

Title: Movement and survival of wild Chinook salmon smolts from Butte Creek during their outmigration to the ocean: comparison of a dry versus wet year

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3 **Abstract**

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

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Introduction

Balancing human demands for water with maintenance of a functioning ecosystem capable of supporting healthy Chinook Salmon populations has become a central challenge facing natural resource managers in California's Central Valley (CCV). Here, four runs of Chinook Salmon (*Oncorhynchus tshawytscha*) 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 fresh water: fall, late-fall, winter, and spring (Healey 1991). Similar to 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 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). Now, 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 are reported inconsistently in additional Sacramento River tributaries and are supplemented by stray spring-run adults from the Feather River Hatchery (Yoshiyama 2001). However, these additional stocks are believed to have been hybridizing with fall-run stocks since the 1960s due to spatial constrictions on previously separate spawning distributions created by dams (CDFG 1998). As a consequence of these various stressors, since 1999 the CCV spring-run Chinook Salmon evolutionarily significant unit (ESU) is state and federally listed as threatened (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 characterized by a wide range of size, timing, and age at which they out-migrate from their natal tributaries to the ocean (e.g., sub-yearling fry

59 and smolt, yearling; CDFG 1998). Such life history diversity has been suggested to convey a
60 stabilizing portfolio effect by providing each population the ability to buffer environmental
61 changes due to anthropogenic forcing or climate, ultimately increasing the resiliency of the
62 entire community (Hilborn et al. 2003; Greene et al. 2010, Schindler et al. 2010). As the largest
63 population of CCV spring-run Chinook Salmon, Butte Creek fish are an important source for
64 promoting diversity in the CCV Chinook Salmon community and have been the focus of
65 considerable investment in the form of population monitoring and restoration efforts. Several
66 restoration actions were implemented in the early 1990s by various state and federal agencies
67 in coordination with water interests and local stakeholders (e.g. CALFED and the U.S. Fish and
68 Wildlife Service's Final Restoration Plan for the Anadromous Fish Restoration Program (AFRP))
69 in order to restore and maintain CCV spring-run Chinook Salmon populations on a long-term
70 basis. The Lower Butte Creek Project (LBCP), for instance, was established in 1997 to improve
71 passage for protected fish species while maintaining the viability of commercial agriculture,
72 private wetlands, government lands, and other habitats (ICF Jones & Stokes 2009). Although
73 increases in returning Butte Creek spring-run Chinook adults have been observed in recent
74 years, the success of those management efforts on enhancing juvenile survival and maintaining
75 population life history diversity has yet to be determined.

76
77 Juvenile mortality during out-migration to the ocean is considered a critical phase to
78 overall population dynamics (Healy 1991; Williams 2006). Tagging and tracking juvenile Chinook
79 Salmon from their freshwater rearing habitats and through riverine systems and into the
80 marine environment can help determine survival rates and identify locations where juvenile
81 mortality is greatest during downstream migration. Acoustic tagging technology has become a
82 well-established tool in estimating movement and survival rates of CCV Chinook Salmon
83 juveniles (Perry et al. 2010; Michel et al. 2013, 2015). While these studies have mainly focused
84 on hatchery smolts that are easily captured, tagged and released in large groups, little is known
85 about the survival and movement of the remaining wild spring-run Chinook Salmon
86 populations. Assessing juvenile mortality of wild spring-run Chinook Salmon is challenging in
87 part due to the small size of these populations and the difficulty in capturing them during their

88 out-migration. However, utilizing survival data from hatchery stocks as a surrogate for wild
89 salmon survival dynamics is often criticized because the two are different in many ways
90 (Kostow 2004). Wild salmon hatch and rear in a completely different environment and face
91 many challenges in their early life that hatchery smolts are able to avoid due to hatchery
92 management and release practices (e.g. predation, water quality). In this paper we detail an
93 acoustic tagging study implemented in lower Butte Creek and extending to the Golden Gate
94 Bridge, aimed at assessing the movement and survival rates of the largest population of wild
95 CCV spring-run Chinook Salmon smolts during their out-migration to the ocean. We were
96 particularly interested in evaluating potential dissimilarities between survival through the
97 Sutter Bypass; a floodplain which has been suggested to be important rearing habitat for
98 juvenile Chinook Salmon (Garman 2013), and the lower Sacramento-San Joaquin River Delta,
99 which is considered a strongly degraded habitat (Nichols et al. 1986). Moreover, previous
100 studies have demonstrated that CCV juvenile out-migration survival can vary strongly among
101 years due to various anthropogenic and environmental factors (Baker and Morhardt 2001;
102 Brandes and McLain 2001; Michel et al. 2015). Therefore, we compared fish movement and
103 locations of high mortality during out-migration for a hydrologically dry year (2015) versus a
104 hydrologically wetter year (2016). We finally discuss the implications of our results on the long-
105 term dynamics of the Butte Creek population and the implementation of future recovery
106 actions.

