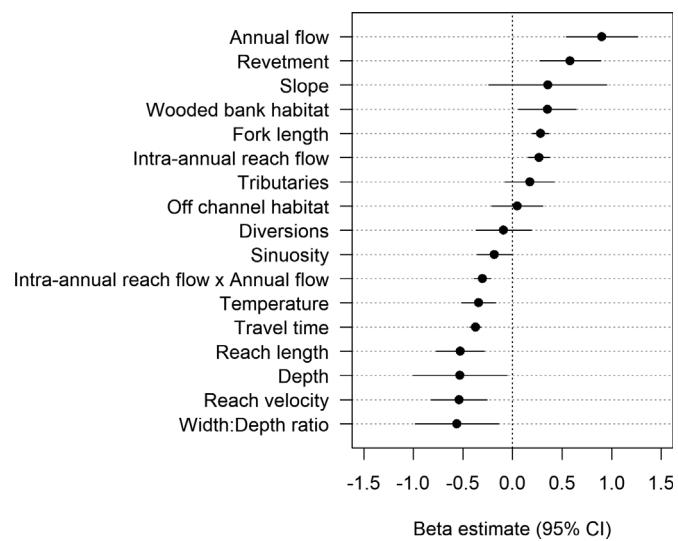
FIGURE 7. Parameter estimates ($\pm$95% CI) of slope coefficients (i.e., β estimates) for each covariate in the selected model. The CIs that overlap zero indicate no significant effect.

In some ways, our results differed from those of previous studies on the late-fall run (Perry et al. 2010; Michel et al. 2015; Henderson et al. 2019) and spring run (Cordoleani et al. 2018; Notch et al. 2020) of Chinook Salmon. We observed stopover behavior in all years, but the region of the river in which stopover behavior occurred appeared to depend on density-dependent habitat availability, with fish exhibiting stopover behavior higher in the river during the wettest year and lower in the river during the driest year (Figure 5). During dry years with lower flow, salmon
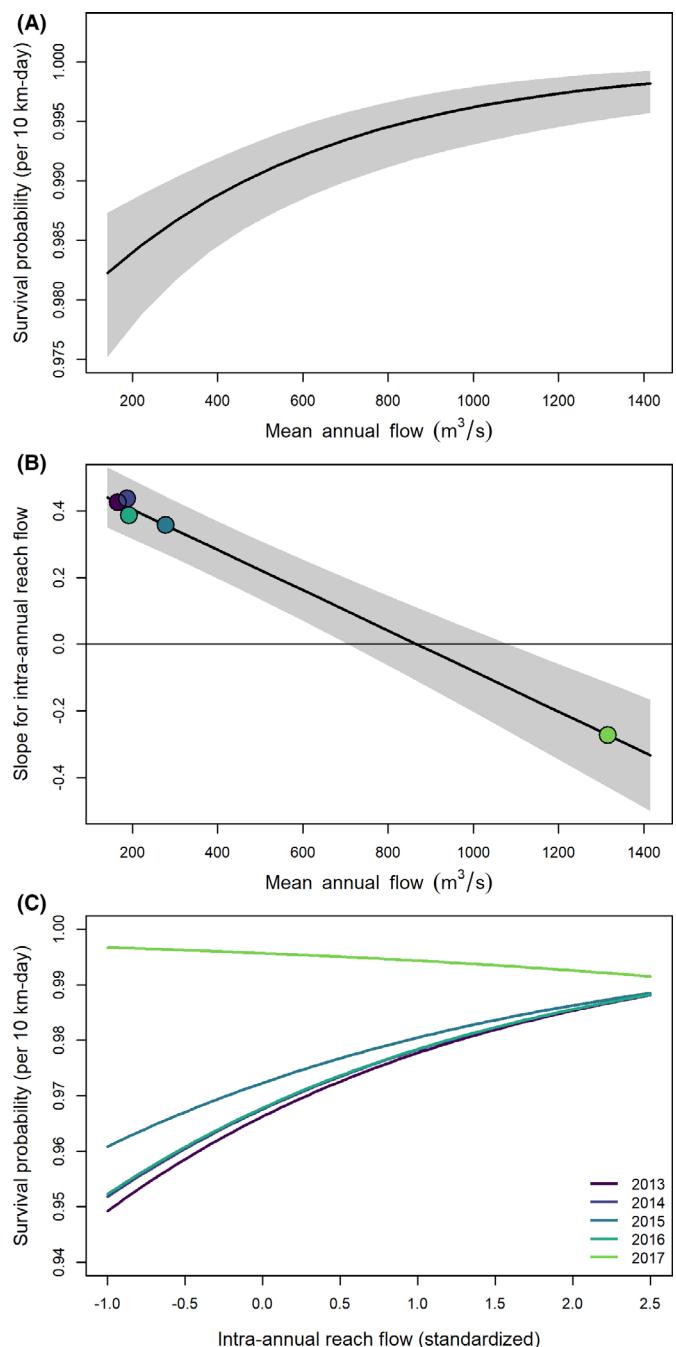

