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ARTICLE

Juvenile Chinook Salmon Survival, Travel Time, and Floodplain Use Relative to Riverine Channels in the Sacramento–San Joaquin River Delta

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Abstract

Floodplains provide multiple benefits to both resident and migratory fish species, including juvenile Chinook Salmon *Oncorhynchus tshawytscha*, but direct comparisons of survival during migration through a floodplain versus riverine routes are scarce. The Yolo Bypass is a broad floodplain of the Sacramento River that floods in about 30% of years in response to large, uncontrolled runoff events. We analyzed data from an acoustic telemetry study conducted in winter 2016 to estimate the proportion of tagged juvenile Chinook Salmon entrained from the Sacramento River into the Yolo Bypass and their spatial distribution within the Yolo Bypass. In addition, we compared survival and travel time of Chinook Salmon that migrated through the Yolo Bypass to those migrating via alternative non-floodplain migration routes at varying stages of a flood event that activated the Yolo Bypass. We found that entrainment into the Yolo Bypass ranged from 1% to 80% among different release groups, with the highest entrainment coinciding with the peak of the March 2016 flooding event. Survival for Chinook Salmon migrating through the Yolo Bypass was similar to survival of those migrating through main-stem migration routes. At the relatively high flows necessary to enable flooding of the Yolo Bypass, survival estimates varied little among release groups and migration routes. Furthermore, mean daily survival rates for Chinook Salmon migrating through the flooded Yolo Bypass were comparable to those of fish migrating through the other non-floodplain routes. Median travel times remained relatively constant during various stages of flooding in the Yolo Bypass. This research should help managers to better understand the potential costs and benefits to floodplain restoration and routing of migrating Chinook Salmon into off-channel habitat.

In riverine environments, floodplains provide ephemeral off-channel habitat that is considered critical to fish species that have evolved to exploit conditions such as pulsed food subsidies and cover from predators (Welcomme 1979; Junk et al. 1989; Bayley 1995; Sparks 1995; Sommer et al. 1997; Lytle and Poff 2004; Balcombe et al. 2007). In lowland reaches of rivers, where flooding is often most extensive and prolonged, floodplains can serve as prime nursery grounds for rearing juveniles, providing heightened availability of trophic resources and elevated growth

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rates relative to the main river channel (Junk et al. 1989; Sommer et al. 2001a, 2001b; Balcombe et al. 2007; Beesley et al. 2012). This is particularly true for Chinook Salmon *Oncorhynchus tshawytscha*, which in numerous studies have been shown to benefit from elevated growth rates in off-channel habitat (Sommer et al. 2001b; Jeffres et al. 2008; Limm and Marchetti 2009; Takata et al. 2017).

Based on this research, restoration of floodplain access and increased floodplain inundation are central to plans and policy for restoring Pacific salmon populations in channelized rivers from California to Washington, including Chinook Salmon in California's Central Valley (DSC 2018; https://resources.ca.gov/Initiatives/California-EcoRestore). However, resource managers remain concerned that actively migrating juvenile Chinook Salmon using reconnected floodplain and other ephemeral off-channel habitat may experience diminished survival due to delayed migration, increased vulnerability to predation, elevated water temperature, or other potential causes of mortality. Compared to the abundant information supporting the growth benefits of floodplain rearing, relatively few studies have examined factors affecting survival within floodplains or the proportion of migrating fish that use floodplain habitat as opposed to main-channel habitat.

The Yolo Bypass is a 323-km^2 floodplain adjacent to the Sacramento River, which historically flooded during the wet season, creating extensive perennial wetlands (Whipple et al. 2012). In the 1930s, an extensive levee system was built to disconnect these lands from the Sacramento River to allow agricultural development. However, Fremont Weir was retained at the upstream end of the Yolo Bypass to allow flood waters onto the historical floodplain during extreme events (mean flooding frequency is 1 in 3 years), thereby preventing flooding of cities and farms downstream. Although the Yolo Bypass does receive some freshwater input from small tributaries outside of these large flood events, direct access for fish transiting the Sacramento River occurs only during flood events.

For migratory fish that are unable to access the Yolo Bypass, the migration seaward leads through a unique configuration of distributary channel junctions located near the upstream extent of tidal influence and featuring levees, armored rip-rap revetments, and water supply pumps (Figure 1). Juvenile Chinook Salmon traveling these areas have lower survival rates compared to migration within the less anthropogenically modified upper reaches of the Sacramento River (Buchanan and Skalski 2013; Michel et al. 2015; Plumb et al. 2019). In contrast, research suggests that the Yolo Bypass could provide benefits to migrating juvenile Chinook Salmon, such as reduced encounters with predators (Ward and Standford 1995; Sommer et al. 2005), diversification of life history strategies (Greene et al. 2010; Schindler et al. 2010; Carlson and Satterthwaite 2011), and a low risk of stranding (Sommer et al. 2005).

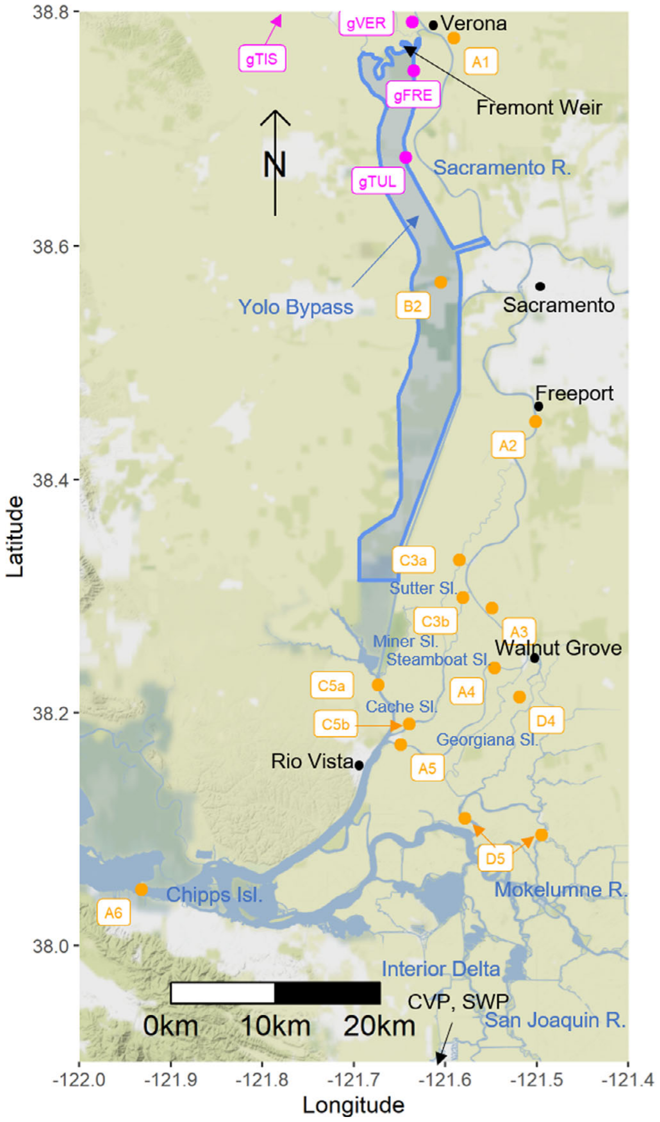

FIGURE 1. Map showing the study area in the Sacramento–San Joaquin River Delta, California, including telemetry stations used for Delta-wide estimates, juvenile Chinook Salmon release sites, and major hydrologic features (Sl. = Slough; Isl. = Island; CVP = Central Valley Project; SWP = State Water Project). Alphanumeric codes represent telemetry stations, and codes beginning with "g" represent release locations; both are labeled as in the model schematic depicted in Figure 3. Place names are included for reference. The Yolo Bypass, indicated by the shaded polygon, is only sometimes flooded.

Despite considerable differences in the physical habitat of floodplain and riverine channels of the Sacramento River, estimates of survival rates and relative use of the Yolo Bypass during flood events are lacking. To date, comparisons of survival among floodplain- or riverine-migrating Chinook Salmon in previous studies have been hampered by sparse data, the inability to separate freshwater survival from ocean survival, or releases of tagged fish occurring in nonflood years (Sommer et al. 2005; Takata et al. 2017; Johnston et al. 2018). Therefore, our study posed three primary questions: (1) "What proportion of juvenile Chinook Salmon migrated along different major migratory pathways at different flows during flooding of the Yolo Bypass?"; (2) "What are the route-specific survival and travel time of juvenile Chinook Salmon using the Yolo Bypass relative to those of fish using other available migratory routes during the same period of time?"; and (3) "What is the spatial distribution and the difference in survival of juvenile Chinook Salmon following different migration paths across the ≤ 4.8-km cross-section of the Yolo Bypass?"

