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Movement and Survival of Wild Chinook Salmon Smolts from Butte Creek During Their Out-Migration to the Ocean: Comparison of a Dry Year versus a Wet Year

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Abstract

California's Central Valley (CCV) Chinook Salmon *Oncorhynchus tshawytscha* stocks have declined substantially since the mid-1800s, with most listed as threatened or endangered or heavily supplemented by hatcheries. As the largest population of CCV wild spring-run Chinook Salmon, Butte Creek fish are an important source for promoting life history diversity in the CCV Chinook Salmon community. However, little information exists on Butte Creek juvenile mortality during out-migration to the ocean, which is considered a critical phase in the overall population dynamics. We used the Juvenile Salmon Acoustic Telemetry System to track the movement of individual fish, and we used a mark–recapture modeling framework to estimate survival of migrating wild Chinook Salmon smolts from lower Butte Creek to ocean entry at the Golden Gate Bridge. Survival and migration varied significantly among years; in 2015, which was a dry year, Chinook Salmon smolts migrated more slowly throughout their migratory corridor and exhibited lower survival than in a wetter year (2016); among locations, fish migrated faster and experienced higher survival in the lower Sacramento River than in the Sutter Bypass and the Sacramento–San Joaquin River Delta. Our data suggest that higher flow at release and larger fish lengths both resulted in increased survival. Our findings shed light on a critical phase of wild spring-run juvenile Chinook Salmon dynamics and could help to inform future restoration and management projects that would improve the survival and abundance of the CCV spring-run Chinook Salmon populations.

Balancing human demands for water with the maintenance of a functioning ecosystem capable of supporting healthy Chinook Salmon *Oncorhynchus tshawytscha* populations has become a central challenge facing natural resource managers in California's Central Valley (CCV). Here, four runs of Chinook Salmon have evolved distinct

life histories to capitalize on the diversity of habitat available in CCV rivers and streams. The runs are named according to the season in which the adults return to freshwater: fall, late fall, winter, and spring (Healey 1991). Similar to stocks in many large West Coast rivers, Chinook Salmon stocks from the CCV have declined substantially since the mid-1800s, mainly due to the construction of large dams and habitat degradation (Yoshiyama et al. 2001). Spring-run Chinook Salmon were once a major component of CCV Chinook Salmon runs and occupied the headwaters of all major CCV river systems where natural barriers were absent (Williams 2006). Presently, self-sustaining spring-run populations survive only in three tributaries of the Sacramento River: Mill, Deer, and Butte creeks (Lindley et al. 2004). Spring-run fish are reported inconsistently in additional Sacramento River tributaries and are supplemented by stray spring-run adults from the Feather River Hatchery (Yoshiyama et al. 2001). However, these additional stocks are believed to have been hybridizing with fall-run stocks since the 1960s due to dam-created spatial constrictions on previously separate spawning distributions (CDFG 1998). As a consequence of these various stressors, the CCV spring-run Chinook Salmon evolutionarily significant unit (ESU) has been state and federally listed as threatened since 1999 (U.S. Office of the Federal Register 1999).

One of the fundamental objectives for managing spring-run populations for future recovery is ensuring that we are supporting and managing for the full range of life history diversity within the ESU (Beechie et al. 2006). Indeed, spring-run Chinook Salmon populations demonstrate unique juvenile rearing plasticity that is characterized by a wide range of size, timing, and age at which they out-migrate from their natal tributaries to the ocean (e.g., out-migration as subyearling fry, subyearling smolts, or yearlings; CDFG 1998). Such life history diversity has been suggested to convey a stabilizing portfolio effect by providing each population the ability to buffer environmental changes due to anthropogenic forcing or climate, ultimately increasing the resiliency of the entire community (Hilborn et al. 2003; Greene et al. 2010; Schindler et al. 2010). As the largest population of CCV spring-run Chinook Salmon, Butte Creek fish are an important source for promoting diversity in the CCV Chinook Salmon community and have been the focus of considerable investment in the form of population monitoring and restoration efforts. Several restoration actions were implemented in the early 1990s by various state and federal agencies in coordination with water interests and local stakeholders (e.g., CALFED and the U.S. Fish and Wildlife Service's Final Restoration Plan for the Anadromous Fish Restoration Program) in order to restore and maintain CCV spring-run Chinook Salmon populations on a long-term basis. The Lower Butte Creek Project, for instance, was established in 1997 to improve passage for protected fish species while maintaining the viability of commercial agriculture, private wetlands, government lands, and other habitats (ICF Jones & Stokes 2009). Although increases in returning Butte Creek spring-run Chinook Salmon adults have been observed in recent years, the success of those management efforts in enhancing juvenile survival and maintaining population life history diversity has yet to be determined.

Juvenile mortality during out-migration to the ocean is considered a critical phase to overall population dynamics (Healey 1991; Williams 2006). Tagging and tracking of juvenile Chinook Salmon from their freshwater rearing habitats, through riverine systems, and into the marine environment can help to determine survival rates and identify locations where juvenile mortality is greatest during downstream migration. Acoustic tagging technology has become a well-established tool in estimating movement and survival rates of CCV Chinook Salmon juveniles (Perry et al. 2010; Michel et al. 2013, 2015). These studies have mainly focused on hatchery smolts that are easily captured, tagged, and released in large groups, whereas little is known about the survival and movement of the remaining wild spring-run Chinook Salmon populations. Assessing juvenile mortality of wild spring-run Chinook Salmon is challenging in part due to the small size of these populations and the difficulty in capturing them during their out-migration. However, the utilization of survival data from hatchery stocks as a surrogate for wild salmon survival dynamics is often criticized because the two are different in many ways (Kostow 2004). Wild salmon hatch and rear in a completely different environment and face many challenges in their early life that hatchery smolts are able to avoid due to hatchery management and release practices (e.g., predation, water quality). In this paper, we detail an acoustic tagging study—implemented in lower Butte Creek and extending to the Golden Gate Bridge—that was aimed at assessing the movement and survival rates of the largest population of wild CCV spring-run Chinook Salmon smolts during their out-migration to the ocean. We were particularly interested in evaluating potential dissimilarities between survival through (1) the Sutter Bypass, a floodplain that has been suggested to constitute important rearing habitat for juvenile Chinook Salmon (Garman 2013); and (2) the lower Sacramento–San Joaquin River Delta (hereafter, the Delta), which is considered a strongly degraded habitat (Nichols et al. 1986). Moreover, previous studies have demonstrated that CCV juvenile out-migration survival can vary strongly among years due to various anthropogenic and environmental factors (Baker and Morhardt 2001; Brandes and McLain 2001; Michel et al. 2015). Therefore, we compared fish movement and locations of high mortality during out-migration for a hydrologically dry year (2015)

versus a hydrologically wetter year (2016). We discuss the implications of our results for the long-term dynamics of the Butte Creek population and the implementation of future recovery actions.