107

108 <A> Methods

109

110 *Study site.*— Butte Creek is a tributary of the Sacramento River that originates at
111 Humboldt Mountain on the western slopes of the Cascade Range at an elevation of more than
112 2,100 meters (Figure 1). The Butte Creek watershed encompasses an area of about 2,900
113 square kilometers and is connected to the Sacramento River at two locations, the Butte Slough
114 Outfall Gates (BSOG) and the downstream end of the Sutter Bypass, a remnant flood basin
115 habitat (Garman 2013). Butte Creek historically entered the Sacramento River at the BSOG, but
116 is now diverted away from the Sacramento River for 40 kilometers into the Sutter Bypass

117 (Figure 1). This bypass is composed of two canals as well as the East-West Diversion weir which
118 is used to control the flow of water going into the east and west side canals of the bypass.
119 Several weirs along both canals divert water for agricultural or managed wetland uses (ICF
120 Jones & Stokes 2009). During high flow conditions, water from the Sacramento River flows into
121 the bypass through Moulton, Colusa and Tisdale weirs in order to prevent flooding of
122 downstream areas.

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

131
132 *Freshwater life history.*— CCV spring-run Chinook Salmon demonstrate a unique diversity
133 in life-history among the stocks of California Chinook Salmon. Adult spring-run Chinook Salmon
134 ascend un-dammed tributaries to elevations between 300 -1,500 meters when the spring
135 freshet allows access, and hold in deep pools over summer before spawning in the fall. CCV
136 spring-run juveniles emerge from the gravel between November and March, depending on
137 water temperatures, and spend 3 to 15 months in fresh water before emigrating to the ocean
138 (CDFG 1998). Spring-run Chinook Salmon juveniles exhibit a wide variety of rearing and out-
139 migration strategies. They can either migrate out of the spawning habitat soon after emergence
140 as fry during high flows in the winter, rear in their natal habitat and out-migrate as smolts
141 during the spring, or remain in the stream for an entire year and out-migrate the following fall,
142 winter, or spring as yearlings (CDFG 1998). Juveniles out-migrating from Butte Creek are
143 assumed to be a mix of fry and smolts, with very few remaining in Butte Creek as yearlings
144 (Clint Garman, California Department of Fish and Wildlife, Personal Communication). Smolt

145 emigration peaks in April and May, but can extend from February through June (Ward et al.
146 2004a, 2004b, 2004c).

147

148 *Acoustic tagging and receivers.*— We used the Juvenile Salmon Acoustic Telemetry
149 System (JSATS; McMichael et al. 2010) to track the movements and estimate survival of
150 migrating wild spring-run Chinook Salmon smolts from Butte Creek. The transmitters (tags)
151 were manufactured by Advanced Telemetry Systems (ATS), JSATS model SS300, with a tag
152 weight in air of 300 mg and size of 10.7 x 5.0 x 2.8 mm. These tags emit a uniquely coded signal
153 at 416.7 kHz at a pulse rate of about 5 seconds, and have an expected life of 32 days at these
154 settings. The JSATS tag we used weighed 300 mg which allowed us to tag juvenile Chinook
155 Salmon that weighed at least 6.0 g (approximate fork length = 80 mm) which resulted in tag
156 burdens $\leq 5\%$. Laboratory studies comparing growth and survival between acoustically tagged
157 and untagged juvenile salmon have suggested that tag burdens of less than 5% do not
158 significantly affect acoustically tagged fish compared to untagged controls (Ammann et al.
159 2013; Brown et al. 2010).

