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ARTICLE

Survival of Juvenile Fall-Run Chinook Salmon through the San Joaquin River Delta, California, 2010–2015

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Abstract

Survival of juvenile fall-run Chinook Salmon *Oncorhynchus tshawytscha* through the San Joaquin River Delta of California (hereafter, "Delta") has been low for most estimates since 2002 and has been consistently low since 2010. From 2010 through 2015, annual estimates of the probability of surviving through the Delta (from Mossdale to Chipps Island, approximately 92 river kilometers) ranged from 0 to 0.05, based on acoustic-telemetry data from smolt-sized hatchery Chinook Salmon. River conditions were poor in most of these years; average daily river discharge into the Delta from the San Joaquin River was <40 m^3/s in four of the six study years. In the high flow year of 2011 (average daily river discharge = 278 308 m^3/s), the juvenile survival probability through the Delta was estimated at only 0.02 (SE $<$ 0.01), suggesting increased flows alone will not be sufficient to resolve the low survival through the Delta. The low survival in this short portion of the salmon's life history makes achieving a minimal smolt-to-adult ratio of $\geq$2% nearly impossible for this fish stock. Over half of the fish surviving through the Delta during 6 years of study were salvaged at the Central Valley Project's water export facility and transported for release just upstream of Chipps Island.

Historically, the Central Valley of California has hosted one of the most diverse populations of Chinook Salmon *Oncorhynchus tshawytscha*. This population has four distinct runs, and the adults return during every month of the year to spawn in every accessible stream (Yoshiyama et al. 1998). The winter and late-fall runs were restricted to the Sacramento River basin, while the fall and spring runs were present throughout both the Sacramento and the San Joaquin River basins (Yoshiyama et al. 1998). Both river basins drain into the California Delta, and eventually into the San Francisco Bay. The largest of these runs is the fall run, which forms the basis of the California and southern Oregon ocean salmon fishery (Williams 2006). The Central Valley's fall-run (FR) Chinook Salmon population consists predominantly of hatchery-reared fish from the Sacramento River basin (Williams 2006; Barnett-Johnson et al. 2007). However, the San Joaquin River basin has two FR Chinook Salmon hatcheries on the Merced River and Mokelumne River, and both basins produce naturally reared fish. Although naturally

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produced FR Chinook Salmon in the San Joaquin River basin have been restricted to the tributaries since the 1940s (Fisher 1994), there is currently an effort to return a self-sustaining population to the San Joaquin River main stem (www.restoresjr.net).

Central Valley FR Chinook Salmon have been listed as a “species of concern” by NOAA Fisheries (NOAA 2010), and in 2008 and 2009, low anticipated adult returns resulted in closure of the ocean fishery south of Cape Falcon, Oregon (NOAA 2008, 2009). Efforts to understand the causes of low survival of FR Chinook Salmon have included measuring juvenile survival through the California Delta, which forms the tidally influenced freshwater portion of the San Francisco estuary (Figure 1). Early coded wire tag studies from 1994 to 2006 provided monitoring of Chinook Salmon survival through the California Delta to Jersey Point for stocks originating in the San Joaquin basin (Brandes and McLain 2001; SJRGA 2007, 2013). Partly in response to low adult returns of FR Chinook Salmon in the mid-2000s, researchers switched to acoustic telemetry because of the smaller sample sizes required and the ability to provide more detailed spatial and temporal information on salmon migration through the California Delta. Acoustic-telemetry studies of juvenile hatchery-reared FR Chinook Salmon in the San Joaquin Delta were implemented starting in 2006 as part of the multiyear Vernalis Adaptive Management Plan (VAMP) and continued after the VAMP study ended in 2011 (SJRGA 2013). We present survival results from 6 years of acoustic telemetry studies from 2010 through 2015 and discuss ramifications of the consistently low passage survival through the San Joaquin Delta.

METHODS

Study Area

The Sacramento San Joaquin Delta (hereafter, “Delta”) is an area of nearly 3,000 km^2 located in the Central Valley of California. It extends from the city of Sacramento on the Sacramento River, and the area near Mossdale Bridge on the San Joaquin River, downstream to the confluence of the Sacramento River and San Joaquin River at the entrance to Suisun Bay at river kilometer (rkm) 64, measured from the Golden Gate Bridge at the exit of the San Francisco Bay (Figure 1). For the purpose of this paper, we use the term “Delta” to refer to the portion of the overall Sacramento San Joaquin estuary that is dominated by the San Joaquin River as it approaches Suisun Bay from the east and south (Figure 1). The Delta is a complex network of natural rivers, natural or artificial cuts, islands, and levees and contains some of California’s most fertile

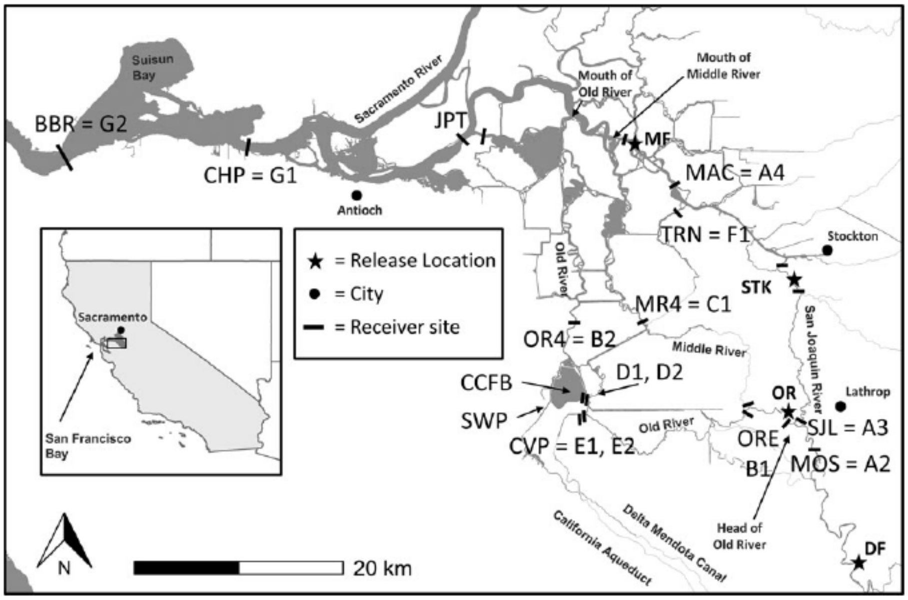

FIGURE 1. The portion of the Sacramento San Joaquin River delta that was studied, including acoustic telemetry receiver sites common to the 2010 2015 studies and key receiver sites added in later years. Inset shows the state of California (light shading) and the Delta and San Francisco Bay (dark shading); detailed area is marked with a rectangle. The study area extended from Mossdale (MOS) to Chipps Island (CHP). Acoustic tagged Chinook Salmon were released at Durham Ferry (DF), Old River (OR), and Stockton (STK) in 2010, DF in 2011 2014, and DF and Medford Island (MF) in 2015. Key sites are DF, MOS, and CHP. Receiver sites with alphanumeric codes (e.g., A2) are used in the model schematic in Figure 2. Site Jersey Point (JPT) was added in 2011. Site Benicia Bridge (BBR) (G2) was added in 2014. Water export facilities are CVP and SWP; CCFB Clifton Court Forebay. Highway 4 receivers are designated OR4 and MR4. The CHP site used a dual array of receivers.

agricultural land. The San Joaquin River skirts the majority of the Delta to the east. The Old River originates (rkm 170) from the San Joaquin River downstream from Mossdale Bridge and moves west and north near the western edge of the Delta until it reconnects with the San Joaquin River (rkm 122) upstream from the confluence with the Sacramento River. The Middle River originates (rkm 158) from the Old River in the south and moves north until it connects with the San Joaquin River (rkm 126) just upstream from the confluence of the San Joaquin and Old rivers (Figure 1).

