

RESEARCH

Survival of Juvenile Chinook Salmon in the Yolo Bypass and the Lower Sacramento River, California

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ABSTRACT

While our knowledge of the range of survival that outmigrating juvenile Chinook Salmon experience in different routes of the Sacramento–San Joaquin Delta has increased in recent years, few studies have focused on their survival during outmigration in the Yolo Bypass, the Delta’s primary floodplain. The Yolo Bypass floodplain provides valuable rearing habitat and growth benefits to juvenile fish in flood

years, and efforts are underway to improve access to the Yolo Bypass and the Toe Drain, its perennial navigation channel, under a broader range of flows and river stages than is currently possible. We compared variation in transit time, and estimated survival between different release groups of fish outmigrating through the Yolo Bypass or through migratory routes in the lower Sacramento River. Tagged late-fall-run juvenile Chinook Salmon were released in both systems in 2012 and 2013. There was no significant difference between the estimated cumulative probability of survival in the Yolo Bypass system and combined routes of the lower Sacramento River in either year (0.312–0.629 vs. 0.342–0.599, 95% credible interval in 2012; and 0.111–0.408 vs. 0.240–0.407, 95% credible interval in 2013, respectively). The Yolo Bypass had a higher coefficient of variation (CV) in travel time relative to the lower Sacramento River routes in both years (0.34 vs. 0.29 in 2012, and 0.44 vs. 0.34 in 2013). This work suggests that in relatively low water years, the estimated survival of outmigrating juvenile Chinook Salmon in the Toe Drain is directly comparable to routes in the lower Sacramento River, and that metrics of behavioral diversity can and should be incorporated into future telemetry studies.

KEY WORDS

Sacramento–San Joaquin Delta, mark–recapture, floodplain, migration, route selection, telemetry

INTRODUCTION

There is substantial spatial variability in the Sacramento–San Joaquin River Delta (hereafter “the Delta”), a complex network of tributaries and tidal channels in the Central Valley of California outflowing to the San Francisco Bay. Juvenile Central Valley Chinook Salmon (*Oncorhynchus tshawytscha*) must navigate the Delta during their downstream migration to the Pacific Ocean. Survival during the juvenile life stage, when outmigration takes place, is a known population constraint (Junge 1970; Brandes and McLain 2001; Williams 2006; Moyle et al. 2017). To investigate the role of different migration corridors in survival, Perry et al. (2010) introduced a conceptual framework for studying population-level survival of juvenile Chinook Salmon outmigrating in the Delta. In this framework, route-specific survival and migration probabilities are estimated simultaneously. When combined with an evaluation of how management actions affect the proportion of the population that migrates via different routes, the framework becomes a powerful conceptual tool for leveraging the results of acoustic telemetry studies (Perry et al. 2016).

A growing number of acoustic telemetry studies fit within Perry et al.’s framework; they focus on estimating the survival and distribution of outmigrating juvenile salmonids across different routes in the Delta (Buchanan et al. 2013, 2018; Perry et al. 2013; Singer et al. 2013; McNair 2015; Michel et al. 2015). The results of these acoustic telemetry studies provide useful insight into relative differences in survival along various migration corridors in the Delta. For example, there are substantial differences between survival in the mainstem Sacramento River and other routes in the northern or interior Delta (Perry et al. 2016). The routes within the lower Sacramento River and north Delta, which include Sutter, Miner, and Steamboat sloughs (Figure 1), generally have higher survival than routes through the interior Delta (Perry et al. 2010, 2016). Routes that go through various interconnecting sloughs and channels of the interior Delta, including Georgiana

Slough (Figure 1), consistently have the lowest combined survival of juvenile Chinook Salmon in the Delta (Newman 2008; Newman and Brandes 2010; Perry et al. 2010; Buchanan et al. 2013), and the mainstem Sacramento River has higher mean survival relative to the rest of the Delta (Newman 2008; Newman and Brandes 2010; Perry et al. 2010, 2016; Singer et al. 2013; Michel et al. 2015). However, survival in most outmigration routes in the Delta is characterized by both inter- and intra-annual variability (Perry 2013; Singer et al. 2013; Michel et al. 2015).

Fewer studies have been conducted on the primary floodplain migration route in the Delta. This route traverses the Yolo Bypass, which lies to the west of the lower Sacramento River below Fremont Weir and terminates at the Cache Slough complex (Figure 1). Fish may enter the Yolo Bypass all year at the southern end; however, fish passage through the Yolo Bypass to the Sacramento River (or vice versa) at the northern end is currently possible only via the overtopping of Fremont Weir (Figure 1). Fremont Weir overtops when the Sacramento River reaches stages greater than 9.8 m (32 ft NAVD88). During overtopping and inundation, the Yolo Bypass represents some of the most important seasonal floodplain habitat available for native fishes in the region (Sommer et al. 2001b; Feyrer et al. 2006). Juvenile Chinook Salmon reared in the Yolo Bypass floodplain have demonstrated better growth and survival than those reared in the mainstem Sacramento River (Sommer et al. 2001a, 2005; Katz et al. 2017; Takata et al. 2017). Since the evidence of floodplain benefits to juvenile fishes is substantial, efforts are underway to increase the proportion of juvenile Chinook Salmon able to access the floodplain across a broader range of Sacramento River stages and flows (DSC 2013; NMFS 2009). Most of these efforts involve proposed modifications to Fremont Weir, with the goal of diverting flow and increasing juvenile fish entrainment into the Yolo Bypass at Sacramento River stages below 9.8 m (32 ft NAVD88), allowing fish to rear and migrate through the Yolo Bypass even in relatively dry years (NMFS 2009; DSC 2013; CDWR and USBR 2017). However, the only perennially-navigable route through the Yolo Bypass in the absence of flood conditions is the Toe Drain, a narrow, shallow channel along the