METHODS

To address the three primary questions, we tracked releases of acoustic-tagged juvenile Chinook Salmon both just prior to and during overtopping of Fremont Weir, when extensive flooding occurred across the full expanse of the Yolo Bypass floodplain. During the flood event, we used paired floodplain and river release locations to track differential survival and we included releases upstream of the weir to estimate the proportion of juvenile Chinook Salmon using the floodplain. Hydrophone arrays transecting the floodplain provided information on spatial distribution of these fish across the floodplain, allowing us to test whether survival depended on spatial location.

Study area.— The Yolo Bypass is situated within the context of the branching network of channels of the north Sacramento–San Joaquin River Delta (hereafter, "Delta"), which affords oceanward-migrating fish several possible routes seaward (Figure 1). Several streams and agricultural drainages that are direct tributaries to the Yolo Bypass continue to flood small portions of the bypass in most years, and a canal along the eastern bypass levee, called the Toe Drain, collects and channels water from these sources year-round. Extensive flooding from the Sacramento River over Fremont Weir, with concurrent passage of migrating juvenile Chinook Salmon onto the floodplain, occurs on average about once every 3 years. When Fremont Weir, located just upstream from Verona, is overtopped, fish can be entrained into the Yolo Bypass, which rejoins the Sacramento River near Rio Vista via Cache Slough. Fish that are not entrained into the Yolo Bypass remain in the Sacramento River and may subsequently enter a number of other migration routes through the Delta. Sutter and Steamboat sloughs diverge from the main-stem Sacramento River downstream from Freeport and rejoin the Sacramento River near Rio Vista. Fish may also migrate through Georgiana Slough and, when its radial gate is open, the Delta Cross Channel near Walnut Grove. These two channels join the Mokelumne River, the lower San Joaquin River, and the channels of the interior Delta, which in turn lead to either of the Central Valley Project or State Water Project export facilities or rejoin the Sacramento River near Chipps Island (Figure 1).

Telemetry array.— Acoustic telemetry stations were deployed throughout the north Delta during the 2016 study period to monitor acoustic-tagged juvenile Chinook Salmon as they migrated to the ocean. Each telemetry station consisted of one or more acoustic tag-detecting hydrophones (VEMCO Models VR2W and HR2). Hydrophones were located just downstream of each major channel junction in each route, with the exception of the Yolo Bypass, where instead an array of 19 hydrophones spaced at about 200-m intervals was deployed along the Interstate-80 (I-80) bridge across the section flooded by the Yolo Bypass, approximately 22 km downstream from the Yolo Bypass entrance at Fremont Weir (Figure 1). Additional hydrophones were located at exits of migration routes, including where Sutter Slough, Steamboat Slough, and the Yolo Bypass rejoin the Sacramento River and where Georgiana Slough converges with the Mokelumne River (Figure 1). Finally, multiple hydrophones were deployed in the Sacramento River near Chipps Island to form a pair of detection arrays at the study area's furthest downstream point (Figure 1). Each telemetry monitoring station was assigned a letter–number-pair designation, with letters A–D designating stations within (A) the main-stem Sacramento River, (B) the Yolo Bypass, (C) Sutter Slough or Steamboat Slough, and (D) Georgiana Slough or the interior Delta. Numbers within a route increased with increasing distance downstream (Figure 1).

Fish tagging and transport.— Fish handling, holding, and tagging procedures were based on a well-established standard operating procedure developed for tagging salmon in the Columbia River basin (Liedtke et al. 2012). Juvenile late-fall-run Chinook Salmon reared at the U.S. Fish and Wildlife Service's Coleman National Fish Hatchery (Anderson, California) were obtained for this study. Fish were held at the hatchery until just prior to tagging, when they were anaesthetized, individually weighed and measured, and surgically implanted with an acoustic transmitter (VEMCO Model V5). To ensure that tag burden did not exceed 5%, in accordance with published recommendations (Martinelli et al. 1998; Liedtke et al. 2012), fish were selected for tagging only if their weight exceeded 13 g. After postsurgery recovery and monitoring, tagged fish were transported to one of several release sites. Tagged fish averaged 165 mm FL (range = 108–218 mm) and 50.0 g (range = 13.4–117.0 g), and average tag burden was 1.48% (range = 0.56–4.85%). Tagging and transport procedures are described in greater detail by Liedtke and Hurst (2017).

Fish release strategy.— Field crews conducted three releases between March 11 and March 18, 2016, with a target sample size of 240 fish each, yielding a total of 717

TABLE 1. Summary of the numbers and sizes of juvenile Chinook Salmon released at one of three general sites in the Sacramento–San Joaquin River Delta, California, during March 2016. All released fish were first surgically implanted with individually identifiable acoustic tags.

Release group	Date(s)	Release location	*N*	Mean FL (mm)	FL range (mm)
1	Mar 11–12	Tisdale	141	166.5	111–208
		Yolo Bypass	99	168.1	118–207
		Verona	0		
2	Mar 15–16	Tisdale	40	168.1	127–218
		Yolo Bypass	100	164.7	109–204
		Verona	100	166.6	113–218
3	Mar 17–18	Tisdale	40	168.4	132–203
		Yolo Bypass	98	169.1	119–211
		Verona	99	169.0	117–210

tagged Chinook Salmon released (Table 1). The three releases were timed to coincide with a flood pulse that was expected to overtop Fremont Weir and flood the Yolo Bypass (Figure 2). River discharge data were obtained from U.S. Geological Survey streamflow monitoring network, stations 11390500, 11425500, 11455315 (USGS 2016).

Because the proportion of Chinook Salmon expected to enter the Yolo Bypass was unknown, for each release group we released 40 fish into the Sacramento River at Tisdale 57 river kilometers (rkm) upstream of Fremont Weir (gTIS; Figure 1), 100 fish directly into the Yolo Bypass downstream of Fremont Weir (gFRE and gTUL), and 100 fish into the Sacramento River 2 rkm downstream of Fremont Weir (gVER). This strategy was implemented for two reasons. First, the release strategy balanced the need for sufficient sample size to estimate survival in each migration pathway while also providing enough fish with which to estimate the proportion entering the Yolo Bypass. Secondly, high flows and the wide floodplain made it logistically impossible to place a telemetry array in the Yolo Bypass close enough to Fremont Weir to estimate entrainment into the Yolo Bypass. The paired-release study design with multiple release sites enabled estimation of this important entrainment parameter. Uncertainty in the timing of initial overtopping led to different release sites for the within-Yolo Bypass releases. For the first release, the 100 fish released into the Yolo Bypass were released into the Tule Canal, which runs along the eastern edge of the Yolo Bypass floodplain, just upstream of I-5 and 10 rkm downstream from Fremont Weir (gTUL). Fish were released into Tule Canal because the Fremont Weir had not yet overtopped and flows were too low within the Yolo Bypass just downstream of the weir. However, for the final two releases, during the overtopping of Fremont Weir, fish were released into the Yolo Bypass 2 rkm downstream of the weir (gFRE; Figure 1).

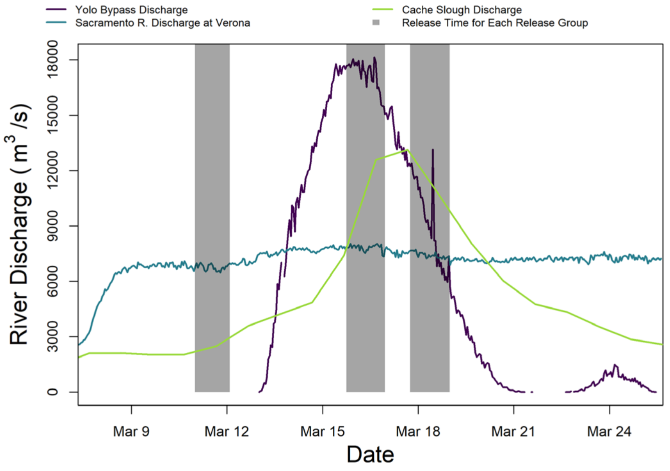

FIGURE 2. Instantaneous river flows (m^3/s) during March 2016 in the Yolo Bypass at Fremont Weir, in the Sacramento River at Verona, and in Cache Slough at the downstream end of the Yolo Bypass. Data were taken from U.S. Geological Survey gauging stations (11390500, 11425500, 11455315) at 15-min intervals. Times of release (gray bars) are indicated for each of three juvenile Chinook Salmon release groups.