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

167 We collected fish using a 2.44 m diameter rotary screw trap (RST) installed at Weir 2 in
168 the Sutter Bypass. We chose Weir 2 as the trapping site to ensure that fish collected and tagged
169 were actively migrating downstream, since it is relatively low in the Butte Creek system.
170 Additionally, this downstream site ensured that the 30 day acoustic tag battery life was utilized
171 efficiently, allowing movement through the Sutter Bypass, Sacramento River, Delta and San
172 Francisco Bay to be recorded. The RST was operated continuously (24 hours per day), and was

173 emptied of fish each morning. All salmonids were measured (fork length (FL) in mm) and fish >
174 80 mm were implanted with an acoustic tag.

175 On the river bank adjacent to the RST, we set up a shaded work station to surgically
176 implant tags before the sun was overhead and temperatures became too warm. The same
177 surgeon implanted tags into the coelom of the fish for both years of the study. Fish were
178 anesthetized (using 90 mg/l tricaine methanesulfonate), weighed, measured, photographed,
179 then placed ventral side up in a padded V-channel. During surgery we irrigated the fish's gills
180 with water containing a maintenance dose of anesthetic (30 mg/l). We made an incision on the
181 ventral side of the fish between the pelvic girdle and pectoral fins with a Sharpoint 3 mm 15°
182 stabbing blade scalpel. The incision was 6–8 mm long and 3 mm off the ventral midline. We
183 inserted the tag into the coelom and oriented it so the tag transducer was posterior. We closed
184 the incision with a single suture of 6-0 Polydioxanone absorbable monofilament and tied with a
185 double-wrapped square knot (i.e. surgeon's knot). We placed tagged fish into a recovery bucket
186 and monitored until they resumed their normal swimming behavior. After surgery, we held fish
187 in holding pens just below Weir 2 for 12 hours before release at 22:00 hours (Pacific Standard
188 Time), primarily to ensure the fish were fully recovered, but also because juvenile salmon tend
189 to migrate at night (Chapman et al. 2013).

190 We also collected tissue samples from all tagged fish to identify their origin by using
191 Genetic Stock Identification (GSI; Clemento et al. 2014). For each fish, we calculated the
192 posterior probability that it originated from a given stock, and assigned the fish to the stock
193 with highest posterior probability. Based on Satterthwaite et al. (2014) and communication
194 with John C. Garza (NMFS-SWFSC), we considered assignments of fish with a maximum
195 posterior probability exceeding 75% as robust stock assignments for this study. We did not
196 assign a stock to fish with posterior probability less than 75%. The genetic analysis was
197 performed at the Southwest Fisheries Science Center in Santa Cruz, CA.

198
199 *Data analysis.*— Tagged fish either completed their migration out of the study reaches or
200 completed a partial migration and died before exiting the detection arrays. We used a spatial
201 form of the Cormack-Jolly-Seber model (CJS; Cormack 1964; Jolly 1965; Seber 1986) to estimate

202 reach-specific survival rates (ϕ_i) and detection probability (p_i). We considered the initial tag
203 location as a “mark” and subsequent detections at downstream receivers as a “recapture”. We
204 used the method of maximum-likelihood to estimate survival and detection probabilities along
205 with their 95% confidence intervals (Lebreton et al. 1992).

206 For consistency between tagging years and because of the low number of fish migrating
207 through the Delta, we selected a subset of receiver locations for the survival analysis, thus
208 creating a total of 9 separate reaches for which survival and detection probability were
209 estimated (Table 1; Figure 1). Furthermore, because the length of reaches along the migratory
210 path is not identical, we standardized survival estimates per 10 km in order to allow inter-reach
211 survival comparisons. Finally, we estimated regional (Sutter Bypass, Sacramento River, Delta
212 and Bay) and overall (from the release site to the Golden Gate Bridge) survival for both years,
213 using methodology described in Michel et al. (2015).