The region of focus in this paper extends from just downstream of the Mossdale Bridge (Mossdale; rkm 174), located on the San Joaquin River approximately 3.8 rkm upstream from where the Old River leaves west from the San Joaquin River (hereafter, "head of Old River"), to Chipps Island (rkm 77), which is legally considered the downstream boundary of the Delta and is located near the entrance to Suisun Bay (Figure 1). Within this study area are several routes that fish may take to get from Mossdale to Chipps Island. The simplest (approximately 92 km) is to remain in the San Joaquin River throughout the Delta, passing the city of Stockton, MacDonald and Medford islands, and Jersey Point. An alternative route (hereafter, "Old River route") is to leave the San Joaquin River at the head of Old River. Fish using this route may either move through the interior Delta via the Old and Middle rivers until they rejoin the San Joaquin River just upstream from Jersey Point or enter one of two water export facilities, where Delta water is actively pumped for export to water users in central and southern California. The entrances to these facilities are located in the southwestern region of the Delta off the Old River. The Central Valley Project (CVP) is located approximately 2 rkm south of the State Water Project (SWP), which is accessed via the Clifton Court Forebay reservoir. Fish that enter these facilities are captured and considered "salvaged"; salvaged fish are then transported by truck to the northwestern Delta and released into the San Joaquin River or Sacramento River approximately 20 rkm upstream from Chipps Island. Fish that remain in the San Joaquin River past the head of Old River (hereafter, "San Joaquin River route") may either remain in the San Joaquin River all the way to Chipps Island or they may leave the San Joaquin River for the interior Delta at various points downstream, including at Turner Cut, Columbia Cut, and the Middle River mouth. Once fish enter the interior Delta, they may move to Chipps Island either in the river (i.e., swimming through Delta waters) or by salvage and trucking from one of the export facilities. Survival was monitored through both the Old and San Joaquin River routes. Additionally, survival was monitored through the region that extended from Mossdale to the Turner Cut junction in the San Joaquin River route (37 rkm) and to the water export facilities or Highway 4 in the Old River route (29 to 38 rkm) (hereafter, "southern Delta").

Tagging, Fish Health, and Release Methods

Juvenile FR Chinook Salmon used in these annual studies came from either the Merced River Fish Hatchery (2010 2013) or the Mokelumne River Fish Hatchery (2014, 2015) (Table 1). All fish were surgically implanted with microacoustic tags. The 2010 and 2011 studies used the Hydroacoustic Technology, Inc. (HTI) Model 795 microacoustic tag (HTI, Seattle; diameter = 6.7 mm, length = 16.3 16.4 mm, average weight in air = 0.65 g); each HTI tag transmitted a pulse every 4 11 s, depending on the unique settings of the tag. The 2012 and 2013 studies used the VEMCO V5-180 kHz tag (VEMCO, Bedford, Nova Scotia; width = 5.6 mm, length = 12.7 mm, average weight in air = 0.66 0.67 g), and the 2014 and 2015 studies used the VEMCO V4-180 kHz tag (width = 5.7 mm, length = 11.0 mm, averaged weight in air = 0.41 0.42 g). The VEMCO tags transmitted the tag identification codes every 25 35 s.

In each study year, between two and seven groups of 133 647 juvenile Chinook Salmon each were tagged and released in April, May, or June; total sample sizes each year

TABLE 1. Release year, hatchery source of study fish, sample size (*N*), release dates, mean (range) FL at tagging, transmitter type (manufacturer and model), mean (range) tag burden (tag weight/fish weight), and mean estimated tag life (SE; days) for release groups of juvenile Chinook Salmon smolts used in the 2010 2015 South Delta tagging studies.

Year	Hatchery	*N*	Release dates	FL (mm)	Tag type	Tag burden (%)	Tag life (d)
2010	Merced	993	April 27 May 20	110 (99 121)	HTI 795 Lm	4.2 (2.8 5.8)	27.3 (7.8)
2011	Merced	1,895	May 17 June 19	111 (94 140)	HTI 795 Lm	4.1 (2.0 6.5)	28.8 (6.7)
2012	Merced	959	May 2 May 22	113 (100 135)	VEMCO V5	3.8 (2.0 5.4)	41.7 (7.5)
2013	Merced	950	May 1 May 19	115 (101 135)	VEMCO V5	3.8 (2.4 5.2)	50.6 (8.6)
2014	Mokelumne	1,918	April 16 May 19	98 (80 119)	VEMCO V4	3.8 (2.0 5.4)	48.9 (10.4)[a]
2015	Mokelumne	1,290	April 15 May 2	98 (83 119)	VEMCO V4	3.7 (1.9 4.8)	40.2 (5.5)

[a] Results are given for the May 2014 tag-life study. Mean estimated tag life for the April 2014 tag-life study was 12.4 d (SE = 4.7).

ranged from 950 to 1,918 (Table 1). The tagging team included three to four surgeons each year; all surgeons received either new-surgeon training or refresher training annually. The average FL at tagging ranged between 98 and 115 mm across years and was highest for 2012 and 2013 and lowest for 2014 and 2015 (Table 1). Tag burden (i.e., the ratio of tag weight to body weight) averaged between 3.7% and 4.2% each year (Table 1). Tag burdens ≥ 5% body weight occurred in 4% to 11% of the fish released in the 2010–2012 studies and in 0 to 1.3% of the fish released in the 2013–2015 studies. The maximum tag burden (6.5%) was observed in 2011 (Table 1); no more than 2% of fish in any year had a tag burden >5.4%.

Tagging was performed at the Tracy Fish Collection Facility in 2010–2012, located at the CVP approximately 40 km by truck from the primary release site (Durham Ferry), at Merced River Hatchery in 2013, and at Mokelumne River Hatchery in 2014 and 2015. The Merced River Hatchery and Mokelumne River Hatchery are located on the Merced and Mokelumne rivers approximately 100 km and 80 km from Durham Ferry, respectively. In 2010–2013, fish were anesthetized in a 70-mg/L solution of tricaine methanesulfonate (MS-222), buffered with sodium bicarbonate; in 2014 and 2015, a 0.03% solution of AQUI-S 20E was used as an anesthetic. Tagging procedures followed those outlined in Adams et al. (1998) and Martinelli et al. (1998) in 2010–2012 and were updated to the standard operating procedures outlined in Liedtke et al. (2012) in 2013–2015. After surgery, fish were transported to the release site in trucks outfitted with tanks designed for dissolved oxygen control and structural stability during transport. A maximum temperature differential between the transport tank and the river water of 5°C was targeted by adding nonchlorinated ice to transport tanks or tempering fish after arrival at the release site (Wedemeyer 1996; Iwama et al. 1997).

In 2011–2014, all fish were released in the San Joaquin River at Durham Ferry, located approximately 21 rkm upstream from Mossdale and 113 rkm from Chipps Island (Figure 1). The release site was located upstream of the study area boundary (Mossdale) to allow fish to become distributed naturally in the river, recover from stress associated with handling and release, and express any handling effects before entering the study area. In 2010, fish were released at Durham Ferry and paired with supplemental releases in upper Old River and in the San Joaquin River near the city of Stockton (Table 2). In 2015, the April release group was released at Durham Ferry, and the May release group was split between Durham Ferry and a release site in the San Joaquin River near Medford Island (50 rkm upstream from Chipps Island).

At the release site, fish were held in the river for approximately 24 h in submerged, 19-L, perforated garbage cans to allow them to acclimate to the river water and recover from surgery. The exception was in 2015, when fish released at Medford Island were held at the hatchery for 24 h after surgery rather than at the release site. A total of four tagged Chinook Salmon died during transport or during holding in the river before release in 2010–2014 (0.06% of those transported). In 2015, two fish (0.15%) died during transport and 12 fish (0.92%) died during holding before release at Durham Ferry. Most of those mortalities in 2015 occurred in late April and early May, when river temperatures were especially high (21.9°C to 24.7°C at the beginning of the holding period). Prerelease mortalities were removed from the release groups and from data analysis. An exception was in 2015, when the tag could not be recovered from five of the prerelease mortalities; however, because the study area began approximately 21 rkm downstream from the release site, those unknown mortalities did not bias Delta survival estimates.

TABLE 2. Site abbreviations, types, and locations in river kilometers (rkm) measured from the Golden Gate Bridge at the mouth of San Francisco Bay. Distances to sites on the San Joaquin River are measured along the main stem of the river.