Each release was timed to distribute released Chinook Salmon as evenly as possible over a single 24-h period as they passed downstream of Fremont Weir. For example, for the second release group, releases into the Yolo Bypass and at Verona were delayed by approximately 12 h to coincide with the arrival time of the upstream group at Fremont Weir.

Data processing.— Data that were downloaded from the acoustic telemetry receivers were postprocessed in two steps. First, potential false-positive detections were identified and removed by requiring at least two independent pulses from a given tag at the same location within a 30-min period in order to be considered a valid detection. Second, detections of tags that may have been consumed by predators were identified and removed from the data set by hierarchical cluster analysis following the adapted methods of Gibson et al. (2015), as reported by the California Department of Water Resources (2016). This process consisted of several steps involving application of clustering to several movement metrics, identification of clusters with evidence of predation, and review of detection histories to identify when suspected predation occurred. The screening resulted in 220 tag detection records that were flagged for review. Manual review of each of these flagged detection histories resulted in truncation of 16 tag detection histories at the point we determined the tag had been consumed by a predator, and subsequent detections were censored from further analysis. A detailed discussion of false-positive and predator detection filtering methods was provided by Pope et al. (2018).

Survival, routing, and travel time analysis.— We designed a statistical model to estimate reach- and route-specific survival for primary out-migration routes through the Delta (Figure 3). We used the general framework of multistate mark–recapture modeling to estimate the parameters of interest (Lebreton et al. 2009). Here, the term “state” refers to juvenile Chinook Salmon migrating through the Delta via different routes. Fish can transition between these routes at discrete junctions, and their survival is dependent on which route they take to traverse the study area. Routes included the Sacramento River (route A), the Yolo Bypass (route B), Sutter and Steamboat sloughs (route C), and the interior Delta via Georgiana Slough (route D). Telemetry monitoring locations were selected so that survival within these four routes was estimable (Figure 1).

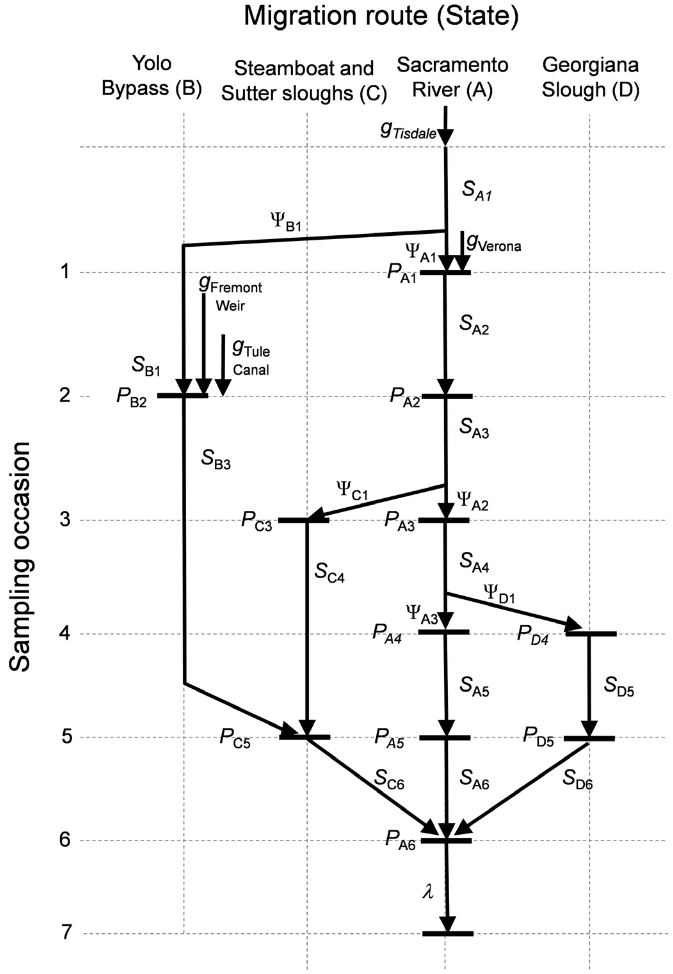

FIGURE 3. Schematic of the multistate mark–recapture model, with parameters indexed by state (migration route) and sampling occasion. Parameters include reach-specific survival probabilities (S), site-specific detection probabilities (P), routing probabilities (Ψ), and the joint probability (λ) of surviving and being detected at telemetry stations downstream of site A6. Chinook Salmon release locations are indicated (g).

The mark–recapture model shown in Figure 3 estimates three types of parameters from detections of tagged juvenile Chinook Salmon, all of which are probabilities constrained between 0 and 1: S_{jt} is the probability of surviving from telemetry station $t - 1$ within route j to telemetry station t (that is, to the next downstream telemetry station); ψ_{jt} is the probability of entering route j at occasion t, conditional on surviving to occasion t; and P_{jt} is the probability of detecting a tagged fish at telemetry station t within route j, conditional on fish and tags surviving to telemetry station jt. All parameters were estimated independently for each of the three releases.

To estimate these parameters, we first summarized telemetry data into an alphanumeric code called a “capture history” that compactly represented the movement history of each tagged individual. For our study, each capture history was eight characters long, with the first character denoting release and the remaining characters each representing detection within a specific route at a sampling occasion, where 0 denotes no detection. For example, the capture history “g_{Tis}AA00DAA” indicates that a fish released at Tisdale was then detected in route A on sampling occasions 1 and 2, not detected on sampling occasions 3 and 4, detected in route D on sampling occasion 5, and detected in route A again on sampling occasions 6 and 7 (Figures 1, 3). Of note in this example is that migration routing can sometimes be inferred even when tags were not detected; here, we know that the individual remained in the Sacramento River at the junction with Sutter and Steamboat sloughs and subsequently migrated through Georgiana Slough into the interior Delta, since its tag was detected at location D5 at the base of the Mokelumne River. Additionally, some release locations are downstream of the first detection opportunity and so have a hyphen as a placeholder to denote the unavailability of detection there (e.g., “g_{Ver}–A00DAA” for a fish released at Verona with the same detection history after occasion 2 as for our previous example).

Each capture history is viewed as one possible outcome from a multinomial distribution and has an associated probability of occurrence defined as a function of the model parameters. This likelihood function has the form

$$L(\psi,S,P|R,n_m) \propto \prod_{m\in M} \pi_m^{n_m}, \tag{1}$$

where M is the set of all possible capture histories; n_m is the number of tagged individuals with capture history m; and π_m is the multinomial cell probability for capture history m, defined in terms of parameters ψ, S, and P.

The equation defining π_m is

$$\pi_m = \left(\prod_{t=F_m}^{L_m} \sum_{j\in J_{mt}} \psi_{jt} S_{jt} \theta_{jt} \right) \times \chi_{K_m L_m}, \tag{2}$$

where J_{mt} is the set of possible routes available at occasion t given capture history m; F_m is the occasion of first possible detection after release for capture history m; L_m is the occasion of last detection for capture history m; K_m is the route in which last detection occurs for capture history m; θ_{jt} represents P_{jt} for route j and occasion t if capture history m indicates detection in route j and occasion t, and represents $1-P_{jt}$ otherwise; and $\chi_{K_m L_m}$ represents the probability of not being detected after detection in route $j=K_m$ at occasion $t=L_m$.

The parameter χ_{jt} is defined recursively (Cormack 1964); $\chi_T=1$ for the final occasion T(here, $T=7$, downstream from Chipps Island) since there are no opportunities for detection after the final occasion, and

$$\chi_{jt} = \sum_{j\in J_{nt}} \chi_{j,t+1} \psi_j \left[S_{jt}\left(1-P_{jt}\right) + \left(1-S_{jt}\right) \right] \tag{3}$$

for occasions $t\in\{1,\ldots,T-1\}$.

For each tagged Chinook Salmon, the time of release and each subsequent time of detection were converted so that each detection provided the time elapsed since the previous detection. Recalling the previous example capture history, "g_{Tis}AA00DAA," travel time data consist of five elapsed travel times associated with each of the five detections in the capture history. The first time represents time elapsed from release to first detection at telemetry station A1 in this example. When one or more consecutive detections are missed, the next detection is associated with the cumulative elapsed time over multiple reaches since the last prior detection. In our example, the time associated with the detection "D" in the fifth digit represents elapsed time from detection at A2 to detection at D5.

These elapsed travel time data were analyzed to estimate independent travel time parameters for each adjacent pair of release–acoustic telemetry locations. For each reach, travel times were modeled as arising from a gamma distribution, so that the likelihood of the recorded elapsed travel time τ_{it} between occasion t and occasion $t+1$ in route j is $Gamma\left(\alpha_{jt},\beta\right)$.