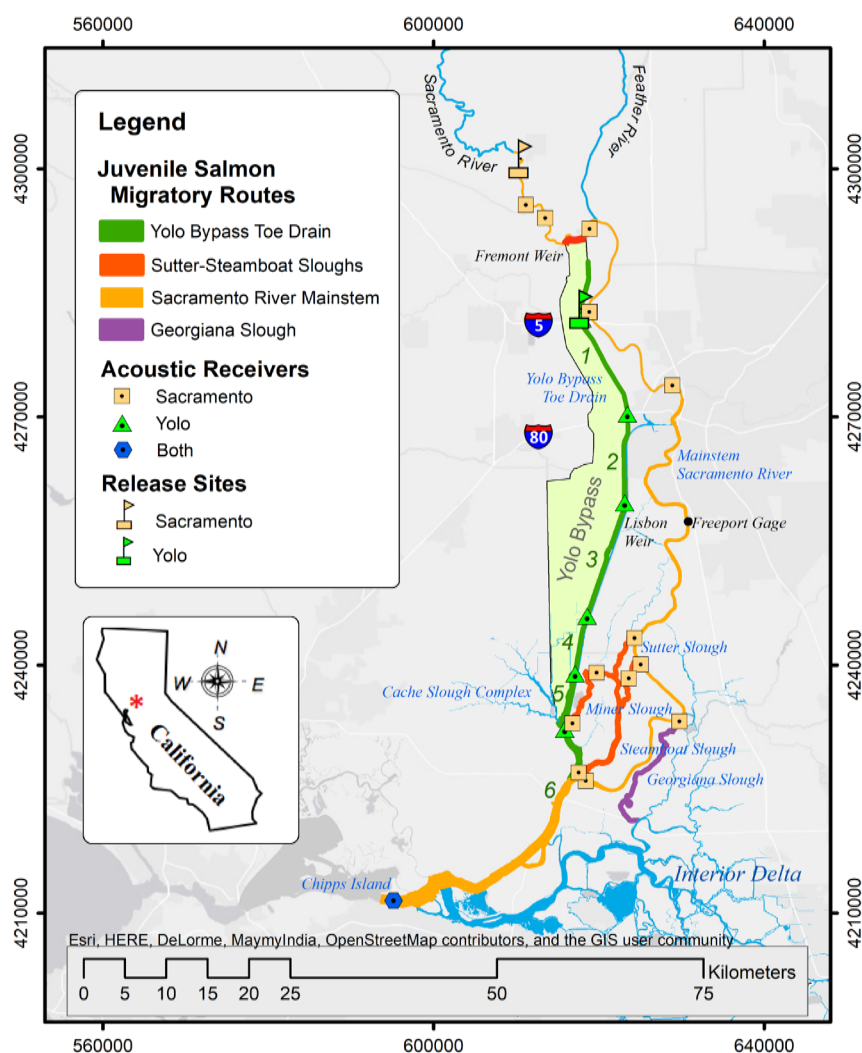


Figure 1 Map of study area for the transit and survival of late-fall-run juvenile Chinook Salmon in the Sacramento River Delta, California, USA. Each migratory route considered in the survival analysis is noted with a different color, along with release locations and acoustic receivers, as deployed in 2012. (See supplementary materials for detailed information about receiver deployment in both years.) Routes along the Sacramento River in the north Delta include Sutter, Steamboat, and Miner sloughs. Georgiana Slough was the only route that provided access to the interior Delta, because the Delta Cross Channel (not identified here) was closed during the study periods. Migratory reaches within the Yolo Bypass route are identified with numbers (1–6) for cross-reference with route-specific survivals presented in Figure 4

eastern edge that terminates in the Cache Slough Complex (Figure 1). The Toe Drain is seasonally prone to high temperatures, and piscivorous fish and birds are present in the channel all year (Sommer et al. 2004). As such, in the absence of flood conditions, the Toe Drain may not be a beneficial migratory corridor for outmigrating juvenile salmon that are entrained into the Yolo Bypass.

Finally, although our knowledge of the range of survival experienced in different routes of the Sacramento–San Joaquin Delta has increased in recent years, the relationship between migration pathway and behavioral diversity is poorly understood. Given the heterogeneous nature of the various migratory routes in the Delta, it is possible that certain routes may be associated

with outmigrating individuals that exhibit higher or lower behavioral diversity. Chinook Salmon are characterized by substantial life history and behavioral variation, which has aided them in species-level resilience and rapid adaptation to unpredictable environments in the past (Moyle 2002). For example, there are four different races of Chinook Salmon in the Central Valley alone (Moyle 2002), each exhibiting distinct migration timing, as well as ocean type, 90-day type, and stream-type life histories (Gilbert 1912; Healey 1991; Higgs et al. 2010). The need to include diversity metrics in Chinook Salmon studies (Johnson et al. 1992; Miller et al. 2010; Carlson and Satterthwaite 2011; Goertler et al. 2016), has been increasingly understood, but

such measurements have been largely missing from acoustic telemetry survival studies.

The goal of the present study was to address two primary questions: (1) in the absence of flood conditions, how does the route-specific probability of survival of juvenile Chinook traveling from within the Yolo Bypass to the end of the upper estuary (at Chipps Island) compare to other routes in the north Delta, and (2) how can indices of behavioral diversity be incorporated within the theoretical framework of telemetry studies that investigate the survival and movement of juvenile Chinook Salmon in the Delta?

MATERIALS AND METHODS

Approach

Our approach was to release acoustically-tagged, juvenile late-fall-run Chinook Salmon and track their movements across an underwater receiver array. This approach, while similar to other landmark telemetry studies in the Delta (e.g., Perry et al. 2010), differs in that the releases across the 2 study years (2012 and 2013) were conducted simultaneously at two locations within two distinct systems in the Delta: the Sacramento River, and the Yolo Bypass (see release site locations in Figure 1). The two systems converge near Rio Vista, California. Chipps Island marked the seaward end of the fish's telemetered downstream migration paths (Figure 1).

Study Systems and Release Sites

The Yolo Bypass system is a 240-square-km (59,000-acre) floodplain in the Central Valley of California that occupies the lower portion of the historical flood basin of the region (Figure 1). The Yolo Bypass also serves as a primary floodplain of the lower Sacramento River (Sommer et al. 2001a, 2001b, 2005). The partially-leveed system has been modified to divert floodwaters from the Sacramento River and its tributaries around the city of Sacramento and surrounding metropolitan areas. The hydrology of the system is complex, with inputs from smaller west-side streams (Putah Creek, Cache Creek, Knights Landing Ridge Cut) as well as seasonal inundation from Sacramento Valley floodwaters via two weirs: Fremont Weir and Sacramento Weir. As previously mentioned, the Toe Drain Canal is the

only perennially-navigable water channel within the Yolo Bypass (Figure 1). During drier periods, when Sacramento River unimpaired runoff is equal to or less than $9.6 \times 10^9 \text{ m}^3$ (7.8 million acre-feet) and the Fremont Weir is not overtopping, the Toe Drain functions as a tidal slough, receiving tidal flows from the Cache Slough complex (which lies just north of the mouth of the Sacramento River; see Figure 1). The extent of the Yolo Bypass migratory route we investigated in this study spanned 90 kilometers, from the Interstate 5 bridge crossing in the upper reaches of the Toe Drain to Chipps Island (Figure 1). Although the full route includes reaches in the lower Cache Slough complex and Sacramento River, the Toe Drain itself terminates within the Yolo Bypass above the Cache Slough complex at approximately River Kilometer (RKM) 114 (measured from the Golden Gate Bridge in the San Francisco Bay).