Site	Site type	Description	rkm
DF	Primary release site	Durham Ferry	195
STK	Release site	Stockton	151
OR	Release site	Old River	164
MF	Release site	Medford Island	128
MOS	Receiver site	Mossdale	174
SJL	Receiver site	San Joaquin at Lathrop	170
ORE	Receiver site	Old River near head	164
TRN	Receiver site	Turner Cut	138
MAC	Receiver site	MacDonald Island	134
CVP	Receiver site, water export facility	Central Valley Project	144
SWP	Receiver site, water export facility	State Water Project	142
OR4	Receiver site	Old River at Highway 4	134
MR4	Receiver site	Middle River at Highway 4	137
JPT	Receiver site	Jersey Point	103
CHP	Receiver site	Chipps Island	77
BBR	Receiver site	Benicia Bridge	57

Each year, between 119 and 227 fish were tagged with inactive tags (i.e., dummy tags) and transported to the release site using identical procedures as the active-tagged fish, held for 48 h at the release site, and then examined for mortality and condition. In 2015, dummy-tagged fish associated with the Medford Island release were held for 24 h at the tagging facility before being transported and assessed at the release site. Of the total number of dummy-tagged fish transported and held, 30 to 90 control fish were examined each year for pathogens, physiological condition, and surgical complications (i.e., loose sutures, open or partially closed incisions, and minor to severe inflammation) in a fish health study performed by the U.S. Fish and Wildlife Service, California Nevada Fish Health Center; 60 to 154 additional untagged control fish were examined for fish health at the hatchery in 2010 and 2011. The fish health assessments occurred after fish were held 29 32 d in 2011, after 72 h in 2015, and immediately after the 48-h holding period in all other years. In addition, tag retention studies in 2012 2015 held between 39 and 75 dummy-tagged fish for 5 to 33 d for an assessment of long-term mortality and tag retention. Fish in the tag retention study were examined for mortality and tag loss at day 5 (in 2012) and days 30 33 (2012, 2014, and 2015). In 2014 and 2015, 75 untagged fish were also held for mortality controls and examined at days 31 33. Tag-retention fish and untagged fish were held in 2013 as well, but faulty mortality reporting made results unusable.

For each study year, in-tank studies were performed to measure the failure rate of the tags used in the study. Between 50 and 102 tags were sampled across manufacturing lots each year using either systematic or stratified random sampling. Tag-life studies typically began several weeks after tagged fish were released to the river. Tank water temperature was maintained with chillers in 2010 (average = 17°C) and with river water pumped from Old River in 2011 2015 to maintain temperatures similar to the Delta environment when tagged fish were migrating.

Acoustic Hydrophone and Receiver Placement

Between 38 and 166 acoustic hydrophones and their associated receivers were deployed at 22 to 43 locations throughout the San Joaquin River and Delta for the 2010 2015 studies. Each hydrophone was connected to a receiver or data logger (receiver) that either stored data for download or connected remotely to online data storage. In 2010 and 2011, HTI technology (receiver models 290 ATR, 291 ATR; data logger models 295-X, 295-I; hydrophone model 590; operating frequency 307 kHz) was used, and VEMCO technology (receiver models VR2W, VR2C, and HR1; 180 kHz; hydrophone was embedded in the receiver) was used in 2012 2015. Each receiver location was composed of 1 to 18 hydrophones to achieve complete coverage of the river channel. Hydrophone spacing across the river channel was based on range tests; at Chipps Island, HTI hydrophone spacing was approximately 150 to 300 m, and VEMCO receiver spacing was approximately 100 to 150 m.

Receiver locations throughout the Delta were determined by the possible routes of juvenile salmon passage and the requirements of the multistate release recapture model to distinguish and estimate movement, survival, and detection processes (described below). Although the technology changed from HTI to VEMCO in 2012 and additional receivers were installed in new locations in later years, the locations of the key receivers remained constant (Figure 1; Table 2). At a minimum, receivers at Mossdale and a dual line of receivers (i.e., dual array) at Chipps Island were required to estimate survival through the Delta from Mossdale to Chipps Island. Additional receiver locations provided estimation of route selection, route-specific survival, and survival in key river reaches (e.g., past the city of Stockton). Dual arrays were placed in both branches downstream from key river distributary points (junctions), in particular the head of Old River (San Joaquin at Lathrop, Old River near head) and Turner Cut (MacDonald Island, Turner Cut) off the San Joaquin River (Figure 1; Table 2). Receivers were also installed at the trash racks and in the holding tank at the CVP water export facility and at the entrance to the Clifton Court Forebay outside the SWP. The Chipps Island receivers were located approximately 20 rkm downstream from the postsalvage release locations for fish that were recovered and trucked from the water export facilities, ensuring that all surviving migrants were required to pass the Chipps Island receivers. Starting in 2011, receivers were placed in the San Joaquin River at Jersey Point, located 26 rkm upstream from Chipps Island; Jersey Point had been used as the downstream survival point in 20 years of coded wire tag studies (Brandes and McLain 2001; SJRGA 2013). In 2014 and 2015, receivers were installed at Benicia Bridge (BBR), 19 rkm downstream from Chipps Island, to provide better estimates of detection probabilities at Chipps Island (Figure 1; Table 2).

Statistical Methods

Data processing and analysis. The raw detection data were processed into detection events for each tag by the U.S. Geological Survey (USGS) lab in Cook, Washington, for the 2010 and 2011 studies, and by the USGS lab in Sacramento for the 2012 2015 studies. The processed detection event data were transferred to the University of Washington, Seattle, where the data were further processed into chronological detection histories identifying the receivers and dates where each tag was detected. Although the study fish were expected to be migrating and therefore to be moving consistently in a downstream (seaward) direction, the tidal nature of the Delta environment means that migrating fish may move upstream temporarily on reverse flows. If such flows expose them to river junctions multiple times, their final route selection may differ from their initial selection at the junction (Perry et al. 2010). Thus, detection histories used the final pass of the tag past a detection site or junction to best represent the fate of the fish.

The possibility of a predatory fish eating a tagged study fish and then passing a receiver with the still active acoustic tag in its gut raised the potential for biased survival