When a tag is not detected at a telemetry station, travel time is missing for the reaches immediately upstream and downstream of the missing detection, since we do not know when the individual arrived. However, the sum of the travel times for each reach is known. This information can help to inform model parameters using the property of the gamma distribution that the sum of gamma-distributed random variables is itself gamma distributed when each variable has the same parameter value β. In our previous example, we know the travel time from station A2 to D5 but not the travel times from A2 to A3, A3 to D4, and D4 to D5. Using properties of the sum of gamma random variables, the overall travel time likelihood for this situation is

$$L(\alpha,\beta|R,\tau) \propto \prod_{i=1}^{R} \prod_{\xi\in\tau_i} \sum_{\lambda\in J_{i\xi}} \psi_{\lambda\xi} \times Gamma\left(\alpha_{\lambda\xi},\beta\right), \tag{4}$$

where τ_i is the set of recorded travel time pairs for individual i; $J_{i\xi}$ is the set of all routes available for individual travel time pair $\tau_{i\xi}$; $\psi_{\lambda\xi} = \prod_{j\in\lambda,t\in\xi} \psi_{jt}$ is the overall probability of traversing all reaches within route λ between stations in travel time pair $\tau_{i\xi}$; and $\alpha_{\lambda\xi} = \sum_{j\in\lambda,t\in\xi} \alpha_{jt}$ is the sum of reach-specific α_{jt} parameters within route λ between stations in travel time pair $\tau_{i\xi}$.

Fundamental parameters for Chinook Salmon survival, routing, and travel time were estimated at the reach scale (that is, over the region bounded by adjacent telemetry stations). However, to compare alternative pathways, we summarize these fundamental parameters over an entire migration route. First, route-specific survival (S_{Route_j}) is defined as survival from the upstream-most telemetry station at Fremont Weir to the downstream terminus at Chipps Island for fish traversing a specific route. Route-specific survival is calculated by taking the product of reach-specific survival probabilities that trace a given migration pathway. Second, the probability of migrating through a specific route (ψ_{Route_j}) is defined as the product of the entrainment probabilities for each junction along that route. Last, the distribution of travel times through an entire migration route is represented as a gamma random variable equivalent to the sum of the gamma random variables for each reach along that route.

Overall Delta-wide Chinook Salmon survival from Fremont Weir to Chipps Island can then be calculated as the sum of the route-specific survival probabilities, weighted by the migration route probabilities. Since one goal is to compare survival through the Yolo Bypass to survival for all other routes, we can similarly calculate non-Yolo Bypass survival ($S_{\mathrm{NON-YOLO}}$), omitting migratory route probability and route-specific survival for the Yolo Bypass route from this calculation. Finally, we also calculate a daily survival for fish migrating via each major route ($\Lambda_{\mathrm{Route}_j}$) as well as for fish migrating via any of the non-Yolo Bypass routes ($\Lambda_{\mathrm{NON-YOLO}}$). The equation used to calculate daily survival is

$$\Lambda_{\mathrm{Route}_j} = S_{\mathrm{Route}_j}^{\frac{1}{\bar{\tau}_{\mathrm{Route}_j}}}, \tag{5}$$

where $\bar{\tau}_{\mathrm{Route}_j}$ is the expected travel time for Route_j in days.

All parameters were estimated simultaneously using Hamiltonian Monte Carlo methods with the Stan modeling software package (Carpenter et al. 2017). Standard normal prior distributions were used for the transformed travel time parameters, $\log(\alpha_{jt}/\beta)$, and all other parameters were given uniform priors between 0 and 1. Four separate Hamiltonian Monte Carlo chains were run in Stan for 2,000 iterations each, discarding the first 1,000 iterations as burn-in. Posterior samples were checked for convergence and mixing, and the resulting sample of 4,000 draws was then reported via the median and 5th and 95th percentiles for each parameter. Posteriors of derived parameters were calculated by applying the formula for a derived parameter to each of the 4,000 sample draws.

Spatial distribution and survival within the Yolo Bypass.— To assess the spatial distribution of juvenile Chinook Salmon migrating within the Yolo Bypass floodplain and its effect on survival, we estimated the cross-stream distribution of acoustic-tagged fish in the Yolo Bypass at the point where I-80 crosses the bypass just west of the city of Sacramento (B2; Figure 1). The linear distance from the east bank to the receiver within the I-80 array that first detected each tagged fish was assumed to represent the cross-stream location within the Yolo Bypass for that fish. A Gaussian kernel density function was applied to these cross-stream location data to estimate the spatial density of Chinook Salmon across the bypass. Separate density estimates were generated for fish released at each of the Tisdale, Fremont Weir, and Tule Canal release sites, since the proximity of each release site to the I-80 detection array (range = 12.5–77.7 km) might potentially influence the cross-stream distribution of fish in the bypass.

Additionally, we tested for differences in survival in the Yolo Bypass as a function of cross-stream spatial location. For this analysis, a Cormack–Jolly–Seber mark–recapture model was fitted to the data (Cormack 1964; Jolly 1965; Seber 1965) to estimate survival within the Yolo Bypass from the I-80 bridge downstream to the detection station at Cache Slough. Each cross-stream position at the I-80 bridge was used as an individual covariate on survival to quantify the magnitude of an east–west gradient on survival.

RESULTS

Survival, Routing, and Travel Time

Survival estimates.— Survival through the Delta from Fremont Weir to Chipps Island varied among routes and release groups, with estimates ranging from 0.564 to 0.843 (Table 2; Figure 4). Among routes, survival was generally lowest for fish migrating through the interior Delta via Georgiana Slough and highest for fish migration through the Sacramento River. For the main-stem Sacramento River, survival estimates ranged from 0.704 to 0.843 among releases, whereas for Georgiana Slough survival ranged from 0.564 to 0.695. Although survival estimates for all non-Yolo Bypass routes were slightly higher for release groups 2 and 3, coincident with higher flow and the overtopping of Fremont Weir, credible intervals overlapped among the estimates and differences were not significant. Survival for the Yolo Bypass route varied little among release groups, ranging from 0.659 to 0.689 (Table 2; Figure 4).

Parameter estimates of survival within individual reaches ranged from 0.650 to 0.991 (Appendix Table A.1). Among reaches, survival was generally highest in upstream riverine reaches, including the Sacramento River above the entrance to Georgiana Slough (reaches A2, A3, A4, and A5), the upper Yolo Bypass from Fremont Weir to the I-80 bridge (reach B1), and Steamboat Slough (reaches C41B and C42B). Survival was generally lowest in tidal reaches, such as the interior Delta from the junction of Georgiana Slough with the lower Mokelumne River to Chipps Island (reach D6) and from the junction of Cache Slough with the Sacramento River to Chipps Island (reach C6).

Migration routing estimates.— The proportion of Chinook Salmon migrating through the Yolo Bypass varied considerably among release groups and influenced the proportion using other migration routes. Estimates of the proportion migrating through the Yolo Bypass ranged from 0.012 to 0.801 and was highest for release group 2, coinciding with peak flows and river stage—and subsequent overtopping—at Fremont Weir. In contrast, estimates of Yolo Bypass entrainment for release groups 1 and 3 were both below 5%.

Migration proportions through each of the other three routes varied little, with the exception of release group 2 when Yolo Bypass entrainment was highest (Figure 5). Median estimates of the proportion migrating via the Sacramento River ranged from 0.115 to 0.458 (Table 3). Migration proportions through Sutter and Steamboat sloughs and Georgiana Slough to the interior Delta were generally lower, with estimates for the proportion migrating via Sutter and Steamboat sloughs ranging from 0.050 to 0.361 and those for the proportion migrating via Georgiana Slough and the interior Delta ranging from 0.031 to 0.233 (Table 3).

TABLE 2. Survival estimates (S) for juvenile Chinook Salmon out-migrating from Fremont Weir to Chipps Island via one of four major routes in the Sacramento–San Joaquin River Delta. Combined survival for non-Yolo Bypass routes indicates average survival for those routes, weighted by the estimated proportion migrating through each route. Lower and upper credible limits (CLs) denote the 5th and 95th percentiles of the posterior distributions for each parameter, respectively.