The other system considered in this study is the lower Sacramento River and its distributaries in the northern Delta. As fish migrate down the Sacramento River from the release site, they may divert from the mainstem channel at Sutter Slough, or further downstream at Steamboat Slough (Figure 1). The fish that take Sutter Slough may then either branch off to Miner Slough, where they will eventually exit at the base of the Cache Slough complex, or they may stay in Sutter Slough and continue southward. Those that stay in Sutter Slough quickly converge with fish that entered Steamboat Slough from the mainstem (Figure 1), and emerge just north of the mouth of the Sacramento River. Fish that remain in the mainstem Sacramento River after these junctions have two more opportunities to divert: first at the Delta Cross Channel (which was closed during this study and was not monitored), and then at Georgiana Slough, which eventually connects to the upper extent of the interior Delta. These migration corridors vary in their levels of aquatic and riparian vegetation, channelization, and bathymetry complexity, but all have been heavily altered over time (Whipple et al. 2012).

There was one release site for each of the two study systems (Figure 1), and all routes terminated at Chipps Island, the endpoint of detection for tagged fish in this study. In the Yolo Bypass system, fish were released near the I-5 bridge into the Toe Drain Canal (RKM 159). Once released in the Yolo Bypass,

Table 1 Summary of release group sample sizes and route distances in each year. The Yolo Bypass route is linear, and thus only one route is possible. In the Sacramento River, fish may stay in the mainstem, divert from the mainstem at Sutter Slough (whereafter they may take either Miner Slough or Sutter Slough—see [Figure 1](#)), divert from the mainstem at Steamboat Slough, or divert from the mainstem at Georgiana Slough. Sutter, Miner, and Steamboat sloughs were grouped into a single route for both years

System	Year	Number of fish released	Route	Route distance (km)
Yolo Bypass	2012	25	Yolo Bypass	90
	2013			
Sacramento River	2012	37	Mainstem	152
			Sutter/Miner/Steamboat Slough	142
			Georgiana Slough	167
	2013	100	Mainstem	152
			Sutter/Miner/Steamboat Slough	142
			Georgiana Slough	167

the Toe Drain is the only route feasible to Chipps Island in dry conditions. This route is termed the “Yolo Bypass” route in [Figure 1](#) and hereafter. Tagged fish in the Sacramento River system were released in the Sacramento River approximately 9 RKM upstream of Fremont Weir (RKM 223). The three migratory routes studied in the Sacramento River system are located within what we hereafter term the “north Delta,” the region of the Sacramento River watershed below Knight’s Landing. The mainstem Sacramento River was one route, and Sutter, Miner, and Steamboat sloughs were grouped together as the second route. The third route was Georgiana Slough. All route distances were measured in km from the release site to the final detection point at Chipps Island, using Google Earth. The Sutter/Miner/Steamboat Slough route was 142 km on average. Georgiana Slough was the longest route, spanning 167 km. The mainstem Sacramento River route was 152 km ([Table 1](#)). All three north Delta routes eventually converge at approximately RKM 77, which is 8 km upstream of the final detection point at Chipps Island.

Fish Release Groups

All fish in the study were yearling late-fall-run Chinook Salmon juveniles, spawned and reared at the Coleman National Fish Hatchery (CNFH). Twenty-five fish were released in the Yolo Bypass in March in 2012 and in 2013 (126.5-mm and 116.0-mm mean fork length, respectively; [Table 2](#)). In the Sacramento River, 37 fish (126.4-mm mean fork length; [Table 2](#)) were released in 2012, and 100 fish (131.3-mm mean fork length; [Table 2](#)) were released in 2013.

Transmitter Implantation

Fish were tagged with 180-kHz acoustic tags (VEMCO®, V5) (5x12-mm, weight 0.65g, power output 143dB). Estimated tag battery life varied by year and release group, but ranged from 30 to 63 days. Acoustic tags were surgically implanted using a modification of the protocol used by Adams et al. (1998). Fish released in the same year were tagged on the same day by the same surgeons. Each fish undergoing surgery was transferred from the aerated holding tank into a 19-L container containing an anesthetic bath of 90 mg L⁻¹ tricaine methanesulfonate (MS-222). When a fish reached Stage 4 anesthesia (Summerfelt and Smith 1990),

Table 2 Summary of tagged fish and release groups

Release group	Number of fish	Mean fork length in mm (SD)	Mean weight in grams (SD)	Mean tag burden % (SD)
Sacramento River 2012	37	126.41 (12.39)	23 (6.18)	3.09 (1.1)
Sacramento River 2013	100	131.3 (14.21)	25.32 (9.04)	2.9 (0.89)
Yolo Bypass 2012	25	126.48 (11.58)	22.28 (5.49)	3.12 (0.89)
Yolo Bypass 2013	25	116 (5.32)	17.06 (2.94)	4.22 (0.69)

it was removed from the anesthetic bath, and mass and length measurements were recorded. Surgeries were conducted on a custom surgical table, which was fitted with an irrigation tube to ensure that water containing a maintenance anesthetic dose of 30 mg L⁻¹ of MS-222 passed continually over the gills of the fish. Once a fish was placed inverted on the surgical table, a 6- to 10-mm incision was made in front of the pelvic girdle, and the tag was inserted into the coelomic cavity. The incision was then closed with one or two interrupted sutures of absorbable monofilament. Surgery times for all release groups ranged from 1.3 to 6.8 minutes, with an overall mean of 2.1 minutes. After surgery, individual fish were placed into another 19-L container where the time to initial recovery, characterized by proper orientation and swimming, was recorded. The fish was then placed in the holding tank and allowed to recover for 24 hours before release. Previous studies with late-fall-run Chinook Salmon from the CNFH have shown that there is minimal tag-related mortality when the tag-weight to body-weight ratio (the “tag burden”) remains below 5.6% (Sandstrom et al. 2013; Ammann et al. 2013). Mean body-weight ratio was less than 4.2% of body weight for each release group (Table 2). Two fish in the Sacramento River 2012 release group exceeded the 5.6% body-weight ratio.