METHODS

Study site.— Butte Creek is a tributary of the Sacramento River that originates at Humboldt Mountain on the western slopes of the Cascade Range at an elevation of more than 2,100 m (Figure 1). The Butte Creek watershed encompasses an area of about 2,900 km^2 and is connected to the Sacramento River at two locations: the Butte Slough Outfall Gates (BSOG); and the downstream end of the Sutter Bypass, a remnant flood basin habitat (Garman 2013). Butte Creek historically entered the Sacramento River at the BSOG but is now diverted away from the Sacramento River for 40 km into the Sutter Bypass (Figure 1). This bypass is composed of two canals as well as the East–West Diversion Weir, which is used to control the flow of water going into the east- and west-side canals of the bypass. Several weirs along both canals divert water for agricultural or managed wetland uses (ICF Jones & Stokes 2009). During high-flow conditions, water from the Sacramento River flows into the bypass through Moulton, Colusa, and Tisdale weirs to prevent flooding of downstream areas.

Once juvenile salmon exit the Sutter Bypass and enter the Sacramento River above the town of Verona, they migrate downstream through the lower Sacramento River, the Delta, and San Francisco Bay before entering the Pacific Ocean. In a wet year, fish could also cross the Sacramento River at the base of the Sutter Bypass and enter the Yolo Bypass through Fremont Weir; however, no water from the Sacramento River spilled into the Yolo Bypass during the 2015–2016 tagging period. The entire migration corridor considered for this study encompassed 249 river kilometers from the release site in the Sutter Bypass to the Golden Gate Bridge.

Freshwater life history.— Central Valley spring-run Chinook Salmon demonstrate a unique diversity in life history among the California stocks of Chinook Salmon. Adult spring-run Chinook Salmon ascend un-dammed tributaries to elevations between 300 and 1,500 m when the spring freshet allows access, and they hold in deep pools over the summer before spawning in the fall. The CCV spring-run juveniles emerge from the gravel between November and March depending on water temperatures, and they spend 3–15 months in freshwater before emigrating to the ocean (CDFG 1998). Spring-run Chinook Salmon juveniles exhibit a wide variety of rearing and out-migration strategies. They can (1) migrate out of the spawning habitat soon after emergence as fry during high flows in the winter; (2) rear in their natal habitat and out-migrate as smolts during the spring; or (3) remain in the stream for an entire year and out-migrate during the following fall, winter, or spring as yearlings (CDFG 1998). Juveniles out-migrating from Butte Creek are assumed to be a mix of fry and smolts, with very few remaining in Butte Creek as yearlings (Clint Garman, California Department of Fish and Wildlife [CDFW], personal communication). Smolt emigration peaks in April and May but can extend from February through June (Ward et al. 2004a, 2004b, 2004c).

Acoustic tagging and receivers.— We used the Juvenile Salmon Acoustic Telemetry System (JSATS; McMichael et al. 2010) to track the movements and estimate the survival of migrating wild spring-run Chinook Salmon smolts from Butte Creek. The transmitters (tags) were manufactured by Advanced Telemetry Systems (ATS): JSATS Model SS300 tags had a weight in air of 300 mg and dimensions of $10.7 \times 5.0 \times 2.8$ mm. The tags emitted a uniquely coded signal at 416.7 kHz with a pulse rate of about 5 s and had an expected life of 32 d at these settings. The tag weight of 300 mg allowed us to tag juvenile Chinook Salmon that weighed at least 6.0 g (approximate FL = 80 mm), resulting in a tag burden no greater than 5%. Laboratory studies comparing growth and survival between acoustically tagged and untagged juvenile salmon have suggested that tag burdens of less than 5% do not significantly affect acoustically tagged fish relative to untagged controls (Brown et al. 2010; Ammann et al. 2013).

To detect the presence of tagged fish, we deployed acoustic receivers at several sites beginning at the capture/release site and ending at the Golden Gate Bridge (Figure 1). We used a combination of receivers manufactured by ATS, Teknologic, and Lotek Wireless. The number of receivers deployed at each location varied from one to five depending on the channel width. Reaches were defined by receiver locations and varied from 0.5 to 100 km in length (Table 1). Each year, we deployed all receivers prior to release of tagged fish and then recovered and downloaded the data at the end of June.

We collected fish by using a 2.44-m-diameter rotary screw trap (RST) installed at Weir 2 in the Sutter Bypass (Table 2). We chose Weir 2 as the trapping site to ensure that fish collected and tagged were actively migrating downstream, as this weir is relatively low in the Butte Creek system. Additionally, this downstream site ensured that the 30-d acoustic tag battery life was utilized efficiently, allowing fish movement through the Sutter Bypass, the Sacramento River, the Delta, and San Francisco Bay to be recorded. The RST was operated continuously (24 h/d) and was emptied of fish each morning. All salmonids were measured (FL; mm), and an acoustic tag was implanted into each fish larger than 80 mm.