214 In order to evaluate year and location effects on out-migrating smolt survival and
215 detection probabilities, we compared the constant model (i.e. constant survival and detection
216 rates through space and time) to models including parameters allowing year and/or reach to
217 vary (e.g. $\sim reach * year$; see Table A1 for list of models). Because it is impossible to measure, or
218 estimate, all potential factors that influence salmon survival, we hypothesized that the fully
219 parameterized model (full model) that included year and reach as factors would have the best
220 fit to the data and provide us with the best estimates of reach survival by year. We therefore
221 used this model to generate reach-specific, regional, and overall survival estimates. However, in
222 order to gain a better understanding of the underlying mortality mechanisms, we also looked at
223 models that included fish characteristics (i.e. fish length and Fulton’s condition factor (K)), and
224 environmental variables (i.e. Sutter Bypass flow and water temperature at release). We used
225 flow data from Butte Slough near Meridian (CDEC station BSL, [http://cdec.water.ca.gov/cgi-
226 progs/stationInfo?station_id=BSL](http://cdec.water.ca.gov/cgi-progs/stationInfo?station_id=BSL)) located downstream of BSOG (closest flow gauge to the
227 Sutter Bypass release site), and temperature data from the Butte1 acoustic receivers (post
228 calibrated at the Southwest Fisheries Science Center, Santa Cruz, CA). All continuous covariates
229 were standardized by subtracting the mean and dividing by the standard deviation.

230 To be able to partition the influence of each covariate of interest on the survival
231 variability through time, we used the base model $\phi(\sim reach)$ and included covariates in an
232 additive framework (see Table 3 for list of models). We deliberately excluded the *year* variable
233 from all covariate models because the inclusion of this variable would have accounted for the
234 majority of interannual variability in survival, and therefore masking any influence of the
235 individual/environmental covariates and providing no information on mechanisms. However,
236 we compared the $\phi(\sim reach + year)$ model to the covariates models in order to assess how much
237 interannual variability explained by the *year* variable could be explained by these covariates
238 instead. Once the relative importance of covariates had been determined from the model
239 selection exercise, we extracted the standardized β parameter coefficients for these covariates
240 to identify the relationship direction between those covariates and fish survival. These β
241 parameter coefficients allow for comparison of the influence of covariates between models,
242 and can be interpreted as the predicted change in survival for 1 standard deviation increase in
243 the covariate. We used the Akaike's Information Criterion corrected for small sample sizes
244 (AICc) for model selection (Akaike 1973; Burnham and Anderson 2002). We performed this
245 analysis using the RMark package (Laake 2013) within program R (version 3.1.1.; R
246 Development Core Team 2013).

247 Finally, in order to obtain additional information on the movements of the tagged fish
248 during their out-migration and relate that to their survival, we estimated the average migration
249 rates for the different regions along the migration pathway. We did this by considering the
250 movement rate of the fish between its last detection in one reach to its first detection at the
251 next reach.

252

253 <A> Results

254 In 2015, we deployed the RST on April 1st and tagged fished for 11 days between April
255 6th and April 16th. In that period of time we tagged and released a total of 141 smolts. In 2016
256 we started tagging on April 14th, and were able to tag and release our target of 200 juveniles by
257 April 18th. In 2015 the mean fork length was 104.75 mm and the mean weight was 13.47 g,
258 whereas in 2016 the average fish tagged was 110.02 mm and 16.68 g (Table 2).

259 Genetic assignment

260 The genetic analysis suggests the smolts tagged in the Sutter Bypass were a mix of
261 CCV fall-run and spring-run origin. In 2015, 6 smolts were confidently identified as CCV fall-run
262 fish and 124 smolts as CCV spring-run fish while in 2016 a higher proportion of fish tagged were
263 genetically classified as CCV fall-run fish (121 fall-run versus 65 spring-run; Table 2). It also
264 appears that, although fall-run smolts were slightly larger in both years, fall-run and spring-run
265 smolt exhibit similar size range (Table 2; Figure A1). We performed an F-test (var.test function
266 in R) to compare fall-run versus spring-run smolt length variances for each year and found no
267 statistical difference between spring-run and fall-run fish length distributions (2015 p-value=
268 0.1489, 2016 p-value= 0.9086). This implies that no length cutoff could be robustly applied to
269 these two runs, and that visual distinction based on length is problematic. Therefore, although
270 not all the fish tagged were spring-run Chinook Salmon, because of their overlapping size range
271 and migration timing we assumed that fall-run juveniles were a good proxy for the purpose of
272 this study.

273 The rotary screw trap used in this study was located below Butte Creek fall-run
274 spawning habitat, it is therefore likely that many of the captured fall-run smolts were wild Butte
275 Creek fall-run Chinook Salmon. In addition, because Sacramento River water spilled into the
276 lower Butte Creek watershed via Moulton, Colusa and Tisdale Weirs several times before the
277 tagging experiment took place, it is also possible that some of the tagged fall-run fish originated
278 from the mainstem Sacramento River or another tributary and used the Sutter Bypass as a
279 migratory corridor.