Fish Transport, Release, and Detection

Tagged fish were transported in large, oxygenated coolers from the CNFH to the release sites. Fish were divided evenly between coolers to keep densities equal and to ensure that all fish were treated similarly; each cooler held 10 to 13 smolts. Before release, temperatures in the coolers were slowly

equilibrated by periodic exchanges of cooler water, at a rate that changed the temperatures in the coolers no more than 1°C per hour. Releases began when the temperature of the first cooler was within 0.5°C of the river. Each cooler release was spread out by 20 minutes to promote dispersal of the fish. The spread would ideally also reduce collisions of acoustic signals that prevent receivers from recording a complete detection, or lead to the creation of false tag codes.

Releases at both sites took place mid-afternoon on March 30, 2012 and on March 6, 2013, respectively, and spanned 1 to 3 hours, including acclimation time. The presence or absence of the released fish was then recorded with an array of 180-kHz-sensitive acoustic receivers (VEMCO® Ltd., VR2W) (Figure 1). The acoustic array consisted of single, autonomous receivers in most locations. However, in locations where the width of the river exceeded the expected detection range of a single receiver, at least two receivers were deployed (one on each side of the channel, as at the base of the Cache Slough complex, or multiple receivers placed at equal intervals across the width of the channel, in the case of the Chipps Island receiver locations). Figure 1 depicts consistent monitor locations between the 2 years of the study; however, the spatial organization of individual reaches and number of receivers differed slightly between years (detailed receiver maps, and other supplementary materials, are included at <https://github.com/Myfanwy/Johnstonetal2018SFEWS>). Where possible, receivers were placed upstream and downstream of the points where fish would be able to transition from one route to another. At Chipps Island, dual lines of receivers allowed the probability of survival and detection in the last reach of each

route to be independently estimated (Skalski 2006; Perry et al. 2016). The acoustic receiver array data were downloaded after the expected life of the acoustic tags had passed (minimum of 30 days).

Range Tests

We completed a continuous, 10-day range test in the Cache Slough complex in 2014. Monitors detected a stationary tag that emitted a coded signal every 10 seconds, with an average of 99% efficiency at 50 meters, 50% efficiency at 175 meters, and 16% efficiency at 300 meters across the testing period, although conditions and detectability varied greatly with noise and hydrologic conditions. Within the Toe Drain, mobile range testing recorded a 100% detection efficiency of a stationary tag at 200 meters. Range testing conducted by a multi-agency group in January of 2012 found detection at Chipps Island to have an efficiency of approximately 97% at 50 m, 70% at 100 m, and 47% at 150 m (Israel et al., unpublished data). Range test data within the mainstem Sacramento River was unavailable, but short-term range tests in Sutter Slough had a 100% detection efficiency at 50 meters and 50% at 150 meters (Israel et al., unpublished data, see “Notes”).

Data Processing

The raw data was imported and initially processed with the software program VUE (Version 2.3, VEMCO, Inc). This was done to: (1) remove potential false detections; (2) identify predation events or shed tags; and (3) correct for any time-drift that occurred in the receivers during deployment. The detections were then exported to R (Version 3.1, R Core Team 2017) and processed into individual encounter histories. Encounter histories are a presence-absence spatio-temporal record for each fish at the acoustic receivers placed along the migratory corridor. For the Sacramento River fish, the encounter history of each fish was used to classify the route the fish had taken (either the mainstem Sacramento River, Sutter/Miner/Steamboat Slough, or Georgiana Slough).

We assumed that the spatio-temporal history of a fish could only display upstream movement for one of two reasons. The first was that the fish was consumed by a predator, in which case the fish would not

resume its downward migration after rapid upstream movements. The second was that the fish was advected or displaced upstream by the tide. Observed tidal advection took place only in the vicinity of the base of the Cache Slough complex (Figure 1), after fish had already selected a route. Several individuals that had taken the mainstem Sacramento River route were detected at the mouth of the Sacramento River, then detected at one or more receivers at the base of the Cache Slough complex. The fish were then either subsequently detected at Chipps Island, or not detected again. The detections constituting these upstream movements were removed from each affected fish's encounter history, so as not to confound the model or the route classification of these fish. In cases where a fish's encounter history evidenced its predation, its detection record was truncated to the last observed downstream location before its upstream movement. A single instance of a shed tag or mortality was evidenced in the Sacramento River 2013 release group; this fish's detection history was truncated to the first detection at its last known receiver location.

Finally, to define the temporal context of environmental conditions examined during the study period, we calculated a “detection window” across all detections in a single year. This was defined as the time elapsed from the first recorded detection to the last recorded detection of any tagged fish, excluding the shed and predated tags. Data on environmental conditions in the following sections were summarized within each study year's respective detection window. We obtained water temperatures and flow in the Toe Drain and the mainstem Sacramento River during the detection windows of both years from the CDEC gauges at Lisbon Weir in the Yolo Bypass and Freeport in the Sacramento River, respectively (Data available from: <http://cdec.water.ca.gov>).

Statistical Analysis

Travel time for individual fish was defined as the total time elapsed (including time spent during tidal advection for those individual fish affected) between the time of release and the time of first detection at the Chipps Island dual receiver array. To provide a metric of behavioral diversity in outmigration, we report the CV on individual travel

times between systems. The larger the CV, the greater the variability present within the measured quantities. Our assumption was that the CV of travel time might provide an indication of whether there was system-level variation in behavioral diversity in outmigrating juvenile Chinook Salmon.

To estimate survival in both systems, we fit a multi-state, multi-level mark-recapture model to the telemetry data. The model estimates the probability of a fish existing in a certain state at each receiver location in its encounter history. A fish is known to be alive at a given upstream location if it is later observed at a location further downstream, and is known to be in a certain route when there are no possible transitions into other routes before the next observation of that fish's path. Since it is possible for a fish to be alive but undetected, the observable states for the model are then: (1) alive and detected in a known route, (2) alive in a known route but undetected at a certain location within that route, (3) dead (or undetected) in a known route, (4) alive with route unknown, and (5) dead (or undetected) with route unknown. In this study, state 4 was not observed in the data.