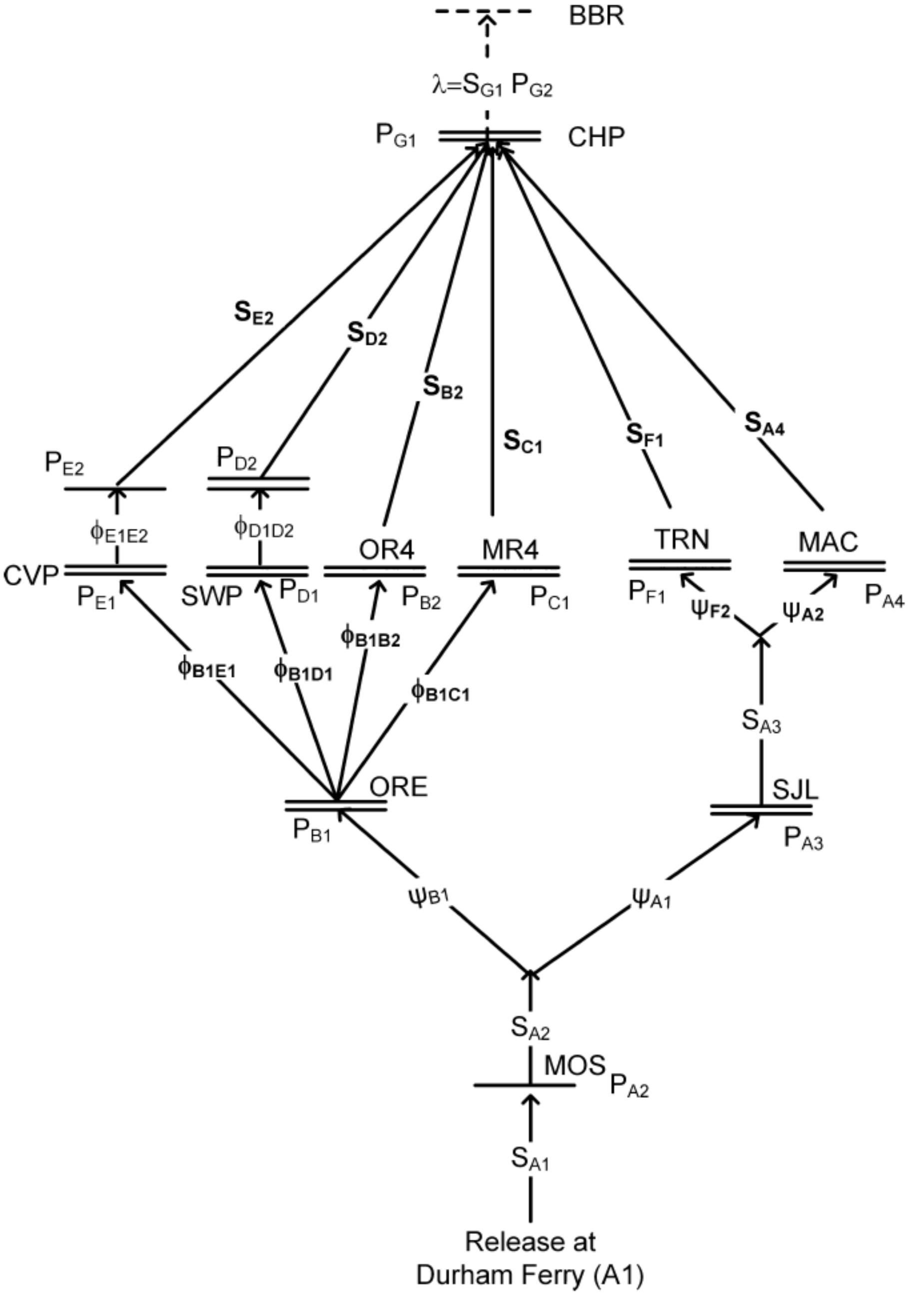

FIGURE 2. Schematic of multistate release recapture model to estimate survival of juvenile Chinook Salmon from Mossdale (MOS) through the Delta to Chipps Island (CHP). The downstream boundaries of the southern Delta are MacDonald Island (MAC) and Turner Cut (TRN) in the San Joaquin River route, and the water export facilities (CVP, SWP) and Highway 4 receivers (OR4, MR4) in the Old River route. Horizontal lines indicate acoustic receivers; parallel lines indicate dual receiver array. Model parameters are probabilities of salmon reach survival (S), detection (P), route selection (ψ), and transition ($\Phi = \psi S$), and the last reach parameter λ SP. Site BBR was available only in 2014 and 2015 (dashed lines).

estimates. Detection data were passed through a "predator filter" to identify and remove likely predator detections. The predator filter was based on assumed behavioral differences between migrating Chinook Salmon smolts and predators such as Striped Bass *Morone saxatilis*, including differences in residence time in the vicinity of a receiver, travel rate between receivers, and movements against river flow. More information on the predator filter is available in Buchanan et al. (2013, 2015, 2016) and SJRGA (2011, 2013).

The filtered detection history data were analyzed using a multinomial, multistate release recapture model to estimate the probabilities of detection (*P*), reach-specific survival (*S*), and route selection (ψ; i.e., "route entrainment") (Buchanan and Skalski 2010; Perry et al. 2010; Buchanan et al. 2013). Different model states were used to represent the different routes through the Delta. Smolt survival was estimated for various regions in the Delta, including (1) through-Delta survival (i.e., Mossdale to Chipps Island), and (2) survival through the southern Delta (i.e., Mossdale to MacDonald Island Turner Cut in the San Joaquin River route, and Mossdale to CVP SWP Old River (OR4) Middle River (MR4) in the Old River route (Figure 1; Table 2). The multistate release recapture model accounts for imperfect detection probabilities (i.e., efficiencies) in estimating survival. An example of the 2010 model can be found in Buchanan et al. (2013), and a schematic of the model common to all study years (Durham Ferry releases) is presented in Figure 2. Pope (2014) included the likelihood equation for the 2011 study year. For Medford Island releases, survival downstream to Chipps Island was estimated with the single-release Cormack Jolly Seber model (Skalski et al. 1998).

For the 2010 study year, the multistate model was fit separately for each of seven release groups, and the averages of parameter estimates weighted by release size were reported. Sparse detections at downstream sites in the 2011 2015 study years required pooling the data from individual releases in those years for fitting the model. The multistate models were fit to the data for each year using maximum likelihood estimation in the software program USER (Lady and Skalski 2009). On occasion, the full model had to be simplified to account for sparse data through certain routes, resulting in loss of some route-specific information but not affecting the estimate of overall through-Delta survival. For some study years, no tag or only one tag was detected at Chipps Island, which prevented estimation of survival to Chipps Island separately from the detection probability. These cases were noted in the results, and the survival estimate was reported under the assumption of 100% detection probability. The 95% upper bound on survival to Chipps Island in these cases was estimated using a binomial error structure (Louis 1981) and an assumed travel time of 7 d.

Each year, potential surgeon effects on survival of tagged fish were assessed by testing for persistent differences between surgeons in survival through multiple reaches using the nonparametric Kruskal Wallis test (Sokal and Rohlf 1995). In the event that a surgeon was observed to have fish with consistently lower survival than that for the rest of the surgical team, the release recapture model was refit to the data without that surgeon's tags.

Survival estimates in the San Joaquin River route and Old River route were compared by using a two-sized Z-test on the log scale and the significance level set at $\alpha = 0.05$. Survival estimates were tested for heterogeneity among years by means of an F-test (Skalski et al. 2014). The hypothesis that survival was higher in the southern Delta (i.e., through the upstream reaches of the Delta) than through the lower (i.e., downstream) reaches of the Delta was tested by comparing the estimates of through-Delta survival to the square of southern Delta survival: δ = (survival through southern Delta^2)/(through-Delta survival). If southern Delta survival is comparable with survival in the downstream reaches, then the ratio δ should be approximately 1. A one-sample t-test was used to compare the ratio δ to 1 on the log scale. Only years with tag detections at Chipps Island were included for the regional comparison.

Tag life and travel time. Tag life was measured as the time between tag activation and failure time in the in-tank studies. In some cases, malfunctioning hydrophones in the tag-life studies required right-censoring the time-to-failure data. Observed tag survival was modeled separately each year using the four-parameter vitality curve (Li and Anderson 2009). Within each study year, possible stratification of tag survival by activation date was assessed using the Akaike information criterion (AIC; Burnham and Anderson 2002), with the exception of the April tag-life study from 2014; homogeneity (i.e., no stratification) of tag survival was concluded in all years except 2014. In 2014, the earliest (i.e., mid-April) release group and April tag-life study both suffered from a manufacturing defect that turned the tags off prematurely; the defect was corrected for later release groups, resulting in a separate tag-survival model for the mid-April release for that year.

The fitted tag-survival models were used to adjust the estimated fish survival probabilities for tag failure using methods adapted from Townsend et al. (2006). In this study, travel time and the probability of tag survival to Chipps Island were estimated separately for the different routes (e.g., San Joaquin River route and Old River route). Standard errors of the tag-life-adjusted fish survival and transition probabilities were estimated using the inverse Hessian matrix of the fitted joint fish-tag survival model. The additional uncertainty introduced by variability in tag survival was not incorporated into the estimated SEs of the survival estimates. In previous studies, however, variability in tag-life parameters was observed to contribute little to the overall uncertainty in the fish survival estimates (Townsend et al. 2006); thus, the resulting bias in the SE values was expected to be small. Because of the high rate of premature tag failure experienced by the mid-April release group in 2014, no attempt was made to adjust the survival estimates for tag failure for that release group. Thus, estimates from the 2014 mid-April release group represent minimum fish survival (Holbrook et al. 2009).

RESULTS

Delta Conditions

Delta inflow from the San Joaquin River is measured at the Vernalis river gauging station, which is located approximately 3 rkm upstream from the Durham Ferry release site. River discharge (flow) at this station was considerably higher in 2011 than in the other years. Average daily flows at Vernalis during 2011 ranged from 278 to 308 m^3/s over the course of the study, whereas average daily flows for the other study years ranged from 11 m^3/s in 2015 to 161 m^3/s in 2010. Daily total water export rates from the Delta (i.e., from CVP, SWP) varied throughout the season, especially in 2011. The average daily export rate during the release periods ranged from 42 m^3/s in 2014 to 277 m^3/s in 2011. Mean daily water temperature in the San Joaquin River near the city of Lathrop (near the head of Old River) varied between years (ANOVA: $P = 0.0155$) and tended to increase throughout each season. Average daily water temperature during the release periods ranged from 15.1°C in 2010 and 2011 to 22.2°C in 2015; the maximum temperature observed at the release site was 24.7°C at Durham Ferry in 2015. The temperature differential between salmon transport tanks and river water was <5°C for 96% of transport trips of tagged fish to the release site (maximum = 6.7°C).