Parameter	Release	Median	Lower CL	Upper CL	Route description
S_{SAC}	1	0.704	0.549	0.867	Sacramento River
	2	0.748	0.634	0.860	
	3	0.843	0.738	0.925	
S_{YOLO}	1	0.689	0.558	0.820	Yolo Bypass to Cache Slough
	2	0.677	0.597	0.767	
	3	0.659	0.574	0.745	
$S_{\mathrm{SUT/STM}}$	1	0.614	0.467	0.761	Sutter Slough or Steamboat Slough
	2	0.697	0.531	0.827	
	3	0.716	0.580	0.836	
S_{GEO}	1	0.564	0.390	0.760	Georgiana Slough to interior Delta
	2	0.695	0.526	0.838	
	3	0.613	0.466	0.760	
$S_{\mathrm{NON\text{-}YOLO}}$	1	0.600	0.490	0.713	All routes combined except Yolo Bypass
	2	0.665	0.564	0.762	
	3	0.735	0.652	0.811	

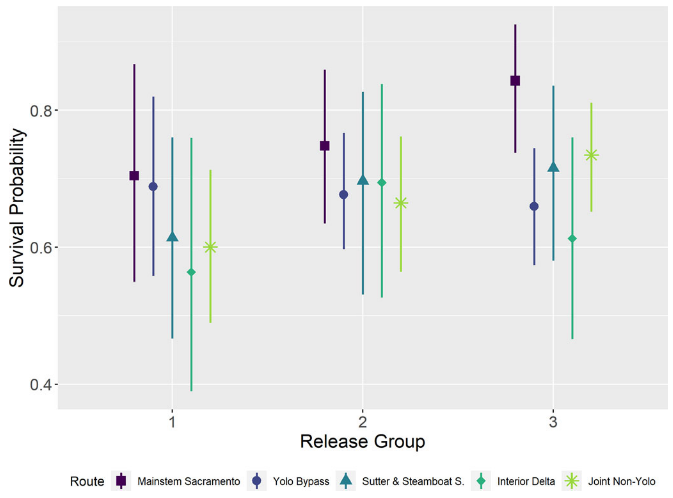

FIGURE 4. Median probability of juvenile Chinook Salmon survival, with upper and lower credible limits (5th and 95th percentiles of the posterior distributions for each parameter, respectively), from Fremont Weir to Chipps Island by route through the north Sacramento–San Joaquin River Delta, California (S. = sloughs).

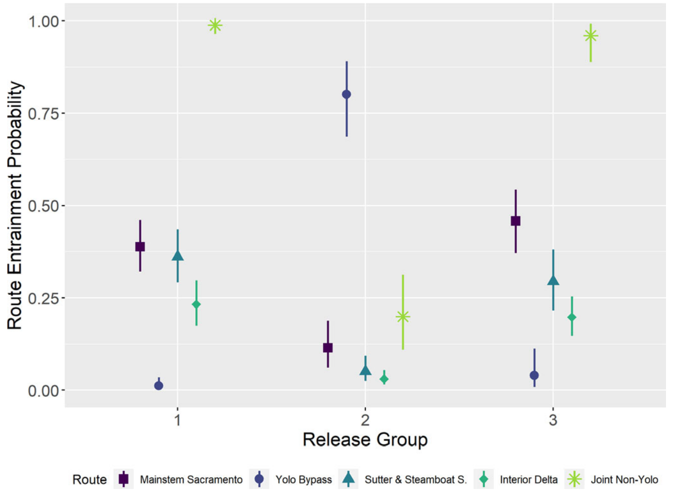

FIGURE 5. Median migratory route probabilities for juvenile Chinook Salmon, with upper and lower credible limits (5th and 95th percentiles of the posterior distributions for each parameter, respectively), from Fremont Weir to Chipps Island in the Sacramento–San Joaquin River Delta, California (S. = sloughs).

Travel time estimates.— Mean travel time estimates varied by route and release group, with estimated mean travel time from Fremont Weir to Chipps Island ranging from 2.70 to 6.40 d (Figure 6). Within any given route, travel time varied little among release groups (Table 4; Figure 6). For all release groups, Chinook Salmon migrating via either the main-stem Sacramento River (mean travel time range = 2.70–3.16 d) or Sutter and Steamboat sloughs (range = 2.71–2.88 d) traveled more quickly to Chipps Island than those migrating via the Yolo Bypass (range = 4.19–5.08 d). Chinook Salmon migrating via the interior Delta exhibited the longest estimated mean travel times (range = 5.41–6.40 d).

Mean daily survival probabilities.— Daily survival rate estimates were generally similar across routes and release groups, ranging from 0.844 to 0.945 (Table 5). Daily survival estimates for the Sutter and Steamboat Slough route were slightly lower than those for other routes, although

TABLE 3. Migratory route probabilities (Ψ) for juvenile Chinook Salmon out-migrating from Fremont Weir to Chipps Island in the Sacramento–San Joaquin River Delta. Lower and upper credible limits (CLs) are as defined in Table 2.

Parameter	Release	Median	Lower CL	Upper CL	Route description
Ψ_{SAC}	1	0.389	0.321	0.461	Sacramento River
	2	0.115	0.061	0.187	
	3	0.458	0.371	0.543	
Ψ_{YOLO}	1	0.012	0.003	0.035	Yolo Bypass to Cache Slough
	2	0.801	0.687	0.890	
	3	0.040	0.008	0.113	
$\Psi_{SUT/STM}$	1	0.361	0.292	0.435	Sutter Slough or Steamboat Slough
	2	0.050	0.025	0.093	
	3	0.294	0.216	0.381	
Ψ_{GEO}	1	0.233	0.175	0.297	Georgiana Slough to interior Delta
	2	0.031	0.015	0.054	
	3	0.198	0.147	0.254	
$\Psi_{NON\text{-}YOLO}$	1	0.988	0.965	0.997	All routes combined except Yolo Bypass
	2	0.199	0.110	0.313	
	3	0.960	0.887	0.992	

credible intervals overlapped. Daily survival in the Yolo Bypass route was similar to that in the main-stem Sacramento River and was not substantially different from daily survival through non-Yolo Bypass routes.

Spatial Distribution and Survival within the Yolo Bypass

The cross-stream distribution of Chinook Salmon within the Yolo Bypass differed between the groups released directly into the Yolo Bypass and the group released in the Sacramento River. In the Yolo Bypass, the cross-stream distribution tended to be increasingly skewed toward the east bank the closer the release site was to I-80 (Figure 7). In contrast, fish that were released in the Sacramento River upstream of Fremont Weir and that entered the bypass volitionally were uniformly dispersed up to about 2 km from the east bank before densities gradually decreased out to 2.5 km (Figure 7). No fish were first detected on the western group of four receivers located 4.2–4.8 km from the east bank; however, it is important to note that since the Yolo Bypass is a seasonally inundated floodplain and not a well-defined river channel, this far western extent of the bypass may not have been flooded during some portion of the study.

Median survival for all tagged Chinook Salmon detected at the I-80 array to Cache Slough was estimated at 0.839 (5% and 95% credible limits [CLs] = 0.784 and 0.887, respectively). The location of first detection within the I-80 array had no significant effect on survival. For example, survival from I-80 to Cache Slough for fish that were first detected at the easternmost receiver of the I-80 array (right side of Figure 7) was estimated at 0.847 (CLs = 0.784, 0.901), while fish that were first detected at the westernmost receiver (left side of Figure 7) had an estimated survival of 0.819 (CLs = 0.690, 0.919).

DISCUSSION

Our results help to gain an understanding of how actively migrating juvenile Chinook Salmon use inundated floodplains such as the Yolo Bypass. We found that the proportion of fish using the Yolo Bypass changed dramatically among release groups during various stages of the flood event. Over 80% of fish from the group that was released during peak flooding ultimately entered the Yolo Bypass, as compared with less than 5% either before or after the peak of the flood event. Despite this large difference in use of Yolo Bypass habitats at different flood stages, we found that survival and mean travel time through the Yolo Bypass were relatively constant among release groups. Furthermore, after accounting for travel time, daily survival rates for fish migrating through the flooded Yolo Bypass floodplain were comparable to those of fish migrating through the riverine main-stem Sacramento River and interior Delta routes. Finally, we found that fish entering the Yolo Bypass from the Sacramento River were widely distributed across the breadth of the floodplain as they migrated downstream.

Our observations contrast with some generally accepted findings from other studies conducted within main-channel riverine environments. Other studies, including those conducted within the Delta, show a positive relationship between river discharge and overall survival for migrating juvenile Chinook Salmon (Perry et al. 2018). In contrast, despite releases occurring across the ascending limb, peak,

TABLE 4. Travel time estimates ($\bar{\tau}$; d) for juvenile Chinook Salmon out-migrating from Fremont Weir to Chipps Island via one of four major routes in the Sacramento–San Joaquin River Delta. Lower and upper credible limits (CLs) are as defined in Table 2.