The probability (p) of observing a fish is then the product of its survival and detection probabilities at a given location:

$$p(\text{observed}) = p(\text{survival})p(\text{detection}) \quad (1)$$

Where "observed" is indicated by a positive detection at a receiver location. If the fish is unobserved at a particular location within its encounter history, but observed at some later downstream location, the model assumes that the fish is alive at all the previous locations along a given route. For these intermediate locations in an encounter history where the fish went unobserved, the model estimates:

$$p(\text{unobserved}) = p(\text{survival}) (1 - p(\text{detection})) \quad (2)$$

When the fish is not known to be alive at a given location (i.e., is *not* observed at that location or at any subsequent location in any route), the model estimates:

$$p(\text{unobserved}) = p(\text{survival}) (1 - p(\text{detection})) + (1 - p(\text{survival})) \quad (3)$$

In this case, since both the probability of survival at the current location and the probability of having died before the current location depend on the fish's previous state(s) at all its prior locations, this quantity is calculated recursively for each fish and location along the route.

For each of the model scenarios above, the probability of surviving from a prior location to a current one is a mixture of one individual-level effect (fork length) and one reach-level effect (length in kilometers). A reach is a stretch of river delimited by an upstream receiver location and a downstream receiver location along a given route. When the routes diverge in the Sacramento River system and fish can choose among one of the three possible routes, the model included estimation of a transition probability ψ_h , where h is one of the three possible routes. In the estimation of ψ_h , the model used only fish that were observed alive in the reach before the transition location.

The survival model was adapted from Kéry and Schaub (2012) and fit in Stan[®] via the rstan interface (Version 2.15.0, Stan Development Team 2016). We chose a Bayesian framework because it offers a straightforward, flexible approach to fitting this computationally-intensive model. We also chose this framework because receiver placement in the Sacramento River changed slightly between 2012 and 2013, and it was not always possible to have receivers above, below, and within each route transition in the Sacramento River in both years (receiver placement details are available from: <https://github.com/Myfanwy/Johnstonetal2018SFEWS>). A Bayesian framework accommodated this by accounting for uncertainty in the survival and detection probabilities for these locations and subsequent reaches. The model makes several assumptions: (1) all transition and detection probabilities are the same for all individuals at a given station across the study period; (2) individual survival is independent; (3) states are recorded without error; (4) a fish cannot be detected once dead; (5) fish proceed downstream after release, and do not backtrack; and (6) survival, detection, and route selection are independent of a fish's previous reach. We used weakly-informative, beta-distributed priors for probability of survival and detection, and weakly-informative, normally-distributed priors

for the effects of fork length and reach length. The survival model was structured as multi-level, with effects estimated at both the route level and the overall system level (either the Yolo Bypass or the Sacramento River system), which facilitated direct comparison of expected cumulative survival between the two systems across years. Differences between systems were calculated as the difference of the posterior probability distribution of expected cumulative survival in one system from that of the other. (In the Sacramento River system, the expected cumulative survival was the average of all three estimated route-level survivals, weighted by their transition probabilities). When the 95% credible

interval—as calculated by the quantile method—of the distribution of differences included zero, we inferred no consistent difference in expected cumulative survival between the systems and years in question. All code and data used to fit the model is available from: <https://github.com/Myfanwy/Johnstonetal2018SFEWS>.

RESULTS

Environmental Conditions

During the study period, average daily water temperature in the Sacramento River ranged from 11–14 °C (mean 13.0 °C) in 2012, and 12–17 °C

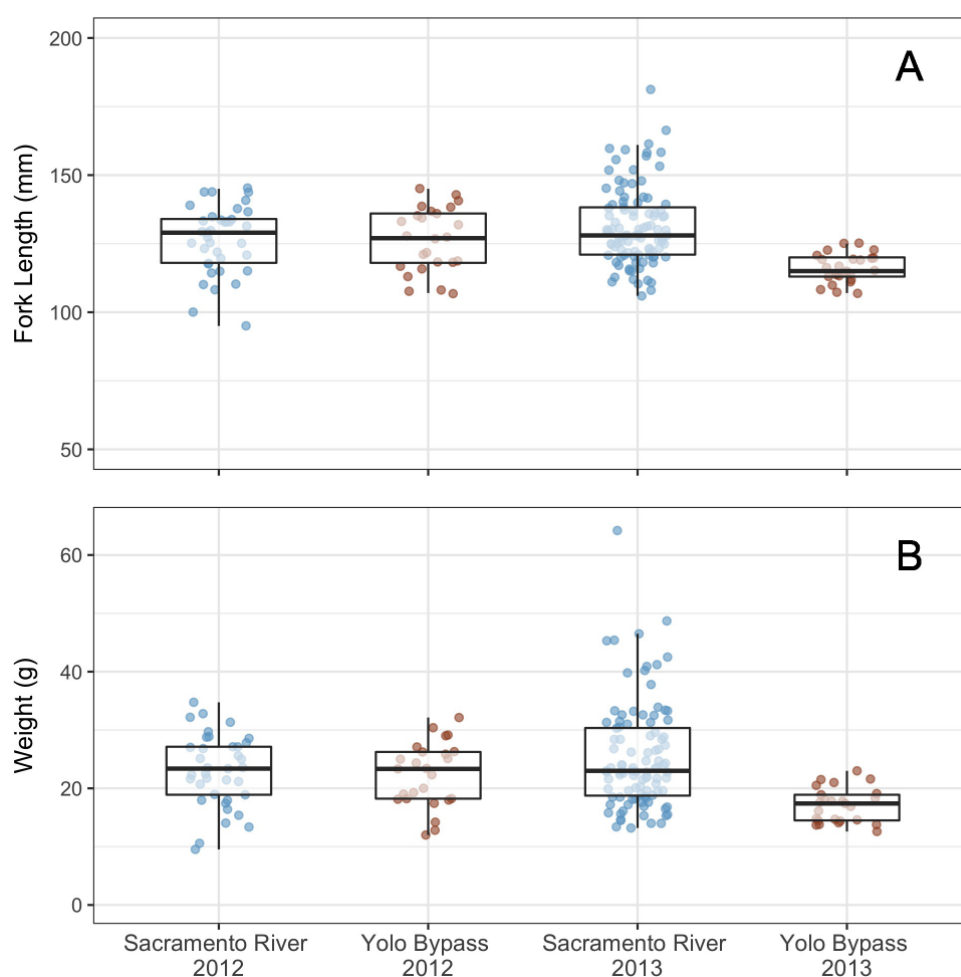


Figure 2 Distribution of fork length and weight of tagged fish across the four release groups in the study. The bolded black line in each box is the median; lower and upper hinges of the boxes correspond to the 25th and 75th percentiles. The upper whiskers extend from the hinge to the largest value no further than $1.5 \times \text{IQR}$ from the hinge (where IQR is the inter-quartile range, or distance between the first and third quartiles). The lower whisker extends from the hinge to the smallest value, $1.5 \times \text{IQR}$ of the hinge, at most. The individual dots are the actual measurements, color-coded by system, jittered and plotted with partial transparency for visual aid.