On the riverbank adjacent to the RST, we set up a shaded work station to surgically implant the tags before
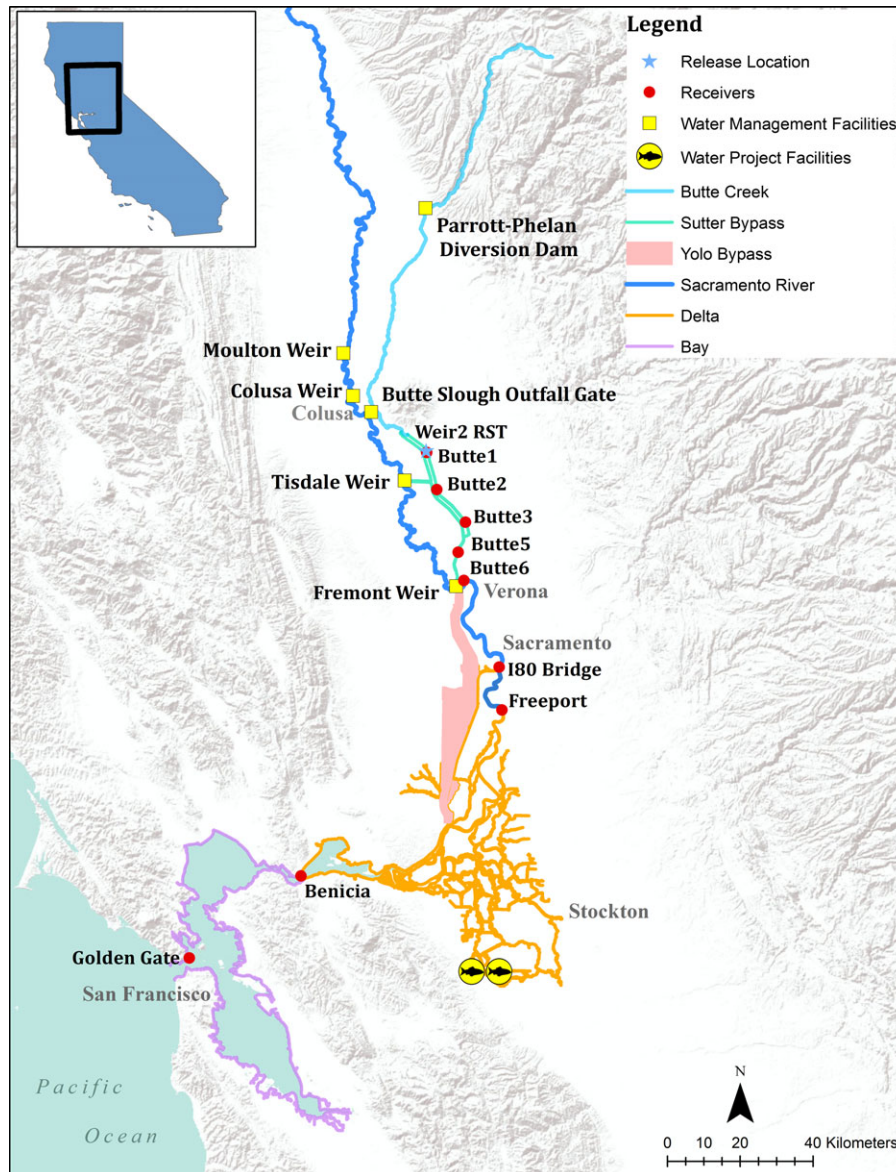
FIGURE 1. Map of California's Central Valley, showing the different regions considered in the study, the release location, and the receiver locations. [Color figure can be viewed at afsjournals.org.]

the sun was overhead and before temperatures became too warm. The same surgeon implanted tags into the coelom of all fish for both years of the study. Fish were anesthetized (tricaine methanesulfonate at a concentration of 90 mg/L), weighed, measured, photographed, and then placed ventral side up in a padded V-channel. During surgery, the fish's gills were irrigated with water containing a maintenance dose of anesthetic (30 mg/L). An incision was made on the ventral side of the fish between the pelvic girdle and pectoral fins with a Sharpoint 3-mm, 15° stabbing blade scalpel. The incision was 6–8 mm long and 3 mm off the ventral midline. The tag was inserted into the coelom and oriented such that the tag transducer was

posterior. The incision was closed with a single suture of 6-0 polydioxanone absorbable monofilament, and the suture was tied with a double-wrapped square knot (i.e., surgeon's knot). We placed each tagged fish into a recovery bucket and monitored the fish until it resumed its normal swimming behavior. After surgery, we held the tagged individuals in holding pens just below Weir 2 for 12 h before releasing them at 2200 hours (Pacific Standard Time), primarily to ensure that the fish were fully recovered but also because juvenile salmon tend to migrate at night (Chapman et al. 2013).

We collected tissue samples from all tagged fish to identify their origin by using genetic stock identification

TABLE 1. Study reach locations where out-migrating Chinook Salmon from Butte Creek (California) were tracked, the distance of each reach from the Golden Gate Bridge (river kilometers [rkm]), the individual reach lengths, and the total region length (km). Weir2_RST represents the rotary screw trap installed at Weir 2 in the Sutter Bypass; Butte1–Butte6 and additional receiver locations are depicted in Figure 1.

Region	Reach	Distance from ocean (rkm)	Reach length (km)	Region length (km)
Sutter Bypass	Weir2_RST to Butte1	249.54–249.05	0.49	
	Butte1 to Butte2	249.05–238.46	10.59	
	Butte2 to Butte3	238.46–226.46	12.00	
	Butte3 to Butte5	226.46–216.98	9.48	
	Butte5 to Butte6	216.98–206.48	10.50	43.06
Sacramento River	Butte6 to I-80 Bridge	206.48–170.74	35.74	
	I-80 Bridge to Freeport	170.74–152.43	18.31	54.05
Sacramento–San Joaquin River Delta	Freeport to Benicia	152.43–52.04	100.39	100.39
San Francisco Bay	Benicia to Golden Gate Bridge	52.04–0.80	51.24	51.24

TABLE 2. Weight (g) and FL (mm; mean, minimum [min], and maximum [max]; SDs in parentheses) of juvenile Chinook Salmon that were captured, tagged, and released at the rotary screw trap in the Sutter Bypass during 2015 and 2016 (CCV = California Central Valley; n = sample size). Group assignment is shown only for fish with genetic stock assignment posterior probabilities exceeding 75%.

Year	Group	n	Mean (SD) weight	Mean (SD) FL	Min FL	Max FL
2015	CCV fall run	6		112.67 (16.85)	84	135
	CCV spring run	125		104.00 (11.73)	80	136
	All	141	13.47 (5.36)	104.75 (12.28)		
2016	CCV fall run	121		114.60 (6.82)	98	128
	CCV spring run	65		103.51 (6.88)	85	122
	All	200	16.68 (7.68)	110.02 (10.93)		

(Clemento et al. 2014). For each fish, we calculated the posterior probability that it originated from a given stock, and we assigned the fish to the stock with the highest posterior probability. Based on Satterthwaite et al. (2014) and communication with John C. Garza (National Marine Fisheries Service [NMFS], Southwest Fisheries Science Center [SWFSC], Santa Cruz), we considered assignments of fish with a maximum posterior probability exceeding 75% as robust stock assignments for purposes of this study. We did not assign a stock to fish with posterior probabilities less than 75%. The genetic analysis was performed at the NMFS-SWFSC.

Data analysis.— Tagged fish either completed their migration out of the study reaches or completed a partial migration and died before exiting the detection arrays. We used a spatial form of the Cormack–Jolly–Seber model (Cormack 1964; Jolly 1965; Seber 1986) to estimate the reach-specific survival rate (φ_i) and detection probability (p_i). We considered the initial tag location as a "mark" and subsequent detections at downstream

receivers as "recaptures." We used the method of maximum likelihood to estimate survival and detection probabilities along with their 95% confidence intervals (Lebreton et al. 1992).