FIGURE 8. Effects of mean annual flow, interannual reach flow, and their interaction on predicted survival of juvenile winter-run Chinook Salmon: **(A)** predicted survival per 10 km per day as a function of mean annual flow, with intra-annual reach flow and the other covariates set to mean values, except for travel time (set to 1 d) and reach length (set to 10 km); **(B)** effect of the interaction between mean annual flow and intra-annual reach flow, showing the slope coefficient for intra-annual reach flow as a function of mean annual flow (symbols represent the slope for intra-annual reach flow for each value of mean annual flow; symbols are slightly jittered vertically to reduce overlap); and **(C)** combined effect of mean annual flow and interannual reach flow on predicted survival per 10 km per day. Shaded regions in panels A and B show the 95% CIs.

that delay migration tend to experience higher mortality (Sturrock et al. 2020). In 2013, a year that was characterized by low flows and a nearly flat hydrograph (Figure 2), the stopover behavior low in the river and the corresponding low survival suggest that fish may not initiate downstream migration without an appropriate migration cue, which usually arrives as a pulse in flow (del Rosario et al. 2013) or, ultimately, as warming temperatures (Figure 4). Salmon are known to avoid high temperatures by timing their migration to occur before or after peak river temperatures (Hodgson and Quinn 2002). Therefore, we might expect that fish migrating in response to high temperatures could suffer indirect effects, such as a reduction in aerobic scope (Eliason and Farrell 2016).

The trade-off between increased exposure to predators and access to good foraging habitat is indirectly supported with a positive association between annual flow and survival (Michel et al. 2015; Perry et al. 2018; Henderson et al. 2019; Zeug et al. 2020). High flows can benefit survival by increasing water turbidity, thus providing cover for juveniles to evade predators (Gregory and Levings 1998), and by offering access to a greater diversity of foraging and refuge habitat that allows fish to slow down higher in the watershed. A positive association of body size with survival is consistent with previous work on other runs (Cordoleani et al. 2018; Henderson et al. 2019; Notch et al. 2020), which suggests that a fish's size can reduce predation as individuals grow beyond the gape limitation of some predators (Nowlin et al. 2006). A caveat is that the increased tag burden of fish in the smaller size range could disproportionately affect the survival of acoustic-tagged fish (Brown et al. 2010; Liss et al. 2016). Although we did not detect a fish size effect for tag shedding or survival rates in the portion of tagged fish that were held and monitored for 60 d, tag burden will disproportionally affect the performance of smaller fish and may contribute to the observed higher survival for larger fish.

Some relationships between other covariates and survival ran counter to our working hypotheses and revealed interesting patterns upon further investigation. First, increased survival was associated with a higher proportion of revetment along the riverbank (Figure 7). However, the positive effect of revetment was only observed where it was predominant along the riverbank in the last five reaches (Figure 6B, reaches 13–17), which had similar habitat and morphology (e.g., deep, narrow, low-gradient channels; Supplementary Material) and downstream of reaches where fish were observed exhibiting slow travel. Fish surviving to these lower reaches are likely larger because of longer feeding durations or upstream size-selective mortality that removed smaller fish. Moreover, fish holding upstream that survived to these lower reaches are more likely to be actively out-migrating, which decreases travel time (Figure 5) and exposure to predators.

Future work that compares the spatial survival of other runs that emigrate at other times may shed some light on the role of revetment, predation, and survival in this part of the river.

Second, while more rapid downstream movement may appear to result in better in-river survival for out-migrating smolts, the negative association between reach velocity and survival suggests that volitional downstream movement may be compromised. Inflection points that indicate a change to downstream migration behavior appear to correspond to sudden changes in the velocity profile of the river (Figure 4). As instream rearing is known to occur for winter-run fish in the main-stem Sacramento River (Freeman et al. 2001) and tributaries (Phillis et al. 2018), we may be observing a switch from resting and feeding to migration behavior in which vulnerability to mortality is higher, at least initially. During the wet year of 2017, when water velocities were high throughout the main channel, better access to low-velocity off-channel and ephemeral tributary habitat throughout the upper and middle Sacramento River may have been key for fish to improve foraging opportunities on prey (e.g., drift) that would otherwise have been advected in the main stem throughout the largest pulse flow periods.

Limitations of observational studies on hatchery-raised salmon in the field can make it difficult to infer how variables might affect wild fish, which initiate their smolt migration earlier in the fall. Natural-origin winter-run fish initiate their downstream migration beginning in July and into autumn, around the time when the first storms of the year arrive in California, following several months of summer conditions characterized by low flows and warm temperatures. These early storms create unique conditions, known colloquially as a "first flush," when accumulated debris and sediment are carried downstream, creating turbid conditions and cover that wild fish could use as refugia from predators. In contrast, our study fish were released during the peak of winter in a single synchronized event with the entire hatchery production of winter run to provide a swamping effect and improve survival. A study on Sockeye Salmon *O. nerka* using a combination of PIT and acoustic tags demonstrated that the estimated survival probability for smolts increased from 50% when migrating with 2,000 conspecifics to 95% when migrating with 350,000 conspecifics (Furey et al. 2016). Because density dependence spreads fish out as they migrate downriver through rearing habitat along channel margins, a predator swamping effect will attenuate at an unknown rate and will likely have different characteristics than natural-origin fish experience. In addition, if density-dependent habitat availability is indeed the primary mechanism that predicts where fish will slow down, natural-origin fish that are not confronted with as many conspecifics at a given time are more likely to exhibit slower travel times in the upper

reaches of the river than that of our study fish. Future studies that release similar numbers of fish at different locations along the river may be able to control for a swamping effect and more closely approximate how natural-origin fish behave.