(mean 14.9 °C) in 2013. In the Yolo Bypass, average daily water temperature was higher than the Sacramento River in both years, ranging from 14–18 °C (mean 15.8 °C) in 2012, and 13–20 °C (mean 16.9 °C) in 2013. Flows at Freeport ranged from 348–1,274 m³s⁻¹ (mean 690 m³s⁻¹) in 2012, and 184–494 m³s⁻¹ (mean 364 m³s⁻¹) in 2013. The Toe Drain is a smaller channel than the Sacramento River, and flows were much lower than those in the Sacramento River, ranging from 22–41 m³s⁻¹ (mean 28 m³s⁻¹) in 2012, and 5–15 m³s⁻¹ (mean 11 m³s⁻¹) in 2013. Overall, these flows were very low compared to typical levels at this time of year (Sommer et al. 2004, 2005).

Fish Condition

Weight and fork length of the tagged fish were similar across years and systems for three out of the four releases (Table 2). Fish in the Yolo Bypass release group during 2013 were shorter in fork length, weighed less on average, and had much less variation in both fork length and weight relative to the other release groups (Table 2; Figure 2).

Detection Window and Travel Time

The detection window was longer in 2013 than it was in 2012 for both systems. In 2013, the detection window in the Sacramento River was 40 days, from March 6 to April 15, versus 17 days in 2012 (from March 30 to April 16). In the Yolo Bypass, the detection window was 25 days in 2013 (March 6 to March 31), versus 17 days in 2012 (March 30 to April 16). Average travel time from both release sites to Chipps Island was shorter in 2012 than in 2013, but similar between the two systems within years (Table 3). The Yolo Bypass system had greater CV of travel time than the Sacramento River system in both years.

Route Selection and Survival

There were no substantial or consistent differences between the estimated cumulative probability of survival in the Yolo Bypass and all routes of the north Delta in either year. Mean estimated survival was slightly higher in the north Delta routes in 2013 compared to the Yolo Bypass route (Table 4);

Table 3 Coefficients of variation in travel time from release site to Chipps Island. N is the number of individual fish from each release group detected at the receiver array at Chipps Island. For the Sacramento River releases, the distance in kilometers is the mean of the total distance traveled by individual fish in that year, including distance traveled by individuals during tidal advection in the Cache Slough complex

Release group	N	Distance in kilometers	Mean travel time in days (SD)	Coefficient of variation in travel time
Sacramento River 2012	17	154	10.9 (3.2)	0.29
Yolo Bypass 2012	13	91	10.7 (3.6)	0.34
Sacramento River 2013	28	151	16.0 (5.4)	0.34
Yolo Bypass 2013	5	91	14.8 (6.5)	0.44

however, in both years the distribution of possible differences between the two systems estimated by the model included zero (Figure 3). This indicates there were no consistent differences in estimated survival between the systems in either year. The lowest estimate of route-level survival was associated with the Georgiana Slough route in 2013 (0.043–0.323, 95% credible interval; Table 4), while the mean estimated cumulative survival in both years was highest for the mainstem Sacramento River route (0.528 and 0.348, respectively; Table 4). In both years, fish had a higher estimated probability of remaining in the mainstem Sacramento River than of diverting into one of the other two routes (Table 5).

The model estimated the effect of both reach length and fork length on individual survival. The values of estimated cumulative probability of survival in Table 4 apply to fish of 130-mm average fork length that transited the length of the routes in this study. The estimated effect of reach length on survival was small and overlapped zero; –0.01 per 10 km (–0.03–0.01, 95% credible interval). The estimated effect of fork length on survival was 0.02 (0.01–0.03, 95% credible interval) per cm.

Table 4 Estimated cumulative probability of survival for each route and year. Estimates reported are from the release site to Chipps Island, a distance of varying lengths for the two systems and differing slightly among the three routes of the Sacramento River (see Table 2). Estimates represent the mean expected cumulative probability of survival for a fish of 130 mm in fork length transiting the distance of a given route. We used the quantile method to calculate credible intervals. The estimate for “All Routes” in the Sacramento River system is the average of the posterior probabilities of each of the three routes in that system, weighted by their estimated route probabilities (see Table 5).

Year	System	Route	Mean estimated cumulative survival	95% credible interval
2012	Yolo Bypass	Yolo Bypass	0.469	0.312–0.629
2012	Sacramento River	Mainstem	0.528	0.370–0.682
2012	Sacramento River	Sutter/Miner/Steamboat Slough	0.392	0.203–0.584
2012	Sacramento River	Georgiana Slough	0.423	0.136–0.684
2012	Sacramento River	All Routes	0.470	0.342–0.599
2013	Yolo Bypass	Yolo Bypass	0.240	0.111–0.408
2013	Sacramento River	Mainstem	0.348	0.243–0.456
2013	Sacramento River	Sutter/Miner/Steamboat Slough	0.364	0.245–0.483
2013	Sacramento River	Georgiana Slough	0.172	0.043–0.323
2013	Sacramento River	All Routes	0.322	0.240–0.407