For consistency between tagging years and due to the low number of fish migrating through the Delta, we selected a subset of receiver locations for the survival analysis, thus creating a total of nine separate reaches for which survival and detection probabilities were estimated (Table 1; Figure 1). Furthermore, because the lengths of reaches along the migratory path were not identical, we standardized survival estimates per 10 km in order to allow inter-reach survival comparisons. Finally, we estimated regional survival (Sutter Bypass, Sacramento River, the Delta, and San Francisco Bay) and overall survival (from the release site to the Golden Gate Bridge) for both years using methodology described by Michel et al. (2015).

To evaluate year and location effects on out-migrating smolt survival and detection probabilities, we compared

the constant model (i.e., constant survival and detection rates through space and time) to models that included parameters allowing year and/or reach to vary (e.g., φ[~reach × year]; see Appendix Table A.1 for a list of models). Because it is impossible to measure or estimate all potential factors that influence salmon survival, we hypothesized that the fully parameterized model (full model) that included year and reach as factors would have the best fit to the data and would provide the best estimates of reach survival by year. We therefore used this model to generate reach-specific, regional, and overall survival estimates. However, to gain a better understanding of the underlying mortality mechanisms, we also looked at models that included fish characteristics (i.e., FL and Fulton's condition factor K) and environmental variables (i.e., Sutter Bypass flow and water temperature at release). We used flow data from Butte Slough near Meridian (California Data Exchange Center [CDEC] station BSL, http://cdec.water.ca.gov/cgi-progs/stationInfo?station_id=BSL), located downstream of the BSOG (the closest flow gauge to the Sutter Bypass release site), and we used temperature data from the Butte1 acoustic receivers (postcalibrated at the NMFS-SWFSC). All continuous covariates were standardized by subtracting the mean and dividing by the SD.

To facilitate our ability to partition the influence of each covariate of interest on survival variability through time, we used the base model, φ(~reach), and included covariates in an additive framework (see Table 3 for a list of models). We deliberately excluded the year variable from all covariate models because the inclusion of this variable would have accounted for the majority of interannual variability in survival, thereby masking any influence of the individual/environmental covariates and providing no information on mechanisms. However, we compared the φ(~reach + year) model to the models including covariates in order to assess how much interannual variability explained by the year variable could be explained by these covariates instead. Once the relative importance of covariates had been determined from the model selection exercise, we extracted the standardized β parameter coefficients for these covariates to identify the relationship direction between the covariates and fish survival. These β parameter coefficients allowed for comparison of the influence of covariates between models; they can be interpreted as the predicted change in survival for a 1SD increase in the covariate. Model selection was conducted by using Akaike's information criterion corrected for small sample sizes (AIC$_c$; Akaike 1973; Burnham and Anderson 2002). We performed this analysis in the RMark package (Laake 2013) within R version 3.1.1 (R Development Core Team 2013).

Finally, to obtain additional information on the movements of the tagged fish during their out-migration and

TABLE 3. Comparison of the ~reach + year survival (φ) model versus models that included reach and individual or environmental covariates (fish length, Fulton's condition factor K, Sutter Bypass flow at release, and water temperature at release). The detection probability (p) was set as a constant for each model (N_{par} = number of model parameters; AIC$_c$ = Akaike's information criterion corrected for small sample size; ΔAIC$_c$ = difference in AIC$_c$ score between the given model and the most parsimonious model). Models are ordered from lowest to highest AIC$_c$. Lower AIC$_c$ scores indicate greater relative model parsimony. The β parameter estimates (defined in Methods) are shown for the two covariate models with substantial support over the reach-only model.

Model	N_{par}	AIC$_c$	ΔAIC$_c$	β
φ(~reach + year), p(~1)	11	1,394.074	0.00	
φ(~reach + release flow), p(~1)	11	1,396.929	2.85	0.24
φ(~reach + fish length), p(~1)	11	1,402.226	8.15	0.17
φ(~reach + release temp), p(~1)	11	1,404.477	10.40	
φ(~reach), p(~1)	10	1,405.719	11.64	
φ(~reach + K), p(~1)	11	1,406.765	12.69	

relate that to their survival, we estimated the average migration rates for the different regions along the migration pathway. We did this by considering the movement rate of each fish between its last detection in one reach to its first detection at the next reach.

RESULTS

In 2015, we deployed the RST on April 1 and tagged Chinook Salmon for 11 d between April 6 and April 16. During that period, we tagged and released a total of 141 smolts. In 2016, we started tagging on April 14, and we were able to tag and release our target of 200 juvenile Chinook Salmon by April 18. In 2015, the mean FL of tagged fish was 104.75 mm and the mean weight was 13.47 g, whereas the averages in 2016 were 110.02 mm and 16.68 g, respectively (Table 2).

Genetic Assignment

The genetic analysis suggested that the smolts tagged in the Sutter Bypass were a mix of CCV fall-run and spring-run origin. In 2015, 6 smolts were confidently identified as CCV fall-run fish, and 124 smolts were identified as CCV spring-run fish; in 2016, a higher proportion of tagged individuals were genetically classified as CCV fall-run fish (121 fall-run versus 65 spring-run fish; Table 2). Although fall-run smolts were slightly larger in both years, fall-run and spring-run smolts appeared to exhibit similar size ranges (Table 2; Appendix Figure A.1). We performed an F-test ("var.test" function in R) to compare fall-run versus

spring-run smolt length variances for each year and found no statistical difference between their length distributions (2015: $P = 0.1489$; 2016: $P = 0.9086$). This implied that no length cutoff could be robustly applied to these two runs and that visual distinction based on length is problematic. Therefore, although not all of the tagged fish were spring-run Chinook Salmon, we assumed that due to their overlapping size range and migration timing, fall-run juveniles served as a good proxy for the purpose of this study.

The RST was located below the spawning habitat of the Butte Creek fall run; it is therefore likely that many of the captured fall-run smolts were wild Butte Creek fall-run Chinook Salmon. In addition, because Sacramento River water spilled into the lower Butte Creek watershed via Moulton, Colusa, and Tisdale weirs several times before the tagging experiment took place, it is also possible that some of the tagged fall-run fish originated from the mainstem Sacramento River or another tributary and used the Sutter Bypass as a migratory corridor.