280

281 Hydrological conditions

282 The 2015 water year, California experienced an extreme drought that was classified as
283 “critical”, while the 2016 water year was considered “below normal” by the California
284 Department of Water Resources (DWR; CDEC data). While 2016 was not considered as a wet
285 year, a series of rain events, leading to the flooding of the Sutter Bypass, occurred during the
286 CCV spring-run smolt out-migration period. Therefore, the hydrological conditions experienced
287 by the migrating smolts changed considerably between the two years of the study. In the spring

288 of 2015, likely because of very dry winter conditions, the flow recorded in the lower Butte
289 Creek system had already dropped substantially and stayed very low during the entire study
290 period, averaging $4.03 \text{ m}^3\text{s}^{-1}$ at BSL (Figure 2A). In 2016 we tagged and released fish after a
291 flood event, and although the flow decreased throughout the study period it remained
292 substantially above the maximum flow value recorded during the same period in 2015. The
293 2016 BSL flow averaged $12.91 \text{ m}^3\text{s}^{-1}$. The same pattern was observed in the Sacramento River
294 reach, with an average flow of $160.29 \text{ m}^3\text{s}^{-1}$ in 2015 and $381.53 \text{ m}^3\text{s}^{-1}$ in 2016 (CDEC station at
295 Verona, http://cdec.water.ca.gov/cgi-progs/stationInfo?station_id=VON; Figure 2A).

296 In 2015, water temperatures in the Sutter Bypass and the Sacramento River increased
297 throughout the tagging experiment (Figure 2B). Water temperature at the Butte1 receiver
298 peaked at 18.5°C during the tagging period, then kept increasing and reached 21°C by the end
299 of April. Similarly, water temperature in the Sacramento River increased from 14°C to 22°C
300 during the month of April 2015 (CDEC station at Verona, [http://cdec.water.ca.gov/cgi-](http://cdec.water.ca.gov/cgi-progs/stationInfo?station_id=VON)
301 [progs/stationInfo?station_id=VON](http://cdec.water.ca.gov/cgi-progs/stationInfo?station_id=VON)). In 2016, the Sutter Bypass water temperature, during the
302 tagging period, varied between 18°C and 19.5°C . The peak water temperature at the Butte1
303 receiver was 21°C on April 21, 2016. The Sacramento River water temperature in 2016 slowly
304 increased throughout the month of April but never exceeded 18°C .

305 306 Fish movement

307 In 2015, 27 of the 141 tagged fish (19.1%) were detected entering the Sacramento River,
308 14 fish (9.9%) were detected entering the Delta and only 1 fish (0.7%) was detected at the
309 Golden Gate Bridge. In 2016, 71 of the 200 tagged fish (35.5%) were detected entering the
310 Sacramento River, 49 fish (24.5%) were detected in the Delta and 4 fish (2%) were detected at
311 the Golden Gate Bridge. Although some variability in movement rates among fish was observed
312 each year, especially in the Sacramento River, most of the tagged smolts moved quickly
313 throughout the migration corridor (Figure 3). On average, it took fish 6 days in 2015 versus 2
314 days in 2016 to transit the Sutter Bypass, and 2 days in 2015 versus 1 day in 2016 to transit the
315 Sacramento River (Table 4). The single fish that survived to the Golden Gate Bridge in 2015
316 migrated through the Delta in less than 5 days and migrated from the release site to the Pacific

317 Ocean in 27 days. In 2016, it took an average of 5 days to migrate through the Delta, and 18
318 days to migrate from release site to the ocean (Table 4).

319 Tagged fish migration rates were higher in the Sacramento River compared to the Sutter
320 Bypass and Delta in both years (Figure 3; Table 4). Based on a Tukey test (TukeyHSD function in
321 R), migration rate in 2016 was significantly higher than in 2015 in the Sacramento River and the
322 Sutter Bypass (Sutter Bypass p-value < 0.001, and Sacramento River p-value < 0.001); migration
323 rates were significantly higher in the Sacramento River compared to the Sutter Bypass in both
324 years (2015 p-value = 0.0, and 2016 p-value = 0.0). We calculated a mean migration rate of
325 10.24 kilometers per day (km d^{-1}) in the Sutter Bypass and 33.21 km d^{-1} in the Sacramento River
326 in 2015 versus estimates of 22.13 km d^{-1} and 56.83 km d^{-1} respectively in 2016 (Table 4). Since
327 only one fish was successfully detected at Benicia (the Delta exit location) and the Golden Gate
328 Bridge in 2015, it was not possible to estimate Delta and Bay travel rate statistics for that year.
329 However, more fish were detected in 2016 and the average movement rate through the Delta
330 was estimated at 22.48 km d^{-1} .