Fish Health and Tag Retention

The 24 72-h mortality rate of dummy-tagged fish ranged from 0 to 2% in all study years. Fish condition after tagging was generally good; however, examination of control fish in the fish health studies found surgical complications (e.g., loose sutures) in some years. Incidence of such complications ranged from 0 to 10% per year except in 2012 (18%). High rates of *Aeromonas Pseudomonas* infection were found in some years (20% in 2015 and 37% in 2012) but may have been due to environmental contamination during sampling (Nichols 2015). Health assessments for control fish in 2010 2013 consistently found evidence of the myxozoan parasite *Tetracapsuloides bryosalmonae*, the causative agent of proliferative kidney disease (PKD). Clinical incidence of PKD in control fish ranged up to 93% (2012); no PKD was detected in sampled fish from 2014 and 2015. For more details on fish health results, see SJRGA (2011, 2013), Nichols (2014, 2015), Buchanan et al. (2015, 2016), and Foott (2015).

Tag retention studies found no tag loss within 30 33 d except in 2015, when 1 of 69 tags (1.4%) was found to have been expelled upon examination on day 31. The mortality rate among dummy-tagged fish used in the tag retention studies and held for 30 33 d in 2014 and 2015 was 0 to 2.4%, respectively, and similar mortality rates were observed among untagged control fish. In 2012, 3 of 39 (7.7%) dummy-tagged fish died by day 5; no other dummy-tagged fish died by the study's end on day 30, and no untagged fish were available for comparison in 2012.

Tag Life and Travel Time

Mean tag life was approximately 12 d in the April 2014 tag-life study, which reflected a manufacturing defect. For all other tag-life studies, mean tag life varied from 27 d in 2010 to approximately 50 d for both the 2013 study and the May 2014 tag-life study (Figure 3).

Median travel time from Mossdale to Chipps Island was approximately 3 to 4 d in 2010, 2011, and 2013 and 5.2 d in 2012 (Table 3). The single tag detected at Chipps Island in 2014 was detected there 4.9 d after detection at Mossdale but came from the faulty tag group and may not represent average travel time of the group. No fish with tags passing Mossdale in 2015 were detected at Chipps Island. Both the shortest (1.1 d) and the longest (12.4 d) travel times through the study area to Chipps Island occurred in 2011. Travel time through the Delta (i.e., Mossdale to Chipps Island) was significantly longer on average in 2012 than in the other 3 years that have estimates ($t_{70} = 2.937$, $P = 0.0045$). Median travel time from Mossdale through the southern Delta to the Turner Cut junction (i.e., to the Turner Cut or MacDonald Island receivers) ranged from 1.3 d in 2014 (three fish) to 3.7 d in 2013 (two fish) (Table 3). Travel times from Mossdale through the southern Delta to either the water export facilities (CVP, SWP) or the Highway 4 receivers (OR4, MR4) tended to be slightly shorter: median travel times ranged from 0.8 d in 2011 to 1.9 d in 2012 (four fish) and 2013 (Table 3). Tags from the 2015 Medford Island release were detected at Chipps Island 2.1 to 8.9 d after release (median time = 3.7 d; Table 3).

Survival Estimates

Annual estimates of the total probability of juvenile salmon surviving from Mossdale to Chipps Island (hereafter, "through-Delta survival") based on acoustic-telemetry data were all ≤0.05 (SE ≤ 0.01) for the 6 years of study (Table 4); there was no significant difference in survival between years ($F_{4,\ \infty} = 1.668$, $P = 0.1542$). Considering the 92-km length of the primary San Joaquin River route through the Delta, a total survival probability of 0.05 translates to a survival probability of 0.97 per kilometer (i.e., 0.03 probability of mortality per kilometer). Nearly half (7 of 17) of the release groups yielded through-Delta survival estimates of ≤0.01, although two 2010 release groups had estimates of 0.10 (SE = 0.03) (Figure 4). During the drought years of 2014 and 2015, only one fish was detected at Chipps Island out of 2,719 released at Mossdale; that single fish came from the April 2014 release group that had defective tags, and represents the joint probability of fish and tag survival and detection. Under the assumption of 100% detection probability at Chipps Island, survival from Mossdale to Chipps Island was 0 for fish released with nondefective tags in 2014 and 2015. Also assuming a binomial error structure, the 95% upper

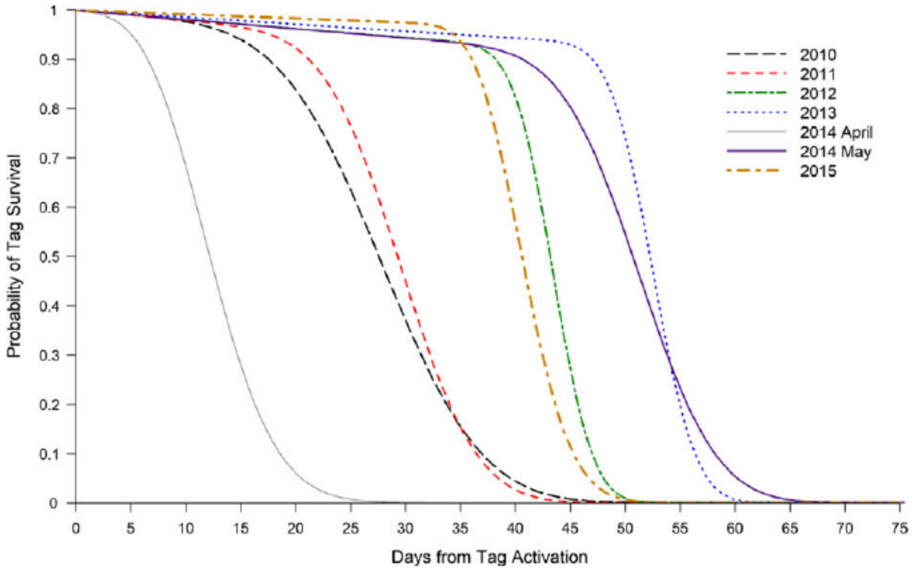

FIGURE 3. Fitted tag survival curves for each year and/or in tank study. The 2010 and 2011 studies used HTI tags, and the 2012 2015 studies used VEMCO tags (see Methods). [Color figure can be viewed at afsjournals.org.]

TABLE 3. Estimated (median, range in parentheses) travel time (days) through the southern Delta and to Chipps Island for study years 2010 2015; number after semicolon number of observations. Travel times are from Mossdale and are for Durham Ferry (DF) releases unless otherwise noted (MF Medford Island release). Turner Cut Junction TRN and MAC acoustic receivers (Figure 1). NA no estimate is available.

Year	Turner Cut Junction	Water export facilities Highway 4	Chipps Island (from Mossdale)	Chipps Island (from release site)
2010	2.5 (1.3 3.7); 81	1.1 (0.5 5.8); 162	3.4 (1.3 7.2); 29	3.8 (1.6 7.6); 29
2011	1.6 (0.7 10.2); 404	0.8 (0.3 10.3); 378	2.9 (1.1 12.4); 27	3.3 (1.4 12.7); 33
2012	2.2 (1.0 7.3); 109	1.9 (1.2 3.9); 4	5.2 (3.7 10.0); 15	5.6 (4.1 10.4); 15
2013	3.7 (3.0 4.3); 2	1.9 (0.4 6.1); 95	3.6 (3.3 7.6); 3	4.0 (3.8 8.1); 3
2014[a]	1.3 (0.9 1.6); 3	1.8 (1.7 1.9); 2	NA; 0	NA; 0
2015 (DF)	2.4; 1	NA; 0	NA; 0	NA; 0
2015 (MF)	NA	NA	NA	3.7 (2.1 8.9); 35

[a] Estimates for 2014 omitted mid-April release group because of a tag-programming error.

bound on survival was 0.01 in 2014 and 0.13 in 2015; the relatively high upper bound in 2015 reflects the low survival from the Durham Ferry release site to Mossdale that year (0.03; Table 5). In the extreme drought year of 2015, survival from the Medford Island release site to Chipps Island was estimated at 0.08 (SE = 0.01); only one fish released at Durham Ferry was detected as far downstream as Medford Island that year. No persistent effects from surgical treatment were detected through multiple reaches in any year ($P \geq 0.3679$ each year).