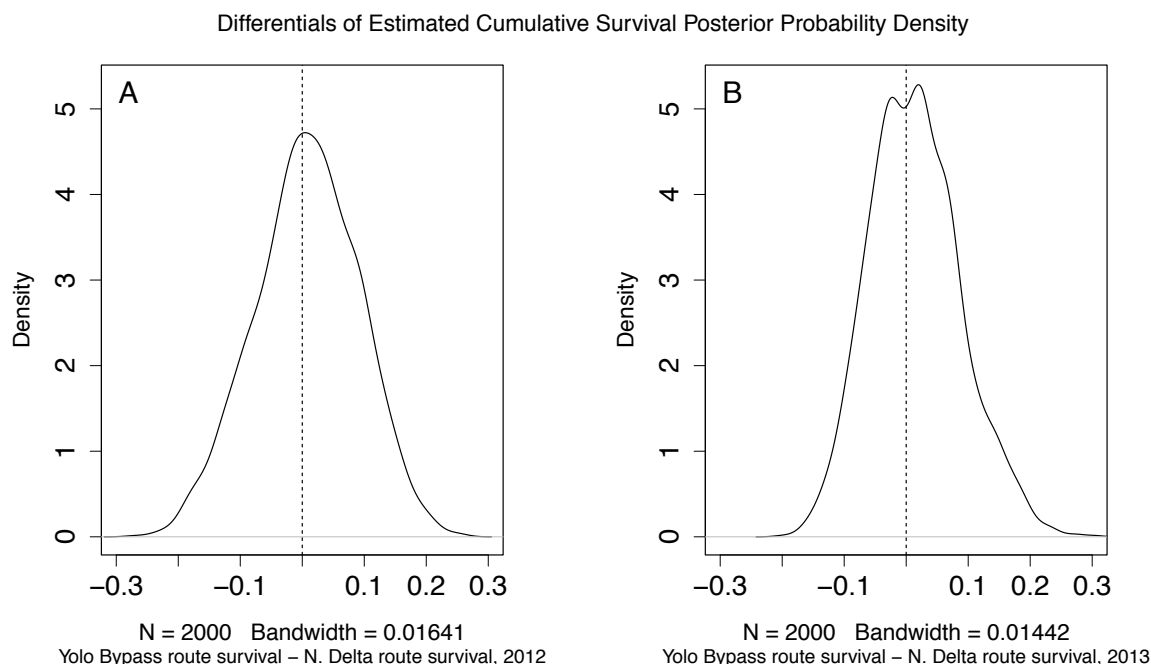


Figure 3 Posterior probability density differentials for estimated cumulative survival between the Yolo Bypass system and the Sacramento River system in both years. The distribution of differences between estimated survival in the north Delta routes from that of the Yolo Bypass route is shown. The distributions overlapped with zero (dotted line) in both years, indicating no conclusive evidence for differences in survival between the two systems. The dotted line at zero has been added for visual reference.

DISCUSSION

The first goal of this study was to estimate and compare juvenile Chinook Salmon survival during outmigration in select routes in the Sacramento River and Yolo Bypass systems. Our estimates of route-level survival from the Sacramento River system were consistent with previous studies in the region (Perry et al. 2010, 2013; Michel et al. 2015; Singer et al. 2013), and the estimated route-level survival through the Yolo Bypass was not consistently or substantially different from those estimated in the north Delta routes in this study (Table 4; Figure 3).

This similarity in estimated survival between the two systems was surprising. Water Year 2012 was classified by the California Department of Water Resources (CDWR) as a Below Normal water year based on measured unimpaired runoff; 2013 was classified as Dry, representing more intense drought conditions (<http://cdec.water.ca.gov>). The dry conditions corresponded to a much larger reduction

of flow in the Toe Drain relative to the Sacramento River, and correspondingly higher temperatures. Lower flows and higher temperatures are both factors that have been linked with low survival in the Delta (Newman et al. 2008; Brandes and McClain 2001; Baker and Morhardt 2001; Baker et al. 1995; Perry et al. 2016). Lower flows during outmigration have been hypothesized to correlate with higher exposure time to predators and elevated temperatures in the Delta for juvenile Chinook Salmon (Perry et al. 2016, 2018). In general, exposure time should correlate negatively with survival for migratory prey (Anderson et al. 2005). Despite being the shortest route studied by 64 km on average (Table 1), the longest average travel times were observed in fish released in the Yolo Bypass route, meaning that this route was associated with the highest exposure times and potential for negatively affecting survival. As a result, we might have expected to observe lower estimated survival in the Yolo Bypass route relative to the north Delta routes, but this was not the

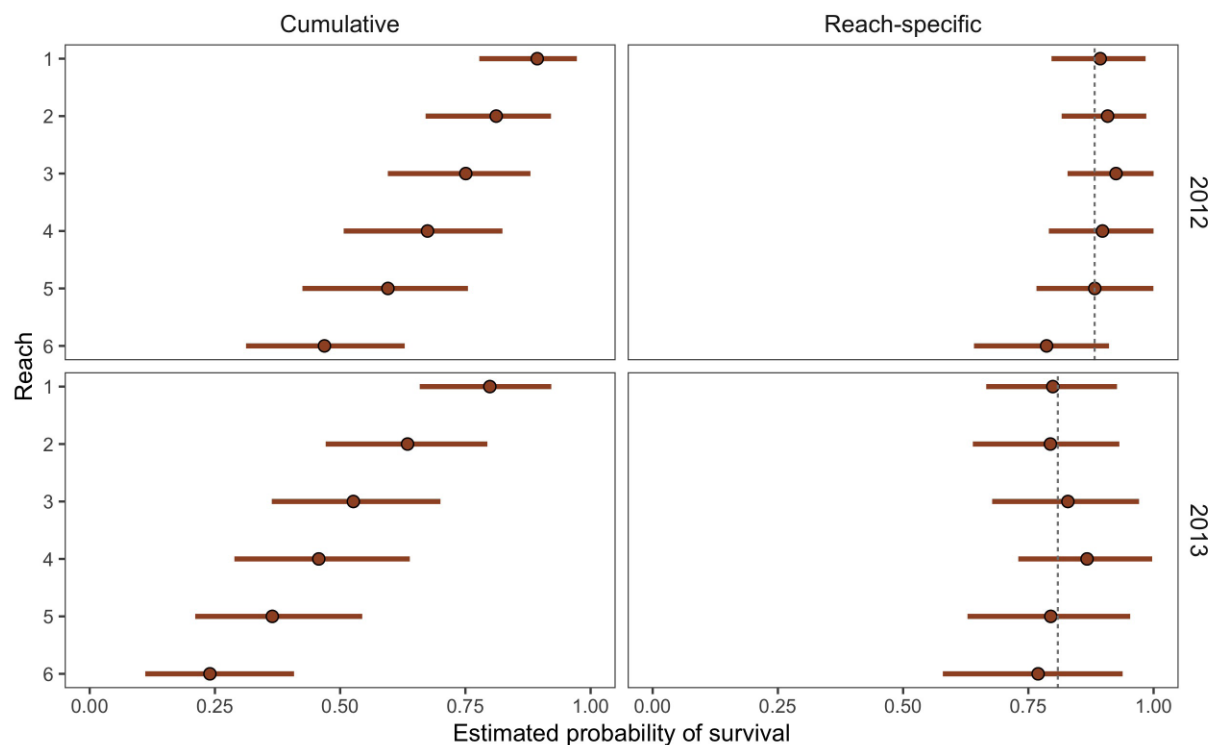


Figure 4 Estimated cumulative vs. estimated reach-specific survival in the Yolo Bypass route in both years. "Middle points represent the estimated mean; whiskers delineate upper and lower 95% credible intervals. The dashed vertical lines in panels B and D indicate overall mean estimated reach-specific survival in the Yolo Bypass that year. Reach identifiers (1–6) correspond to those indicated on Figure 1.