Hydrological Conditions

During the 2015 water year, California experienced an extreme drought that was classified as "critical," whereas the 2016 water year was considered "below normal" by the California Department of Water Resources (CDWR; CDEC data). Although 2016 was not considered a wet year, a series of rain events leading to the flooding of the Sutter Bypass occurred during the CCV spring-run smolts' out-migration period. Therefore, the hydrological conditions experienced by the migrating smolts changed considerably between the 2 years of the study. In spring 2015, likely because of very dry winter conditions, the flow recorded in the lower Butte Creek system had already dropped substantially and stayed very low during the entire study period, averaging 4.03 m³/s at the BSL station (Figure 2A). In 2016, we tagged and released fish after a flood event, and although the flow decreased throughout the study period, it remained substantially above the maximum flow value recorded during the same period in 2015. The 2016 BSL flow averaged 12.91 m³/s. The same pattern was observed in the Sacramento River reach, with an average flow of 160.29 m³/s in 2015 and an average of 381.53 m³/s in 2016 (CDEC station at Verona, http://cdec.water.ca.gov/cgi-progs/stationInfo?station_id=VON; Figure 2A).

In 2015, water temperatures in the Sutter Bypass and the Sacramento River increased throughout the tagging experiment (Figure 2B). Water temperature at the Butte1 receiver peaked at 18.5°C during the tagging period, then kept increasing and reached 21°C by the end of April. Similarly, water temperature in the Sacramento River increased from 14°C to 22°C during April 2015 (CDEC station at Verona, http://cdec.water.ca.gov/cgi-progs/sta

tionInfo?station_id=VON). In 2016, water temperature in the Sutter Bypass during the tagging period varied between 18°C and 19.5°C. The peak water temperature at the Butte1 receiver was 21°C on April 21, 2016. The Sacramento River water temperature in 2016 slowly increased throughout the month of April but never exceeded 18°C.

Fish Movement

In 2015, 27 (19.1%) of the 141 tagged fish were detected as entering the Sacramento River, 14 fish (9.9%) were detected as entering the Delta, and only 1 fish (0.7%) was detected at the Golden Gate Bridge. In 2016, 71 (35.5%) of the 200 tagged fish were detected as entering the Sacramento River, 49 fish (24.5%) were detected in the Delta, and 4 fish (2%) were detected at the Golden Gate Bridge. Although some variability in movement rates among fish was observed each year, especially in the Sacramento River, most of the tagged smolts moved quickly throughout the migration corridor (Figure 3). On average, fish took 6 d in 2015 versus 2 d in 2016 to transit the Sutter Bypass, and they took 2 d in 2015 versus 1 d in 2016 to transit the Sacramento River (Table 4). The single fish that survived to the Golden Gate Bridge in 2015 migrated through the Delta in less than 5 d and migrated from the release site to the Pacific Ocean in 27 d. In 2016, it took an average of 5 d for fish to migrate through the Delta and 18 d for them to migrate from the release site to the ocean (Table 4).

Tagged fish migration rates were higher in the Sacramento River compared to the Sutter Bypass and the Delta during both years (Figure 3; Table 4). Based on a Tukey's honestly significant difference test ("TukeyHSD" function in R), the migration rate in 2016 was significantly higher than that in 2015 within the Sacramento River ($P < 0.001$) and the Sutter Bypass ($P < 0.001$); migration rates were significantly higher in the Sacramento River compared to the Sutter Bypass during both years (2015: $P = 0.0$; 2016: $P = 0.0$). We calculated mean migration rates of 10.24 km/d in the Sutter Bypass and 33.21 km/d in the Sacramento River during 2015 versus estimates of 22.13 and 56.83 km/d, respectively, during 2016 (Table 4). Since only one fish was successfully detected at Benicia (the Delta exit location) and the Golden Gate Bridge in 2015, it was not possible to estimate Delta and San Francisco Bay travel rate statistics for that year. However, more fish were detected in 2016, and the average movement rate through the Delta was estimated at 22.48 km/d.

Survival Estimates

The full model, which was strongly supported as the single best model (AIC$_c$ = 1,383.726; the difference in AIC$_c$ value [ΔAIC$_c$] between the best model and the second-best model was greater than 8; Table A.1), included
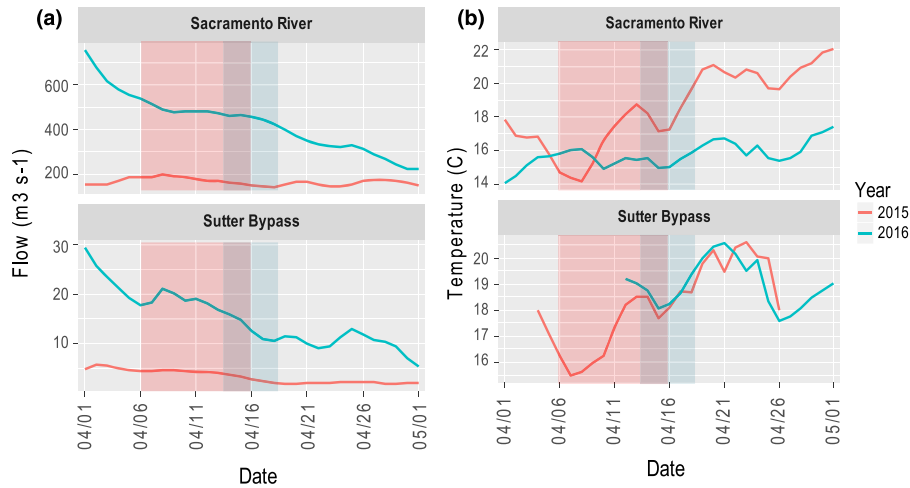
FIGURE 2. (A) Mean daily flow (m³/s) in April 2015 and 2016 for the Sacramento River (California Data Exchange Center [CDEC] Verona station: http://cdec.water.ca.gov/cgi-progs/stationInfo?station_id=VON) and Sutter Bypass (CDEC station BSL [Butte Slough near Meridian]: http://cdec.water.ca.gov/cgi-progs/staMeta?station_id=BSL); and (B) mean daily water temperature (°C) during April 2015 and 2016 for the Sacramento River (CDEC Verona station) and Sutter Bypass (Butte1 site; Advanced Telemetry Systems receiver thermistor). The shaded rectangles indicate the tagging and release time periods in Sutter Bypass for 2015 (in red) and 2016 (in blue). [Color figure can be viewed at afsjournals.org.]

FIGURE 3. Box plot of region-specific movement rates (km/d) for out-migrating Chinook Salmon in 2015 and 2016 (Delta = Sacramento–San Joaquin River Delta). The horizontal bold line represents the median value; vertical whiskers represent the 95th percentiles; and dots denote extreme values.

survival as a function of reach × year and a constant detection probability. This suggested that out-migrant smolt survival varied by location and year. Additionally, although the best model supported a constant detection probability, the spatially explicit models (i.e., $p[\sim reach]$) suggested that detection rates throughout the migratory

TABLE 4. Overall and region-specific percent survival, mean migration rate (km/d), and mean migration time (d), along with SE or SD (in parentheses), for juvenile Chinook Salmon tagged during each year (NA = not applicable).