Parameter	Release	Median	Lower CL	Upper CL	Route description
$\bar{\tau}_{SAC}$	1	3.163	2.936	3.393	Sacramento River
	2	2.696	2.457	2.942	
	3	2.945	2.732	3.169	
$\bar{\tau}_{YOLO}$	1	4.186	4.001	4.381	Yolo Bypass to Cache Slough
	2	5.084	4.827	5.361	
	3	4.531	4.294	4.785	
$\bar{\tau}_{SUT/STM}$	1	2.885	2.659	3.127	Sutter Slough or Steamboat Slough
	2	2.792	2.376	3.443	
	3	2.712	2.465	2.983	
$\bar{\tau}_{GEO}$	1	5.608	5.158	6.073	Georgiana Slough to interior Delta
	2	6.401	5.694	7.148	
	3	5.405	4.933	5.890	

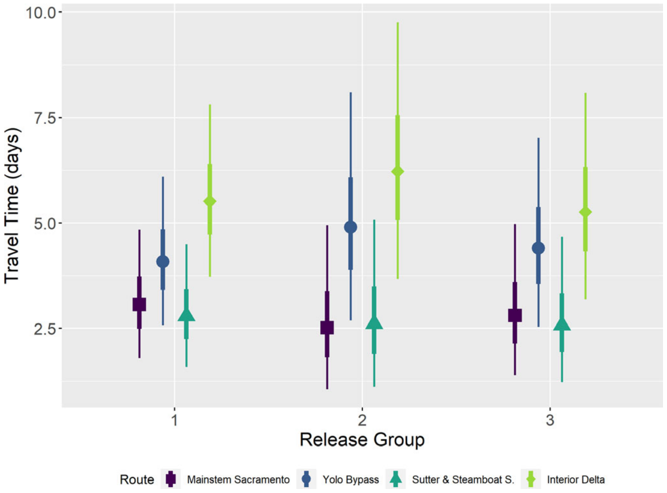

FIGURE 6. Route-specific travel time quantiles for juvenile Chinook Salmon from Fremont Weir to Chipps Island in the Sacramento–San Joaquin River Delta, California (S. = sloughs). Dots indicate medians, thick lines show 25th–75th percentiles, and ends of thin lines show 5th and 95th percentiles. Travel time quantiles are derived from a *Gamma*(α, β) distribution, where α and β are the median posterior values.

and descending limb of the 2016 flood event, estimates of survival through all routes in our study varied little over widely varying discharge conditions (Figures 2, 4). Additionally, travel time for juvenile Chinook Salmon migrating via the Yolo Bypass was consistent across release groups despite release group 1 occurring before the overtopping of Fremont Weir and for which tagged fish were released directly into the Tule Canal (Figure 6).

Given the high flows necessary to overtop Fremont Weir and inundate the Yolo Bypass, it should perhaps be unsurprising that we found little change in survival and travel times among release groups within the non-Yolo Bypass migration routes. Studies showing a positive flow–survival relationship in the Sacramento River have also found decreasing marginal increases in survival at the higher end of the range for historical flows (Perry et al. 2018). Once Freeport flow rises above approximately 1,500 m^3/s, there is little additional benefit to survival with increasing flow. Flows at Verona, which are generally lower than those at Freeport as Verona is upstream of the confluence with the American River, were well above 5,000 m^3/s for the entirety of our study period (Figure 2). At this range of flows, travel times are low and survival is high throughout the Delta, and both are insensitive to variations in flow around these high levels. In contrast, within the Yolo Bypass survival and travel time were similar even for the group released directly into Tule Canal before the overtopping of Fremont Weir. This first release group experienced much lower flows than the two later release groups, suggesting that survival and travel times through the Yolo Bypass may be relatively insensitive to flow even at much lower levels.

Differences in patterns of survival and travel time between the Yolo Bypass and the main-stem Sacramento River may be explained to some degree by the differing relationships between discharge, water velocity, and channel morphology within floodplains as compared to main-channel riverine environments. Unlike a constrained river channel, water velocities across a floodplain are relatively insensitive to increased flow since larger flows are likely to spread out over a greater extent of the floodplain. While migrating fish in constrained main-channel habitat will experience water velocities roughly proportional to river discharge, those in a floodplain are likely to experience similar water velocity over a wide range of discharge

TABLE 5. Daily survival estimates (Λ) for juvenile Chinook Salmon out-migrating from Fremont Weir to Chipps Island via one of four major routes in the Sacramento–San Joaquin River Delta. Non-Yolo Bypass estimates and lower and upper credible limits (CLs) are as defined in Table 2.

Parameter	Release	Median	Lower CL	Upper CL	Route description
Λ_{SAC}	1	0.895	0.826	0.956	Sacramento River
	2	0.898	0.843	0.946	
	3	0.944	0.902	0.974	
Λ_{YOLO}	1	0.915	0.870	0.953	Yolo Bypass to Cache Slough
	2	0.926	0.903	0.949	
	3	0.912	0.883	0.937	
$\Lambda_{\mathrm{SUT/STM}}$	1	0.844	0.768	0.910	Sutter Slough or Steamboat Slough
	2	0.880	0.794	0.935	
	3	0.884	0.815	0.937	
Λ_{GEO}	1	0.903	0.844	0.952	Georgiana Slough to interior Delta
	2	0.945	0.904	0.973	
	3	0.914	0.866	0.951	
$\Lambda_{\mathrm{NON\text{-}YOLO}}$	1	0.884	0.836	0.927	All routes combined except Yolo Bypass
	2	0.907	0.873	0.938	
	3	0.920	0.891	0.945	

conditions. Thus, we expect that travel times and survival will remain similar in this type of floodplain environment, whereas in a constrained river channel we should expect travel time to decrease—and survival consequently to increase—with increasing discharge and water velocity.

Our results are consistent with the XT model of survival put forth by Anderson et al. (2005) and with other research linking increased travel time with increased mortality among migrating fishes. The XT model of salmon migration predicts that migration pathways of longer distance (the “X”) or longer residence time (the “T”) will result in more predator encounters and a lower probability of survival, so long as migration pathways have similar predator density and habitat conditions. Research in the Columbia and Snake rivers over several decades has found increased travel times leading directly to increased mortality (Raymond 1979; Smith et al. 2003). Floodplains like the Yolo Bypass are typically characterized by slower water velocity, and the wide expanse of the floodplain relative to river channels presents opportunities for longer, more tortuous pathways. Although credible intervals overlapped and differences were not significant, we found that overall travel time was higher and survival probability was slightly lower for the Yolo Bypass migration route than for the faster-flowing, channelized, main-stem river (Figures 4, 6). In contrast, daily survival rates did not differ consistently between any migration routes, even routes through regions that have exhibited the lowest overall survival probability in this and other acoustic telemetry studies (Table 5; Perry et al. 2013, 2018). This suggests that the lower overall survival rates for some Delta routes may be primarily an issue of longer travel times for those routes rather than an issue of higher daily mortality risk due to such factors as higher predator density. Although other studies have identified significant local variation in predator densities, they have also found that on a larger scale there are predation risks present within most, if not all, of the routes available to migrating juvenile Chinook Salmon (Nobriga et al. 2005; Nobriga and Feyrer 2007). This finding has important implications for management because in recent years, a key focus of management effort has been the reduction of location-specific predator density. However, if the primary driver of route-specific survival in the Delta is residence time and not daily mortality risk, management for Chinook Salmon smolts focusing on

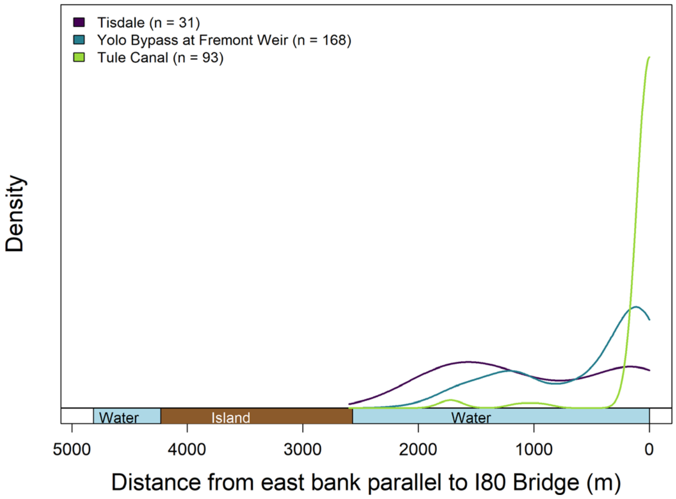

FIGURE 7. Cross-stream distribution of tagged juvenile Chinook Salmon within the Yolo Bypass at the I-80 bridge, separated by release site.

reducing residence time and for presmolt Chinook Salmon focusing on improving other important biological responses besides predation risk, such as somatic growth, may be more productive. These alternative management objectives can be accomplished by actions that (1) guide smolts away from high-residence-time routes like the south Delta route and (2) increase presmolt access to areas with demonstrated beneficial rearing conditions, such as the Yolo Bypass.