Of the acoustic tags released at Durham Ferry and detected at Chipps Island since 2010, the majority of the fish passed through the CVP en route to Chipps Island; the exception was in 2012, when a temporary rock barrier blocked most access to the Old River and the direct route to the CVP was closed (Table 4). The barrier was also installed at the head of Old River in 2014 and 2015, and the large majority of fish used the San Joaquin River route in those years (Table 5). In years without the rock barrier, the probability of selecting the San Joaquin River route ranged from 0.23 (SE = 0.02) in 2014 to 0.58 (SE = 0.01) in 2011 (Table 5). Survival from Mossdale to Chipps Island was low through both the San Joaquin River route and the Old River route in all years. In the 2 years in which there was a statistically significant difference ($P \leq 0.0267$) in route-specific survival, the Old River route had the higher survival when data was combined across release groups (Table 5). When compared on the scale of the individual release groups, only three releases showed survival differences between routes: the Old River route had the higher survival for the two June

TABLE 4. Estimates (SE in parentheses) of (1) probabilities of Chinook Salmon survival from Mossdale to the Turner Cut Junction, the water export facilities Highway 4 receivers, through the entire southern Delta, and through the Delta to Chipps Island, (2) detection probability at Chipps Island (conditional on presence), and (3) the percentage of tags released at Durham Ferry (DF) and detected at Chipps Island that came through the CVP; MF Medford Island release. Estimates are weighted averages for 2010 and estimated from pooled release groups for 2011 2015. When provided, *n* number of tags detected at downstream boundary of reach. Turner Cut Junction TRN and MAC acoustic receivers (Figure 1). NA no estimate is available.

Year	Turner Cut Junction	Water export facilities Highway 4	Total southern Delta	Chipps Island	Detection at Chipps Island	CVP detection percentage (%)
2010	0.32 (0.02)	0.77 (0.05)	0.56 (0.03)	0.05 (0.01)	1.00 (0.00)	65.5
2011	0.48 (0.02)	0.66 (0.02)	0.56 (0.01)	0.02 (<0.01)	0.99 (0.01)	63.6
2012	0.24 (0.02)	0.42 (0.16)	0.24 (0.02)	0.03 (0.01)	1.00 (0.00)	6.7
2013	0.02 (0.01)	0.27 (0.02)	0.21 (0.02)	0.01 (0.01)	1.00 (0.00)	66.7
2014[a]	0.01 (<0.01)	0.12 (0.05)	0.02 (0.01)	0.00 ($n = 0$)	NA	NA
2015 (DF)	0.05 (0.05; $n = 1$)	0.00 ($n = 0$)	0.05 (0.05)	0.00 ($n = 0$)	NA	NA
2015 (MF)	NA	NA	NA	0.08 (0.01)[b]	0.93 (0.05)	NA

[a] Estimates for 2014 omitted mid-April release group because of a tag-programming error.

[b] Survival estimate from release at Medford Island.

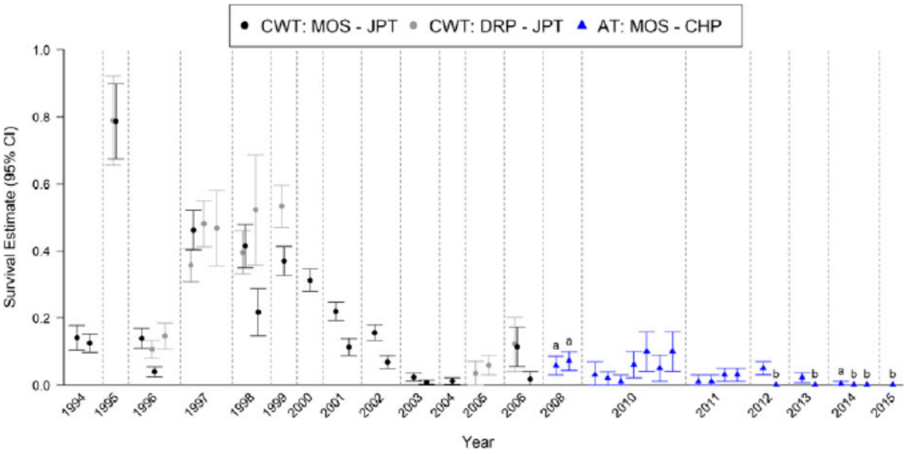

FIGURE 4. Estimated survival of release groups of juvenile hatchery fall run Chinook Salmon from Mossdale (MOS) or Dos Reis Park (DRP, 3.7 rkm downstream from the receivers at San Joaquin at Lathrop) to either Jersey Point (JPT) or Chipps Island (CHP) from coded wire tag (CWT) and acoustic telemetry (AT) studies. Intervals are 95% CIs, truncated to 0 if necessary. The letter a estimates that represent minimum survival because of premature tag failure (Holbrook et al. 2009); letter b no detections at Chipps Island; Delta survival was not estimated in 2009 (SJRGA 2010). (Adapted from Figure 5 1 in SJRGA 2013.) [Color figure can be viewed at afsjournals.org.]

releases in 2011, and the San Joaquin River route had the higher survival for the late April release in 2010 (SJGRA 2011, 2013). Estimated survival through the southern Delta (i.e., through the upstream region of the Delta) tended to be considerably higher than through-Delta survival (Table 4). Survival was also higher in the southern Delta than in the lower (i.e., downstream) reaches of the Delta ($t_3 = 3.670$, $P = 0.0350$). Nevertheless, even the upstream region of the Delta had low survival in recent years. Estimated salmon survival to the Turner Cut junction was only 0.02 (SE = 0.01) in 2013, 0.01 (SE $\leq$ 0.01) in 2014, and 0.05 (SE = 0.05) in 2015, compared with 0.24 to 0.48 (SE = 0.02) in 2010 2012 (Table 4); the annual differences were highly significant ($F_{5,\,\infty} = 58.237$, $P < 0.0001$).

DISCUSSION

The annual through-Delta survival estimates from 2010 to 2015 obtained from these acoustic-tag studies were ≤0.05, and some were 0; release-level estimates were ≤0.10. These acoustic-tag survival estimates continue a pattern of declining survival observed in coded wire tag studies dating back to 2002 (Figure 4). However, low survival was observed in earlier years as well (e.g., 1994; Figure 4). Obvious questions arise in response to these low survival estimates. How do these levels of survival compare with salmonid survival through similar environments in other river systems? What are the possible causes and population effects of low survival? How representative and reliable are the survival estimates, and what are the implications for managers?

TABLE 5. Estimates of the probability of Chinook Salmon survival from the Durham Ferry (DF) release site to Mossdale (MOS), the probability of selecting the San Joaquin River (SJR) route at the head of Old River (OR), and the probability of survival in the two major routes from Mossdale to Chipps Island (SJR route and OR route), and the P value from the two sided Z test on the log scale for the hypothesis of equal survival in the two routes. Estimates are weighted averages for 2010 and estimated from pooled release groups for 2011 2015. NA no test was performed.

Year	DF to MOS	Select SJR route	SJR route	OR route	P-value
2010	0.94 (0.01)	0.47 (0.02)	0.04 (0.01)	0.07 (0.01)	0.0267
2011	0.87 (0.01)	0.58 (0.01)	0.01 (<0.01)	0.04 (0.01)	0.0001
2012	0.50 (0.02)	0.98 (0.01)	0.03 (0.01)	0.11 (0.10)	0.2000
2013	0.50 (0.02)	0.23 (0.02)	0.01 (0.01)	0.01 (0.01)	0.8120
2014[a]	0.16 (0.01)	0.92 (0.02)	0.00 ($n = 0$)	0.00 ($n = 0$)	NA
2015	0.03 (<0.01)	0.92 (0.08)[b]	0.00 ($n = 0$)	0.00 ($n = 0$)	NA

[a] Estimates for 2014 omitted mid-April release group because of a tag-programming error.

[b] Assumption of 100% detection probability in Old River Route ($n = 1$).