Year	Region	Percent survival (SE)	Mean (SD) migration rate (km/d)	Mean (SD) migration time (d)
2015	All	0.7 (0.7)	NA	NA
	Sutter Bypass	19.1 (3.3)	10.24 (4.61)	5.75 (4.28)
	Sacramento River	51.8 (9.6)	33.21 (14.31)	1.88 (0.73)
	Sacramento–San Joaquin River Delta	7.1 (6.9)	NA	NA
2016	All	3.0 (1.2)	33.69 (15.32)	18.44 (3.93)
	Sutter Bypass	35.5 (3.4)	22.13 (6.21)	2.15 (0.81)
	Sacramento River	69.0 (5.5)	56.83 (16.26)	1.09 (0.57)
	Sacramento–San Joaquin River Delta	12.2 (4.7)	22.48 (8.03)	5.18 (2.59)

corridor were consistently high, ranging from 0.851 to 1.000. For all model exercises presented in this paper, detection probability was therefore set to be constant through space and time and was estimated at 0.993.

After including individual and environmental variables in the analysis, the $\varphi(\sim reach + year)$ model was selected as the best model, emphasizing the strong year effect on smolt survival (Table 3). The model that incorporated Sutter Bypass flow at release as a covariate was substantially better supported ($\Delta AIC_c > 3$) over the base model $\varphi(\sim reach)$. Furthermore, it shared similar support ($\Delta AIC_c < 3$) relative to the $\varphi(\sim reach + year)$ model (which benefited from a free parameter), suggesting that the flow model explained much of the variation in interannual survival. The model including fish length also had substantial support over the base model ($\Delta AIC_c < 6$) and suggested a positive influence of fish length on survival. However, the models including water temperature at release and Fulton's K were not better supported than the base model, indicating that these covariates had no detectable influence on survival.

We used the full model (i.e., $\varphi[\sim reach \times year]$) to estimate survival per 10 km, per region, and cumulatively. Overall, survival through the entire migratory corridor (from the release site to the Golden Gate Bridge) was better in 2016 (3.0%) than in 2015 (0.7%; Table 4). At the regional level comparing 2015 to 2016, survival increased in the Sutter Bypass from 19.1% to 35.5%, in the Sacramento River from 51.8% to 69.0%, and in the Delta from 7.1% to 12.2% (Figure 4; Table 4). For both years, the highest regional survival was observed in the lower Sacramento River, while the lowest estimate was for the Delta region. However, the length of each region varied considerably (the Delta region was about twice as long as the Sutter Bypass and Sacramento River regions; Table 1),

and survival often decreases proportionally with increasing region length.

Rates of survival per 10 km varied dramatically between reaches within the Sutter Bypass, the Sacramento River, and the Delta, and some similar survival patterns were observed between years (Figure 5). In the Sutter Bypass, relatively low survival was observed between the release site (the RST at Weir 2 ["Weir2_RST" in Table 1]) and the first receiver (Butte1; 27.1% in 2015) and between the Butte3 and Butte5 receivers (39.3% in 2015; 65.1% in 2016). Survival was higher in the other reaches of the Sutter Bypass, ranging from 72.5% to 94.0% in 2015 and from 79.8% to 84.7% in 2016. In the Sacramento River for 2015, survival decreased from the first reach (Butte6 to the I-80 Bridge; 91.9%) to the second reach (I-80 Bridge to Freeport; 82.5%), whereas it increased in 2016 (92.6% and 95.1%, respectively). Survival in the Delta was lower than in the Sacramento River for both years (76.8% in 2015; 81.1% in 2016). Finally, due to the low number of tagged fish surviving to the Golden Gate Bridge ($n = 1$ in 2015; $n = 4$ in 2016), the 2015 survival rate in the San Francisco Bay could not be estimated, and the 2016 San Francisco Bay survival rate should be used for discussion purposes only.

DISCUSSION

This is the first study to investigate the survival and migration rates of wild Butte Creek spring-run Chinook Salmon smolts during their out-migration to the Pacific Ocean. The acoustic telemetry system used in this study had high detection probabilities (>85%) at all receiver locations. The mark–recapture models provided estimates of survival at fine spatial scales during a dry water year and a wet water year. We showed that Chinook Salmon smolts migrated faster throughout their migratory corridor
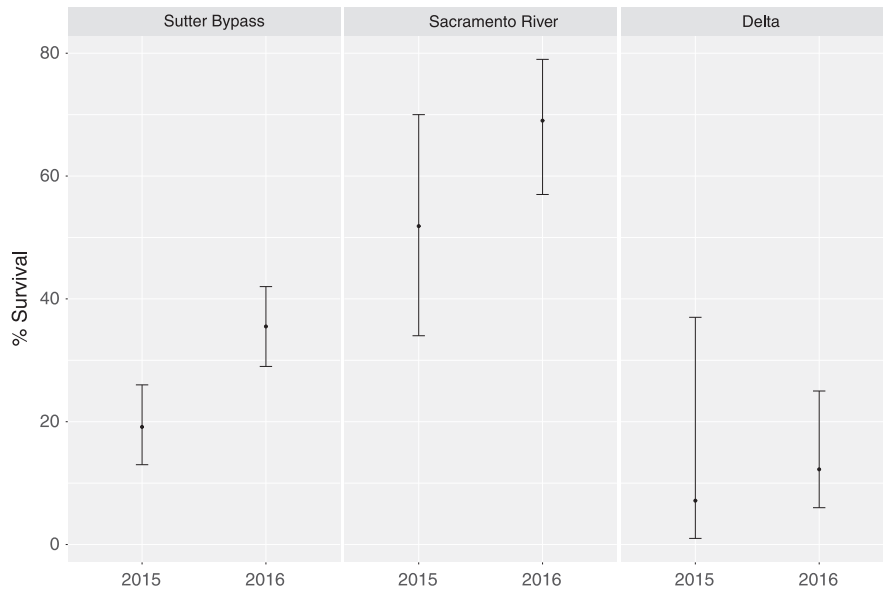
FIGURE 4. Region-specific survival rates (%; mean ± 95% confidence interval) for out-migrating Chinook Salmon in 2015 and 2016 (Delta = Sacramento–San Joaquin River Delta).
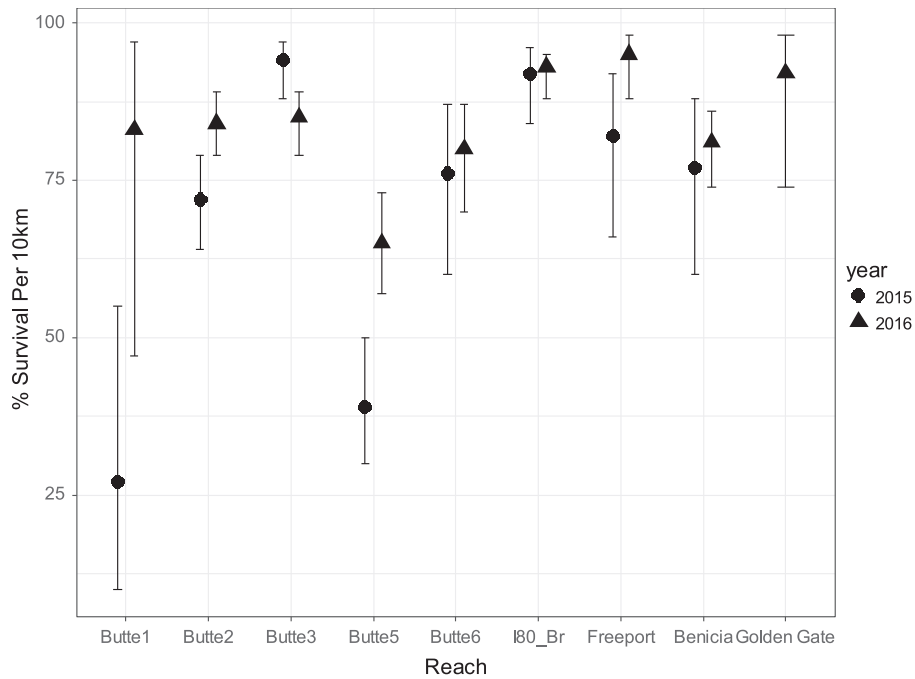