Management Implications

Flow management is often used as a primary tool for mitigating impacts to fish. When high flows are not available, maintaining functional flows through flow pulses offers managers another way to improve survival under low-flow conditions (Michel et al. 2021). Figure 8B describes how the slope of the intra-annual reach flow–survival relationship changes with mean annual flow. This relationship can be used by managers to determine, at a given level of annual flow, whether a flow pulse is likely to produce a measurable effect on survival. For example, when flow is less than about 700 m^3/s, given the confidence interval, pulse flows will have a high probability of having a positive effect on survival. The relationship also indicates what the magnitude of the effect may be. For example, when mean annual flow is 600 m^3/s, a pulse flow is going to have half the effect of a pulse event than when mean annual flow is 200 m^3/s. Of course, there are no observations between 300 and 1,300 m^3/s, and collecting these data in a targeted way is recommended to determine whether the relationship at higher flows is nonlinear.

As climate change induces more variability and a higher frequency of hot and dry conditions, facilitating migration with pulse flows is likely to become harder to achieve due to water scarcity and a lack of habitat diversity throughout the watershed (Lindley et al. 2007). This means that the resilience of declining salmon populations will increasingly depend on habitat restoration (Herbold et al. 2018). While habitat restoration can take months or years to achieve, depending on the scale of the activity, more information is needed to understand which characteristics of holding habitat cause fish to alter emigration. Some of the ways that winter-run fish interacted with spatial covariates appeared to change as they moved downstream, possibly because of selection, given that hatcheries release naïve juveniles into the upper river, or because of switching from holding to out-migration behavior. It is therefore important for resource managers to consider that how fish perceive the value of habitat variables can change in response to density-dependent effects and as the fish develop and mature, exhibiting behavioral and physiological plasticity as they undergo smoltification.

In this study, off-channel habitat was inaccessible during all years except 2017, which is likely why we were unable to detect an effect of access to off-channel habitat on survival. Natural-origin winter-run fish, which begin to rear and out-migrate during late fall and winter, when natural flows are more variable, may have better access to ephemeral off-channel habitat (Bellido-Leiva et al. 2021). We detected low survival and slow travel times in a middle section of the river with a large extent of potential off-channel habitat (Figure 1) where bare banks predominated (Figure 3), suggesting a location where juveniles may be responsive to targeted restoration efforts (around reaches 7–12), such as connecting off-channel habitat at lower flow thresholds.

The positive effect of wooded bank habitat on survival throughout the study area suggests that restoration activities that increase cover and bank complexity along the shoreline of the main-stem river could improve foraging and resting habitat (Zajanc et al. 2013). Indeed, vegetation has been shown to have the largest effect on smolt movement rates in the Sacramento River, with fish slowing down in areas having increased cover (Zajanc et al. 2013; McNair 2015). Wooded bank habitat on the Sacramento River has been lost over the past 50 years, primarily due to bank protection projects like the Sacramento Riverbank Protection Project. Since 1961, over 225 km (140 mi) of revetment (riprap) have been constructed on the riverbank, with only 7% of shaded riparian cover remaining in the lower Sacramento River (USFWS 2004). In our study, fish moved quickly through areas with heavy revetment and they exhibited slower movement in areas with wooded habitat. Moving slowly allows the fish time to rest and feed on their journey to sea.

In conclusion, out-migration survival of winter-run juveniles on the Sacramento River was best described by an intra-annual flow model with a mix of time-varying spatial covariates, reach-specific habitat features, and individual effects. Years with higher flow showed a strong association with increased survival, and years with lower flow showed a more positive flow–survival relationship at the reach scale. Wooded bank habitat had a positive association with survival, despite having been replaced by revetment along more than 90% of the riverbank in the Sacramento River. Evidence for instream holding behavior, which is known to be an important life history trait in juvenile winter-run fish, was indicated by slow travel times that appeared to respond to density-dependent habitat availability. Consistent slow travel times were observed in a section of the river between Red Bluff and Colusa, which coincided with the greatest extent of potential off-channel habitat that was connected during the high flows of 2017. Other habitat features did not have a consistent effect on survival across the migration corridor, as they displayed either a positive association with survival in the upper river and a negative association with survival in the lower part of the river or vice versa, indicating a dynamic relationship between the fish's physiological/behavioral developmental characteristics and their environment. With increased variability in drought and flood severity associated with climate change, it will become more important

to disentangle the behavioral factors that affect out-migration timing (Munsch et al. 2019) and survival (Johnson et al. 2017), particularly as demands for freshwater put additional pressure on native fishes like Central Valley Chinook Salmon at the southern extent of their range.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.