Entrainment into the Yolo Bypass differed greatly between the two releases conducted during significant overtopping of the Fremont Weir entrance to the Yolo Bypass. Over 80% of Chinook Salmon included in release group 2 were estimated to have migrated through the Yolo Bypass (Figure 5) when flow into the Yolo Bypass at Fremont Weir was at its peak, but less than 5% of fish in release group 3 migrated through the Yolo Bypass despite overtopping of Fremont Weir. Release group 3 was conducted only 2 d after release group 2, while Yolo Bypass flow at Fremont Weir was declining but still substantial. These widely varying entrainment estimates indicate a threshold in flow or stage height beyond which a pronounced change in entrainment probability occurs. This contrasts with patterns seen at other major junctions in the Delta, where the proportion of fish migrating via each route changes gradually with changing flows and tends to be bounded away from zero (Perry et al. 2015, 2018).

This apparent threshold pattern may be explained to some extent by the cross-stream distribution of migrating juvenile Chinook Salmon within the Sacramento River. An analysis of fine-scale movement of acoustic-tagged juvenile Chinook Salmon, conducted as a complement to this study, found that as discharge over Fremont Weir increased, mean cross-sectional fish position moved closer to the weir (Blake et al. 2017). In contrast, as flows near Fremont Weir decreased but were still great enough to provide substantial flow into the Yolo Bypass, mean fish position moved away from the bank formed by the weir and toward the Sacramento River centerline. Thus, we posit that at certain overtopping flow levels, Chinook Salmon are not close enough to Fremont Weir to become entrained over the weir and into the Yolo Bypass even though a substantial fraction of river flow is entering the bypass. It is possible that the dynamic cross-stream distribution of juvenile Chinook Salmon near the junction of the Sacramento River with the entrance to the Yolo Bypass serves to impose a critical threshold below which relatively few fish are entrained into the bypass but above which the entrained proportion rises rapidly and disproportionately in response to further increased flows.

The ways in which floodplains and constrained channels respond differently to changing flow conditions provide a plausible explanation for many of our findings. However, several reasons explain why our study may not be generalizable to other systems or to all juvenile salmon populations in the Sacramento River system. First, we only measured survival over a single flood event. Flooding at different times of year will likely feature differing environmental conditions, such as temperature, which could have disparate impacts on migrating juvenile Chinook Salmon. Nonetheless, we were able to characterize variability in floodplain survival relative to main-stem river survival over ascending, peak, and descending stages of the flood event. Second, our study focused on migrating juvenile Chinook Salmon smolts only. At this stage, salmon are actively migrating toward the ocean, and as such their survival is likely to benefit from minimizing their residence time as they move through the Delta, a finding that is supported by our study. In contrast, rearing Chinook Salmon fry use nearshore habitat over a longer period than do migrating smolts and so have different requirements for survival than the fish in our study. However, to the extent that the Yolo Bypass floodplain contains large areas of shallow-water habitat, Chinook Salmon fry could also benefit from increased flood event frequency.

Even within the Chinook Salmon smolt life stage, our results may not reflect the variability of behaviors and outcomes, particularly for smaller-sized juveniles, since tag burden considerations limit the minimum size of fish available for tagging. Different-sized fish may migrate at different rates and may use floodplain and main-stem habitats differently. For example, comparison of center-channel trawls with beach seine catch and snorkel surveys in the Delta showed that larger Chinook Salmon, particularly smolts, migrated in deeper water, while smaller fish were typically found in shallower water (Munsch et al. 2016, 2019). The larger smolts typical of our tagged study fish may maximize their survival exclusively through rapid migration in either main-stem or floodplain habitat. Smaller smolts, however, may accrue survival and growth opportunities through the availability of shallow-water, low-velocity habitat on floodplains, in contrast to riprapped main channel. Conversely, smaller and slower smolts may be more susceptible to predation, as smaller fish are vulnerable to a broader predator field (Hambright 1991; Reimchen 1991; Mihalitsis and Bellwood 2017) and slower fish may suffer a greater number of predator encounters (Anderson et al. 2005). Because of size limitations imposed by tag burden considerations, our study cannot distinguish between the benefits and risks of increased floodplain habitat access for smaller juvenile Chinook Salmon. It is important that resource managers consider outcomes of actions within a broader context, which may require balancing the maximization of short-term survival for a single life history against the maximization of life history diversity, population stability, and resilience. Broader consideration of pathway influence on salmon populations should account for life history diversity and the portfolio effect, whereby populations that are capable of greater phenological diversity in spatial and temporal rearing strategies are better equipped to persist in regions with heterogeneous and unpredictable environmental conditions (Greene et al. 2010; Schindler et al. 2010; Carlson and Satterthwaite 2011).

The difference in cross-stream distribution of tagged juvenile Chinook Salmon from different release sites as they migrated through the Yolo Bypass raises the potential for violation of assumptions in our mark–recapture model. Because locating a telemetry array just downstream of Fremont Weir in the Yolo Bypass was logistically impossible, we relied on a paired-release study design to estimate the probability of entrainment into the Yolo Bypass. Paired-release studies are a common method used to estimate demographic parameters at a point of interest when cost or logistics dictate limited recapture opportunities (Ploskey et al. 2007). In particular, paired-release designs have been used extensively to estimate survival through multiple Columbia River basin hydropower systems, where high-precision estimates of survival are mandated by federal regulations (Skalski et al. 2001).

The paired-release design assumes that fish released at the downstream release site exhibit postrelease behavior similar to that of fish released farther upstream as they migrate past the same point. Differing cross-stream distributions would seem to indicate different behavior between these two groups. However, Perry (2010) conducted a sensitivity analysis for a paired-release design elsewhere in the Delta to determine how varying degrees of violation of this assumption affected estimation of an associated entrainment probability. The study found that mild to moderate violations of the assumption resulted in only a slight bias in the estimated probability and that a severe violation was required to induce a bias greater than a few percentage points. Ultimately, although we are confident that our study design is robust and that our parameter estimates are valid, there is a possibility that some measure of bias was introduced via different behavior among fish released at different sites.

Despite factors that may limit the scope of inference, our analysis provides support for the idea that movement and survival patterns of juvenile Chinook Salmon vary with channel morphology differences between floodplain and constrained main-channel habitats. Broad-scale metrics that are often considered as important indicators of juvenile salmon survival (e.g., flow) may be less important in explaining these differences than metrics that are more closely tied to the immediate environment of migrating fish (e.g., water velocity). While differences in flow have been demonstrated as important in explaining both survival and migration route in networks of constrained main-channel habitats, in floodplains flow may not be a reliable predictor of either survival or migration route. Further studies explicitly aimed at understanding these relationships should provide additional tools for managers seeking to improve juvenile Chinook Salmon habitat and population survival. Additional research on the applied potential benefits of access to the Yolo Bypass for various life stages would contribute valuable information to managers faced with decisions affecting juvenile Chinook Salmon.

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Appendix: Reach-Specific Parameter Estimates

TABLE A.1. Directly estimated parameters for reach-specific survival and detection probability, junction-specific entrainment probability, and reach-specific gamma-distributed travel time parameters for juvenile Chinook Salmon. Listed parameters follow the nomenclature from the model schematic depicted in Figure 3. Lower and upper credible limits (CLs) denote the 5th and 95th percentiles of the posterior distributions for each parameter, respectively.

Parameter	Release	Median	Lower CL	Upper CL	Location description
			Probability of reach survival		
S_{A1}	1	0.939	0.885	0.983	Tisdale to Verona
	2	0.962	0.876	0.997	
	3	0.983	0.930	0.999	
S_{A2}	1	0.982	0.935	0.999	Fremont Weir to Freeport
	2	0.980	0.929	0.998	
	3	0.991	0.963	0.999	
S_{A3}	1	0.977	0.921	0.998	Freeport to Sutter/Steamboat Slough
	2	0.982	0.936	0.998	
	3	0.988	0.954	0.999	
S_{A4}	1	0.976	0.928	0.997	Sutter/Steamboat Slough to Georgiana Slough
	2	0.969	0.898	0.998	
	3	0.981	0.930	0.999	
S_{A5}	1	0.975	0.905	0.998	Georgiana Slough to above Rio Vista
	2	0.960	0.875	0.996	
	3	0.976	0.910	0.998	
S_{A6}	1	0.793	0.628	0.965	Above Rio Vista to Chipps Island
	2	0.863	0.750	0.965	
	3	0.920	0.822	0.989	
S_{B1}	1	0.980	0.946	0.997	Fremont Weir to I-80 bridge
	2	0.910	0.862	0.947	
	3	0.933	0.875	0.981	
S_{B3}	1	0.851	0.784	0.905	I-80 bridge to Cache Slough
	2	0.878	0.821	0.922	
	3	0.773	0.692	0.844	
S_{C41A}	1	0.658	0.074	0.979	Sutter Slough to Miner Slough
	2	0.795	0.328	0.983	
	3	0.898	0.131	0.994	

TABLE A.1. Continued.