FIGURE 5. Reach-specific rates of survival per 10 km (%; mean ± 95% confidence interval) for out-migrating Chinook Salmon in 2015 and 2016.

in 2016 (a wetter year) than in 2015 (a dry year). This difference is likely due to higher flow velocities, both in the Sutter Bypass and in the Sacramento River, during 2016 compared to 2015. The mean migration rate to the ocean (Golden Gate Bridge) was 33.7 km/d for 2016, which is faster than the total mean migration rate reported for

Sacramento River late-fall Chinook Salmon (14.3–23.5 km/d in 2007–2009) by Michel et al. (2013).

Survival to the ocean was also higher in 2016 (3.0%) than in 2015 (0.7%; Table 4). However, these survival rates are lower than most of the survival estimates obtained by Michel et al. (2015) for acoustic-tagged late-

fall-run Chinook Salmon yearlings (survival per year ranged from 2.8% to 15.7%). The survival rates we report are also low in comparison with the 2015 and 2016 survival rates estimated by Faulkner et al. (2016, 2017) for populations of wild spring/summer Chinook Salmon from the Snake River (a tributary of the Columbia River) migrating through a much longer watershed than in our study (mean survival rates through the entire 910-km watershed = 38.3% in 2015 and 33.0% in 2016). However, the fish tracked by Michel et al. (2015) and Faulkner et al. (2016, 2017) were larger in size than the fish we tagged in the Sutter Bypass, and we have shown that fish length influences out-migrant survival. Similar to our study, Notch (2017) found very poor survival (0.3%) to the ocean for acoustic-tagged, wild-caught smolts from Mill Creek, an upper Sacramento River tributary. This suggests that out-migration survival of spring-migrating wild Chinook Salmon smolts can be very low and may represent a bottleneck to the recovery of these populations.

In the Sutter Bypass, there were two reaches with substantially lower survival than the other reaches: (1) from the release site to Butte1 during 2015; and (2) between the receivers Butte3 and Butte5 in both years. These two reaches had the lowest survival per 10 km among all reaches in 2015, and the Butte3–Butte5 reach had the lowest survival per 10 km among all reaches in 2016. Common to both these reaches are in-river diversion weir structures (i.e., at the start of Weir2_RST–Butte1 reach and in the middle of Butte3–Butte5 reach). Studies have shown that Striped Bass *Morone saxatilis* and Sacramento Pikeminnow *Ptychocheilus grandis*—both of which are considered major predators of juvenile salmon in the CCV —tend to congregate below in-river diversion weirs and are effective at preying upon disoriented salmon smolts that pass over these structures (Brown and Moyle 1981; Tucker et al. 2003; Sabal et al. 2016). Various nonnative (e.g., Largemouth Bass *Micropterus salmoides*, Striped Bass, and Channel Catfish *Ictalurus punctatus*) and native (e.g., Sacramento Pikeminnow) predators of salmon have been reported in the lower Butte Creek watershed (ICF Jones & Stokes 2009). These predators were also caught in the RST during the present study in both years. If predators are generally concentrated below these diversion weirs, and furthermore if predator concentrations were enhanced during the low-flow conditions in 2015, this may explain the lower survival of juvenile Chinook Salmon in these two reaches.

Similarly, predation could play an important role in the Sacramento River and Delta reaches, as spring-run smolt out-migration timing overlaps with the Striped Bass spawning season. Adult Striped Bass migrate into the San Joaquin and Sacramento rivers in large numbers during the spring to spawn, and they are likely to prey on juvenile out-migrants during that time (Turner 1976; Tucker

et al. 2003). The increase in survival observed for 2016 in the Sutter Bypass and the Sacramento River corroborates the assumption that an increase in flow induces an increase of fish transport as well as a potential increase in turbidity, which could both reduce spatiotemporal exposure to predation (Gregory and Levings 1998; Michel et al. 2013 and references therein). The higher flow observed in the Sacramento River in comparison to the Sutter Bypass could explain the higher survival and faster migration rate observed in this region.

On the contrary, the relatively low survival and slower migration rates observed in the Delta could be explained by the complex network of natural and man-made tidally influenced channels that salmon smolts must navigate on their journey to the ocean, thus increasing their exposure to potential predators (Nichols et al. 1986). Perry et al. (2010) demonstrated that survival through the Delta was dependent on the fish route selection, which depends strongly on natural flow conditions and the amount of water exported for state and federal water projects. Poor Delta water quality has also been suggested to influence the survival of out-migrating Chinook Salmon smolts by decreasing their swimming performance and presumably their predator evasion capabilities (Lehman et al. 2017).