case. Although differences in route lengths, travel time, flow conditions, and water-quality conditions likely all interplayed in complex ways to affect estimated survival, these results suggest that survival in the Yolo Bypass may be higher under drier conditions than would be expected. As a migratory route, the Yolo Bypass represents an alternative to the branching channels along the Sacramento River, and provides valuable rearing habitat and growth benefits to juvenile fish in flood years (Sommer et al. 2001a). Although the tagged fish in this study were relatively large smolts, and therefore unlikely to have spent time rearing during their outmigration, this study provides initial evidence that the Yolo Bypass may represent a suitable migratory corridor for fish that are diverted into the Toe Drain in the absence of inundated conditions.

Differences in reach-specific survival in the Yolo Bypass between years signaled possible changes in underlying environmental conditions related to lower cumulative survival in 2013. In 2012, the lowest estimated reach-specific survival in the Yolo Bypass route took place in the final reach (Figure 4). Note that while it belongs to the Yolo Bypass route, this particular reach exists outside the boundaries of the Yolo Bypass itself, meaning that estimated reach-specific survival within the confines of the Yolo Bypass was very high in 2012. In 2013, however, estimated survival was lower than it was in 2012 across all reaches in the Yolo Bypass route, not just the ones outside the Yolo Bypass boundaries (Figure 4). Larger sample sizes in future studies of

survival in the Yolo Bypass would permit greater certainty in reach-specific survival estimates, and help to establish whether reach-specific survival varies between years, as has been found in studies in the rest of the Delta (Singer et al. 2013; Michel et al. 2015).

Estimated cumulative survival also differed between the four release groups in the study. Among release groups, the Yolo Bypass 2013 release group had the lowest estimated cumulative survival (0.111–0.408, 95% credible interval; Table 4). Considering this, it is worth noting that the fish in this release group were smaller and more homogenous than the other release groups (Figure 2; Table 2). Because survival was found to be positively associated with fork length, the lower survival estimated in the Yolo Bypass 2013 release group may have been partly attributable to their smaller mean fork length.

Previous work has shown that population-level survival depends upon the proportion of fish that use each migratory route, and the survival within those routes (Perry et al. 2010, 2013). For example, survival in the Georgiana Slough route is typically very low (Newman and Brandes 2010; Perry et al. 2010; Singer et al. 2013), which can lead to a population-level survival estimate being deflated when a large proportion of fish migrate through Georgiana Slough. In the present study, Georgiana Slough's negative contribution to Delta-level survival was greater in 2013 when fish had an estimated 0.18 (0.15–0.20 95% credible interval) probability of taking the route, versus in 2012 when the estimated

Table 5 Migration route probabilities for each route and year for the Sacramento River system releases. We calculated 95% credible intervals using the quantile method

Year	Route	Route probability	95% credible interval
2012	Mainstem	0.550	0.487–0.614
2012	Sutter/Miner/Steamboat Slough	0.350	0.291–0.409
2012	Georgiana Slough	0.100	0.066–0.142
2013	Mainstem	0.525	0.496–0.555
2013	Sutter/Miner/Steamboat Slough	0.299	0.271–0.328
2013	Georgiana Slough	0.176	0.155–0.198

route-selection probability was 0.10 (0.07–0.14 95% credible interval) (Table 5). This may have been from the reduction in flow in 2013, which could have led tidal effects on river flow to be more pronounced at the junction of Georgiana Slough and the Sacramento River than in 2012, causing more fish to be diverted into Georgiana Slough. This study builds on the evidence that route selection or entrainment probabilities vary between – and even within – years (Perry et al. 2010).

The second goal of this study was to incorporate a metric of behavioral diversity for tagged outmigrating fish in the two study systems, by examining the degree of variation present within travel time from respective release sites to Chipps Island. We found that the Yolo Bypass route had higher CV of travel time relative to the north Delta routes in both years (Table 3), despite being the shortest route studied. Travel time and the migration rate of juvenile Chinook Salmon in the Delta is highly variable (Williams 2012), and may differ according to origin (hatchery or wild), race, migration type, and stock – all key components of the diversity we observe in Central Valley Chinook Salmon that helps foster stability and resilience in the population (Lindley et al. 2007; Williams 2006; Carlson and Satterthwaite 2011). Too little is known about how different migratory strategies of juvenile salmonids correspond to variation in travel time, and 2 years of data is certainly not enough to allow for conclusions about whether a particular environment or route is associated with higher behavioral diversity. We hope, however, that by incorporating a behavioral diversity metric in this study, we might further efforts to quantify behavioral diversity in telemetry studies.

Finally, while the results of this study provide an initial comparison of estimated survival and variation in transit time between outmigrating fish in the Yolo Bypass and the Sacramento River, the broad applicability of acoustic telemetry studies to multiple runs of Chinook Salmon and juvenile life stages of other fish species is still debatable. The majority of acoustic telemetry studies on the survival of juvenile Chinook Salmon in the Delta (present study included) have been conducted on hatchery-origin, late-fall-run fish, which are unlikely to represent all migrants in the system (Perry et al. 2016). Previous studies have documented differences in survival, migration behavior,

and estuarine residence between hatchery and wild Chinook Salmon (Beamish et al. 2012; Kostow 2004; Williams 2006; Williams 2012; Levings et al. 1986). More telemetry studies across runs, sizes, migration strategies, and life stages are needed to draw robust conclusions about differences in survival between the Sacramento River and Yolo Bypass systems.

CONCLUSION

Our results provide insight into juvenile Chinook Salmon survival through several outmigration routes in the Delta during low flow periods. This work suggests that in relatively low water years, estimated survival of outmigrating late-fall-run juvenile Chinook Salmon through the Yolo Bypass is directly comparable to estimated survival in routes of the north Delta. Given these results, the known benefits of the Yolo Bypass to juvenile fish under flood conditions, and current proposals to improve access and habitat along the migratory corridor, the Yolo Bypass should continue to be considered a viable migratory route for juvenile Chinook Salmon in the Sacramento–San Joaquin Delta even in the absence of flood conditions. Finally, future telemetry studies should consider including indices or metrics of variation, so that the relationship between behavioral diversity and population resilience might be better understood.

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