Parameter	Release	Median	Lower CL	Upper CL	Location description
S_{C42A}	1	0.885	0.655	0.991	Miner Slough to Cache Slough
	2	0.813	0.450	0.984	
	3	0.867	0.587	0.988	
S_{C6A}	1	0.832	0.682	0.977	Cache Slough to Chipps Island
	2	0.851	0.772	0.950	
	3	0.922	0.837	0.989	
S_{C41B}	1	0.939	0.758	0.995	Upper Steamboat Slough
	2	0.935	0.757	0.995	
	3	0.893	0.149	0.995	
S_{C42B}	1	0.917	0.717	0.994	Lower Steamboat Slough
	2	0.936	0.762	0.994	
	3	0.950	0.815	0.996	
S_{C6B}	1	0.810	0.587	0.974	Steamboat Slough exit to Chipps Island
	2	0.958	0.827	0.997	
	3	0.865	0.704	0.977	
S_{D5}	1	0.955	0.863	0.994	Georgiana Slough to lower Mokelumne River
	2	0.923	0.786	0.988	
	3	0.954	0.866	0.994	
S_{D6}	1	0.650	0.452	0.861	Lower Mokelumne River to Chipps Island
	2	0.840	0.662	0.970	
	3	0.686	0.528	0.836	
			Probability of remaining in or entering river reach		
Ψ_{A1}	1	0.988	0.965	0.997	Sacramento River at Fremont Weir
	2	0.199	0.110	0.313	
	3	0.960	0.887	0.992	
Ψ_{A2}	1	0.650	0.270	0.950	Sacramento River at Sutter/Steamboat Slough
	2	0.751	0.546	0.887	
	3	0.712	0.267	0.998	
Ψ_{A3}	1	0.625	0.538	0.711	Sacramento River at Georgiana Slough
	2	0.787	0.705	0.854	
	3	0.698	0.619	0.770	
Ψ_{B1}	1	0.012	0.003	0.035	Yolo Bypass entrance
	2	0.801	0.687	0.890	
	3	0.040	0.008	0.113	
Ψ_{C1A}	1	0.015	0.001	0.310	Sutter Slough entrance
	2	0.041	0.010	0.131	
	3	0.160	0.001	0.368	
Ψ_{C1B}	1	0.335	0.049	0.420	Steamboat Slough entrance
	2	0.208	0.103	0.323	
	3	0.128	0.001	0.365	
Ψ_{D1}	1	0.375	0.289	0.462	Georgiana Slough entrance
	2	0.213	0.146	0.295	
	3	0.302	0.230	0.381	
			Probability of detection		
P_{A1}	1	0.613	0.539	0.683	Sacramento River at Verona
	2	0.649	0.373	0.877	
	3	0.716	0.588	0.823	
P_{A2}	1	0.105	0.066	0.154	Sacramento River at Freeport
	2	0.072	0.038	0.120	
	3	0.157	0.110	0.213	

TABLE A.1. Continued.

Parameter	Release	Median	Lower CL	Upper CL	Location description
P_{A3}	1	0.840	0.768	0.899	Sacramento River below Steamboat Slough
	2	0.182	0.117	0.266	
	3	0.245	0.178	0.324	
P_{A4}	1	0.325	0.225	0.436	Sacramento River below Georgiana Slough
	2	0.063	0.024	0.130	
	3	0.102	0.050	0.176	
P_{A5}	1	0.982	0.926	0.999	Sacramento River near Rio Vista
	2	0.662	0.535	0.806	
	3	0.840	0.718	0.944	
P_{A6}	1	0.831	0.705	0.977	Sacramento River at Chipps Island
	2	0.960	0.871	0.997	
	3	0.939	0.869	0.993	
P_{B2}	1	0.945	0.900	0.976	Yolo Bypass at I-80 bridge
	2	0.976	0.943	0.993	
	3	0.864	0.791	0.921	
P_{C3A}	1	0.207	0.007	0.889	Sutter Slough near entrance
	2	0.337	0.061	0.880	
	3	0.052	0.003	0.848	
P_{C5A}	1	0.988	0.950	0.999	Cache Slough near Rio Vista
	2	0.992	0.967	0.999	
	3	0.989	0.953	0.999	
P_{C3B}	1	0.067	0.021	0.359	Steamboat Slough near entrance
	2	0.168	0.062	0.392	
	3	0.054	0.003	0.811	
P_{C5B}	1	0.872	0.718	0.969	Steamboat Slough near Rio Vista
	2	0.669	0.400	0.911	
	3	0.755	0.541	0.962	
P_{D4}	1	0.977	0.905	0.998	Georgiana Slough near entrance
	2	0.963	0.842	0.997	
	3	0.976	0.900	0.998	
P_{D5}	1	0.969	0.886	0.997	Lower Mokelumne River
	2	0.955	0.828	0.996	
	3	0.969	0.883	0.997	
			Travel time parameters		
α_{A1}	1	3.318	2.941	3.727	Tisdale to Verona
	2	1.420	0.945	1.943	
	3	2.608	2.153	3.121	
α_{A2}	1	2.130	1.678	2.600	Fremont Weir to Freeport
	2	1.260	0.921	1.608	
	3	1.722	1.410	2.060	
α_{A3}	1	1.029	0.684	1.418	Freeport to Sutter/Steamboat Slough
	2	0.495	0.241	0.832	
	3	0.546	0.291	0.839	
α_{A4}	1	0.711	0.563	0.879	Sutter/Steamboat Slough to Georgiana Slough
	2	0.426	0.223	0.683	
	3	0.520	0.341	0.743	
α_{A5}	1	1.025	0.788	1.288	Georgiana Slough to above Rio Vista
	2	0.561	0.300	0.871	
	3	0.625	0.397	0.883	

TABLE A.1. Continued.

Parameter	Release	Median	Lower CL	Upper CL	Location description
α_{A6}	1	6.458	5.594	7.392	Above Rio Vista to Chipps Island
	2	2.163	1.772	2.590	
	3	3.610	3.100	4.149	
α_{B1}	1	1.784	1.550	2.033	Fremont Weir to I-80 bridge
	2	3.236	2.840	3.674	
	3	3.385	2.970	3.831	
α_{B3}	1	7.473	6.713	8.268	I-80 bridge to Cache Slough
	2	3.329	2.923	3.768	
	3	3.628	3.172	4.117	
α_{CAA}	1	2.279	0.637	13.032	Sutter Slough to Miner Slough
	2	1.178	0.412	2.520	
	3	1.094	0.346	6.637	
α_{CAB}	1	2.470	0.548	14.671	Sutter Slough to Steamboat Slough
	2	1.242	0.287	7.015	
	3	0.971	0.365	7.064	
α_{C6A}	1	5.784	5.140	6.482	Cache Slough to Chipps Island
	2	2.749	2.389	3.140	
	3	3.838	3.364	4.341	
α_{CBB}	1	0.993	0.485	1.658	Upper Steamboat Slough to lower Steamboat Slough
	2	0.629	0.291	1.115	
	3	0.997	0.382	6.642	
α_{CBA}	1	1.683	0.740	3.407	Upper Steamboat Slough to Miner Slough
	2	5.616	0.738	13.455	
	3	1.065	0.355	6.919	
α_{C6B}	1	5.869	4.805	7.049	Steamboat Slough exit to Chipps Island
	2	2.003	1.477	2.632	
	3	3.124	2.491	3.824	
α_{D5}	1	2.287	1.856	2.757	Georgiana Slough to lower Mokelumne River
	2	1.323	0.967	1.731	
	3	1.872	1.497	2.295	
α_{D6}	1	13.980	11.995	16.026	Lower Mokelumne River to Chipps Island
	2	8.211	6.766	9.772	
	3	8.237	6.991	9.636	
β	1	3.596	3.277	3.948	Entire Delta
	2	1.835	1.640	2.036	
	3	2.392	2.155	2.644	