It is important to note that our study focused on a single rearing and out-migration life history strategy in which spring-run and fall-run juveniles leave the tributaries as smolts. The results of this study might not be representative of other life history strategies where juveniles out-migrate as fry, parr, or yearlings. Smolts evolved to out-migrate with spring snowmelt freshets during April and May; however, various human-induced and environmental constraints, such as the homogenization of hydrology due to dams, elevated water temperatures associated with dams, and water diversions in the Delta peaking during the spring, are now likely diminishing the benefits of this life history strategy and leading to lower out-migration survival. Given these constraints, life histories that are characterized by earlier out-migration (fry or parr) might exhibit higher relative survival. However, due to their small size, which precludes acoustic tagging, very little is known about these earlier out-migrant life histories. Studies that aim to quantify the proportion of returning adults with the different out-migration life histories (e.g., Sturrock et al. 2015) would be needed to place the smolt out-migration life history studied here into a broader context.

Our results have strong implications for the management of threatened CCV spring-run Chinook Salmon populations. Butte Creek currently supports the most abundant population of spring-run Chinook Salmon in the CCV and provides a key component for the diversity and viability of the spring-run stock. The Sutter Bypass has been designated by National Oceanic and Atmospheric Administration (NOAA) Fisheries as a critical

habitat for CCV spring-run Chinook Salmon and is considered an important rearing habitat and migratory corridor (Johnson and Lindley 2016). Therefore, to clearly identify the effects of fish characteristics and environmental variables in relation to juvenile movement and survival, a longer time series with increased sample size is necessary. Moreover, further investigation on salmon predation (especially at in-river structures) and improved water quality monitoring in the Sutter Bypass (i.e., water temperature, flow, and turbidity along the bypass) are critical to facilitate a clear assessment of the reasons for low survival in some of the reaches. This type of information will help target restoration and management projects on specific areas within the Sutter Bypass that could improve spring-run juvenile survival and ultimately lead to increased abundances of adults returning to spawn in Butte Creek. This information could also benefit other runs of CCV Chinook Salmon that use the lower Butte Creek system as a nursery and migratory corridor when accessible and would ultimately promote CCV Chinook Salmon stock diversity and stability.

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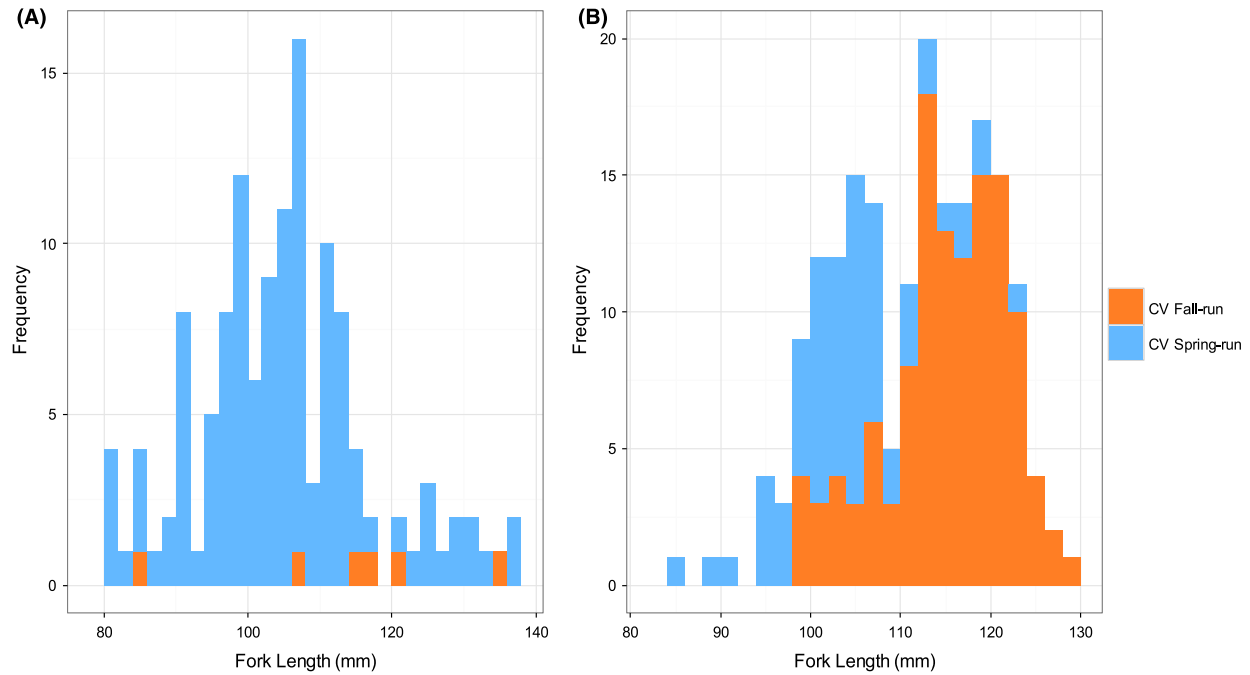
Appendix

FIGURE A.1. Length frequency histograms of out-migrating Chinook Salmon with genetic distinction that were tagged in the Sutter Bypass during **(A)** 2015 and **(B)** 2016. CV = Central Valley. [Color figure can be viewed at afsjournals.org.]

TABLE A.1. Comparison of constant versus year- and/or reach-varying survival (φ) and detection (p) models for out-migrating Chinook Salmon (N_{par} = number of model parameters; AIC_c = Akaike's information criterion corrected for small sample size; ΔAIC_c = difference in AIC_c score between the given model and the most parsimonious model). Models are ordered from lowest to highest AIC_c. Lower AIC_c scores indicate greater relative model parsimony.

Model	N_{par}	AIC_c	ΔAIC_c
φ(~reach × year), p(~1)	19	1,383.726	0.00
φ(~reach × year), p(~reach)	27	1,392.249	8.52
φ(~reach + year), p(~1)	11	1,394.074	10.35
φ(~reach × year), p(~reach + year)	28	1,394.997	11.27
φ(~reach + year), p(~reach)	19	1,402.255	18.53
φ(~reach + year), p(~reach + year)	20	1,403.608	19.88
φ(~reach), p(~1)	10	1,405.719	21.99
φ(~reach × year), p(~reach × year)	36	1,409.928	26.20
φ(~reach), p(~reach + year)	19	1,416.271	32.55
φ(~reach), p(~reach)	18	1,416.436	32.71
φ(~reach + year), p(~reach × year)	28	1,420.496	36.77
φ(~reach), p(~reach × year)	27	1,429.291	45.56
φ(~year), p(~reach)	11	1,568.503	184.78
φ(~year), p(~reach + year)	12	1,570.401	186.67
φ(~1), p(~reach)	10	1,577.198	193.47
φ(~year), p(~reach × year)	20	1,586.445	202.72
φ(~1), p(~reach × year)	19	1,594.144	210.42
φ(~1), p(~reach + year)	11	1,658.943	275.22
φ(~year), p(~1)	3	1,678.890	295.16
φ(~1), p(~1)	2	1,682.151	298.43