Direct comparison of these survival results to other river systems is challenging because of structural differences between the Delta environment and other riverine systems. However, comparisons can be made using survival estimates scaled by migration distance and translated to the length of the Delta, i.e., approximately 92 rkm along the San Joaquin River from Mossdale to Chipps Island (Buchanan et al. 2013). Many acoustic-telemetry studies have estimated survival of yearling Chinook Salmon in the lower river and estuary of the Columbia River (reviewed in Dietrich et al. 2016): scaled to the length of the Delta, the Columbia River survival probability estimates averaged 0.84 and ranged from 0.23 to 1.0 (see Dietrich et al. 2016 for data). Thus, the studies of yearling Chinook Salmon in the Columbia River show considerably higher survival through the lower river and estuary than has been observed for subyearling FR Chinook Salmon through the Delta. For subyearling FR Chinook Salmon from the Columbia River basin, lower river and estuary survival estimates are available from 2002 and 2003 (Clemens et al. 2009) and from 2009 and 2010 (McMichael et al. 2010, 2011; Harnish et al. 2012); extrapolated to the length of the Delta, the Columbia River subyearling FR Chinook Salmon estimates ranged from 0.61 to 0.88. Welch et al. (2008) reported survival of outmigrating yearling Chinook Salmon from 2004 to 2006 through 330 to 395 km of the Thompson Fraser River system and estuary, British Columbia, which, when scaled to the length of the Delta, ranged from 0.37 to 0.74. Thus, there is evidence that survival of juvenile Chinook Salmon into and through estuaries from two other large river systems on the West Coast of North America have considerably higher survival rates than FR Chinook Salmon from the San Joaquin River system, even though five Chinook Salmon populations in the Columbia River basin have warranted listing as endangered under the U.S. Endangered Species Act (U.S. Office of the Federal Register 2010).

In the Columbia River basin, a minimum smolt adult return ratio (SAR) of 2% (0.02) has been recommended for population sustainability (NPCC 2014). The release-specific Delta survival estimates for the San Joaquin River FR Chinook Salmon had a maximum of 0.10 and averaged approximately 0.025 (Figure 4). If SAR ≥ 0.02 is required for population persistence, then a minimum survival probability of 0.2 (i.e., 0.02/0.10) is required through the remainder of the salmon's life history until adult return. Using a low-end Delta juvenile survival value of 0.025, SAR of 0.02 requires post-Delta survival of 0.80. These calculations assume juvenile survival from the tributaries to the Delta is 1.0, which is not the case (Brandes and McLain 2001; Zeug et al. 2014). Additionally, survival through the bays can be lower than survival through the Delta itself for late-fall-run Chinook Salmon (Michel et al. 2015), and Lindley et al. (2009) concluded that ocean conditions contributed heavily to the fall-run salmon fishery collapse in 2007 and 2008. Thus, Delta survival as low as 0.025 to 0.10 is likely not being compensated by higher survival rates in other life stages. At current Delta survival rates, the San Joaquin River component of the Central Valley FR Chinook Salmon population may not persist.

The potential for low Delta survival of San Joaquin River FR Chinook Salmon to affect the persistence of the overall Central Valley FR Chinook Salmon population is also a concern. There is little or no genetic distinction among naturally spawning populations of FR Chinook Salmon in the Central Valley or among the individuals spawned at different hatcheries (Williamson and May 2005; Lindley et al. 2009). The common hatchery practice of trucking juveniles around the Delta may contribute to adult straying, and eggs are sometimes moved from one hatchery to another between basins (Williams 2006, 2012). Furthermore, most existing estimates of Delta survival of FR Chinook Salmon from the Sacramento River are considerably higher than those for FR Chinook Salmon from the San Joaquin River: estimates of Sacramento River FR Chinook Salmon survival from Freeport (on the

Sacramento River) to Benicia Bridge have ranged from 0.26 to 0.39 in 2012 to 2014 and in 2016, although an estimate as low as 0.05 was observed in 2014 (A. Ammann, NOAA Fisheries, personal communication; G. Singer, University of California Davis, personal communication; S. Zeug, Cramer Fish Sciences, personal communication). These observations suggest that the San Joaquin River basin may be a sink for the Sacramento River component of the overall Central Valley FR Chinook Salmon population, rather than a self-sustaining subpopulation (e.g., Johnson et al. 2012). If so, then persistently low survival of the smolt migrant component of the San Joaquin River population puts further strain on the Central Valley population as a whole and reduces total escapement and harvest.

The reasons behind the low Delta survival of FR Chinook Salmon from the San Joaquin River are varied and speculative. Historically, the population decline of Chinook Salmon from the mid-1800s was caused by overfishing, mining, damming, and water diversions (Yoshiyama et al. 1998). Since then, the Delta environment has been heavily modified from a combination of saltwater, brackish, and freshwater marshes to a complex system of river channels maintained by levees that protect agricultural, industrial, and residential land (Nichols et al. 1986). Additionally, a large proportion of the fresh water entering the Delta is extracted for municipal and agricultural use. A multiyear drought likely contributed to the survival estimate of 0 in 2014 and the high mortality before fish even reached the Delta in 2015 (Table 5). Salmon survival estimates from Durham Ferry to Mossdale varied significantly between years ($F_{5,\,\infty} = 708.563$, $P < 0.0001$), and the point estimates for this reach declined for all years of the study except one (Table 5), consistent with the expected drought effects. The prospects of climate change make such extreme drought events more likely in the future (Cvijanovic et al. 2017).

Nevertheless, high river flows alone do not guarantee high survival (e.g., Romer et al. 2013). In particular, 2011 was a wet year, yet total through-Delta survival was low (0.02). The 2011 study fish were released in mid-May through mid-June that year, which coincided with captures of wild Chinook Salmon in the Mossdale trawl (SJRGA 2013), but also occurred just after the end of peak river flow at Vernalis; thus, it is possible that the study fish in 2011 missed the period of primary benefit of high flows for Delta survival. It is notable, however, that survival through the upstream reaches of the Delta was higher in 2011 (e.g., 0.48 from Mossdale to the Turner Cut junction) than in other years, as expected for a high-flow year, whereas survival through the downstream reaches of the Delta was ≤ 0.06 (e.g., approximately 0.05 probability of mortality per kilometer from the Turner Cut junction to Chipps Island). This pattern of higher mortality in the downstream versus upstream Delta reaches was also observed for late-fall-run Chinook Salmon from the Sacramento River in 2011 (Michel et al. 2015) and suggests spatial variability in mortality factors within the Delta. This possibility is supported by the observation that the majority of tagged FR Chinook Salmon from the San Joaquin River detected at Chipps Island when all routes were available (i.e., no rock barrier at the head of Old River) came through salvage at the CVP rather than migrating entirely through Delta waters; this is because salvaged fish avoid the downstream reaches of the Delta.

Fish condition may also account for some of the results observed in these studies. In particular, the high incidence of PKD observed in the fish from the Merced River Hatchery used in 2010 2013 may have contributed to high mortality in those years. This kidney disease is progressive, potentially fatal, and develops faster at higher water temperatures (Ferguson 1981). It is common in fish from the Merced River Fish Hatchery (Foott et al. 2007) and also prevalent in the natural-spawning population (Nichols and Foott 2002). However, no PKD was observed in the study fish from the Mokelumne River Hatchery in the drought years of 2014 2015, when survival was particularly low.

The observed decline in salmon survival coincides with a well-documented decline in populations of many Delta organisms (Sommer et al. 2007). Referred to as the pelagic organism decline (POD), this phenomenon indicates an ecosystem-wide shift in the ecological community of the Delta. Nonnative species such as Largemouth Bass *Micropterus salmoides*, the aquatic weed *Egeria densa*, and the overbite clam *Corbula amurensis* have become well established in the Delta and have altered the food web (Kimmerer et al. 1994; Sommer et al. 2007; Healey et al. 2008). Striped Bass and Largemouth Bass are known predators of juvenile salmonids and also support a popular sport fishery in the Delta (Nobriga and Feyrer 2007; Cavallo et al. 2013). In the 2010 2015 studies, the predator filter identified a minimum of 20% to 64% of the tagged FR Chinook Salmon detected between Mossdale and Chipps Island as being predated upon. Because the predator filter identifies only those predation events that were followed by movement past an acoustic receiver, the actual predation rate within this region was likely even higher. The hypothesis that faster-moving fish have reduced exposure time to predators and consequently higher survival (e.g., Anderson et al. 2005) was not supported here on the scale of the entire Delta, where travel time varied between years (longest in 2012), but total Delta survival did not (Tables 3 and 4); further investigation of a predator exposure or travel time hypothesis is warranted on smaller spatial scales.

The extent to which the results of the acoustic-telemetry study represent the San Joaquin River FR Chinook Salmon population depends on the composition of the study fish, release timing, and fish condition. The fish used in the acoustic-telemetry studies were all smolt-sized subyearlings reared at state-run hatcheries on the Merced or Mokelumne rivers, tributaries to the San Joaquin River. They were expected to pass quickly through the Delta to San Francisco Bay and the near ocean and then return to the Central Valley to spawn as adults approximately 2.5 years later. The majority of salmon in the Central Valley are reared in hatcheries (Barnett-Johnson et al. 2007), but fish from the state-run hatcheries are sometimes trucked around the Delta as juveniles and thus avoid within-Delta mortality (Miller et al. 2010). The natural-spawned population from the San Joaquin basin is not trucked and includes fish that migrate as smolt-sized fish, as well as those that migrate from the tributaries to the San Joaquin River or Delta as either fry- or parr-sized fish (Miller et al. 2010). Recent chemical analysis of otoliths from returning adult wild FR Chinook Salmon from the Stanislaus River in the San Joaquin River basin suggest that fish that exit the Stanislaus River as parr (i.e., rear in the lower San Joaquin River or Delta) sometimes have higher survival to adult return than do fish that exit the Stanislaus River as smolts, which are expected to be better represented by the acoustic-telemetry study fish (Sturrock et al. 2015). However, trawl sampling at Mossdale concurrent with the acoustic-telemetry studies in 2010 and 2011 found Chinook Salmon of comparable length to our study fish, suggesting that our studies effectively represented a detectable component of run-of-river fish in timing and fish size (SJRGA 2011, 2013). Thus, the low survival estimates observed in the acoustic-telemetry studies may be considered to represent the Delta survival of the smolt-sized migrant component of the natural-spawned population, to the extent to which hatchery fish may represent natural fish. Introgression of genes from the hatchery population into the natural population may limit the actual differences in survival between the wild and hatchery populations, but questions remain of surrogacy assumptions in applying results from hatchery fish to the wild population (Murphy et al. 2011). In particular, a number of authors have found hatchery fish to have different survival estimates than naturally produced fish (e.g., Berejikian et al. 1999; Buchanan et al. 2010). Even allowing for differences between study fish and the wild population, the low survival observed for the hatchery-reared release groups suggests that Delta conditions are poor and that a sizeable component of the natural-spawned population from the San Joaquin River basin may also experience low Delta survival. A loss of this population component would contribute to the loss of diversity and resilience overall in Central Valley FR Chinook Salmon and put the population and ocean fisheries at added risk of collapse (Lindley et al. 2009; Carlson and Satterthwaite 2011).

The reliability of the low survival estimates observed here depends on detection probabilities (efficiencies) at Chipps Island, the predator filter, and tagging and handling effects. These survival estimates were generated using a release recapture model that separates survival from detection processes; in particular, the dual receiver array at Chipps Island, either alone or combined with the Benicia Bridge receivers (if present), provided the data structure necessary to estimate the detection probability at that site. Thus, the efficiency of the detection process does not confound the survival probability estimates. Detection probabilities at Chipps Island were estimated to be high (>0.90) for all years with estimates (Table 4). The lack of detections in 2014 prevented estimation of the detection probability for that year; however, the very low survival ($S = 0.01$) estimated to the Turner Cut junction in 2014 suggests that the lack of Chipps Island detections was caused by low survival rather than failure of the detection system.

The survival estimates reported reflect detection data after filtering for likely predator detections. Without implementing the predator filter, the only year with a different Delta survival estimate was 2010, when the unfiltered survival estimate was 0.11 instead of 0.05 (SE = 0.01; SJRGA 2011, 2013; Buchanan et al. 2013, 2015, 2016). The possibility that the low survival probability estimated for the high-flow year of 2011 was a result of positively biased detection probabilities or inaccuracies in the predator filter was explored and discounted; even assuming a Chipps Island detection probability as low as 0.75 and omitting the predator filter, the estimated survival probability from Mossdale to Chipps Island in 2011 would have been 0.03 instead of 0.02.

Possible tagging and handling effects are of concern in any tagging study. In the 6 years of this study, tag burden, tagging and handling procedures, and temperature controls during fish handling were within recommended guidelines (e.g., Wedemeyer 1996; Iwama et al. 1997; Anglea et al. 2004; Brown et al. 2006). The possibility of acute mortality effects due to surgery or transport conditions was assessed by examining dummy-tagged fish after being held for at least 48 h at the Durham Ferry release site after transport. The 48-h mortality rate of these dummy-tagged fish was <2% for all years. Additionally, the mortality rate of active-tagged fish during transport and holding prior to release was minimal in 2010 2014 (0.06% of all tagged fish transported). Together, these results suggest that surgery, handling, and transport caused minimal acute mortality. There was higher mortality during holding at the Durham Ferry release site in 2015 (0.92%). However, river temperatures were abnormally high (≤24.7°C) during the holding period and may account for the prerelease mortality in that year even in the absence of additional stress from surgery or handling

(Marine and Cech 2004). Furthermore, the 21 rkm between the primary release site at Durham Ferry and the upstream boundary of the study area (Mossdale) allowed any acute mortality effects of handling to be expressed outside of the study area. Survival probability estimates from Durham Ferry to Mossdale ranged from 0.03 (SE < 0.01) in 2015 to 0.94 (SE = 0.01) in 2010 (Table 5). Although these estimates reflect possible handling effects, they also reflect river conditions such as low flows and high temperatures that affect both tagged and untagged fish. These considerations suggest that any acute mortality effects of surgery and handling were not reflected in survival estimates in the study area.

The possibility of chronic mortality effects due to surgical errors or variation in surgeon skill was examined by testing for differences in survival estimates of fish among surgeons each year. Although estimated survival was sometimes lower for fish tagged by a particular surgeon in a given reach and year (e.g., from Stockton to Turner Cut in 2012), there was no indication that any fish processed by any individual surgeon had consistently lower survival through multiple reaches in any year. The potential impact of surgical complications (e.g., loose sutures) on estimates of total Delta survival was investigated by adjusting observed estimates of fish survival to Chipps Island (Table 4) by the rate of surgical complications identified from dummy-tagged fish. Such adjustment depended on the conservative assumption that all fish that had surgical complications died within the study area (i.e., neither during the 24-h holding period at the release site nor in the 21 rkm between Durham Ferry and Mossdale) and would not have died without the surgical complications. Even using the maximum observed rate of surgical complications (18% in 2012), the adjusted annual estimates of total Delta survival increased by only 0.01, e.g., from 0.03 to 0.04 in 2012. The mortality and tag loss rates observed from the tag retention studies produced similar results. Thus, the low survival estimates found in these 6 years of study were unlikely to have been an artifact of the tagging process and were more likely to reflect the Delta environment. Similarly, the fact that survival estimates were ≤0.05 regardless of changes in tag and acoustic receiver technology, fish source, and tagging location suggests that low survival is a persistent and pervasive characteristic of this population under current Delta conditions.

Management Implications

Given the complex host of factors contributing to low Chinook Salmon survival in the Delta and the concurrent needs of other California residents, both aquatic and terrestrial, piscine and human, the actions required to improve survival will not be simple. Uncertainty about the minimum Delta survival necessary for population persistence complicates assessment of management action potential and performance; for example, a hypothetical target survival probability as high as 0.50 would likely prompt different approaches than would a lower hypothetical target of 0.10. A more comprehensive understanding of the structure of the Central Valley metapopulation generally, and specifically the San Joaquin River salmon population structure, performance, and requirements, as well as spatially explicit knowledge of regions and causes of high mortality, will be necessary to develop effective recommendations. However, the removal of up to 60% of the river water either upstream or in the Delta (Nichols et al. 1986) may limit any benefits of additional management actions on salmon survival. Managers should be careful to consider the survival both of salmon that use the Delta primarily as migrants and of population components that may rear in the Delta in order to promote the diversity of life histories in the FR Chinook Salmon population and the buffering benefit of the "portfolio effect" (Miller et al. 2010; Schindler et al. 2010; Carlson and Satterthwaite 2011; Sturrock et al. 2015). A priority on habitat quality within the Delta, combined with efforts to improve survival through all portions of the salmon life history, is likely to be required if this population is to persist.

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