331
332 Survival estimates

333 The full model, strongly supported as the single best model ($\text{AICc} = 1383.726$, and ΔAICc
334 of the second best model greater than 8; Table A1), includes survival as a function of *reach* *
335 *year*, and a constant detection probability. This suggests that outmigrant smolt survival varies
336 by location and year. Additionally, although the best model supported a constant detection
337 probability, the spatially-explicit models (i.e. $p(\sim\text{reach})$) suggested that detection rates
338 throughout the migratory corridor were consistently high, ranging from 0.851 to 1. For all
339 model exercises presented in this paper, detection probability was therefore set to be constant
340 through space and time, and was estimated to be 0.993.

341 After including individual and environmental variables in the analysis, the $\phi(\sim\text{reach} +$
342 *year*) model was selected as the best model, emphasizing the strong year effect on smolts
343 survival (Table 3). The Sutter Bypass flow at release covariate model was substantially better
344 supported ($\Delta\text{AICc} > 3$) over the base model $\phi(\sim\text{reach})$. Furthermore, it shared similar support
345 ($\Delta\text{AICc} < 3$) to the $\phi(\sim\text{reach} + \text{year})$ model (which benefitted from a free parameter), suggesting

346 that the flow model explained much of the variation in interannual survival. The model
347 including fish length also had substantial support over the base model ($\Delta AICc < 6$), and
348 suggested a positive influence of fish length on survival. However, the models including water
349 temperature at release and condition factor (K) were not better supported than the base
350 model, suggesting that these covariates had no detectable influence on survival.

351
352 We used the full model (i.e. $\phi(\sim reach * year)$) to estimate survival per 10km, per region
353 and cumulatively. Overall, survival through the entire migratory corridor (from the release site
354 to the Golden Gate Bridge) was better in 2016 than in 2015 (3.0% versus 0.7%; Table 4). At the
355 regional level comparing 2015 to 2016, survival increased in the Sutter Bypass from 19.1% to
356 35.5%, in the Sacramento River from 51.8% to 69.0%, and in the Delta from 7.1% to 12.2%
357 (Figure 4; Table 4). For both years, the highest regional survival was observed in the lower
358 Sacramento River, while the lowest estimate was for the Delta region. However, the length of
359 each region varied considerably (the Delta region is about twice as long as the Sutter Bypass
360 and Sacramento River regions; Table 1), and survival often decreases proportionally with
361 increasing region length.

362 Per 10km survival rates varied dramatically between reaches within the Sutter Bypass,
363 Sacramento River and Delta, and some similar survival patterns were observed among years
364 (Figure 5). In the Sutter Bypass, relatively low survival was observed between the release site
365 and the first receiver (Weir2_RST – Butte 1 in Table 1; 27.1% in 2015) and between Butte3 and
366 Butte5 receivers (39.3% in 2015 and 65.1% in 2016). Survival was higher in the other reaches of
367 the Sutter Bypass, ranging from 72.5% to 94.0% in 2015 and 79.8% to 84.7% in 2016. In the
368 Sacramento River for 2015, survival decreased from the first reach (Butte6 - I80_Br) to the
369 second reach (I80_Br – Freeport), whereas it increased in 2016 (91.9% and 82.5% in 2015, and
370 92.6% and 95.1% in 2016). Survival in the Delta was lower than in the Sacramento River for
371 both years (76.8% in 2015 and 81.1% in 2016). Finally, due to the low number of tagged fish
372 surviving to the Golden Gate Bridge (n=1 in 2015, and n=4 in 2016) the 2015 survival rate in the
373 San Francisco Bay could not be estimated, and the 2016 San Francisco Bay survival rate should
374 be used for discussion purpose only.

375

376 <A> Discussion

377 This is the first study to investigate the survival and migration rates of wild Butte Creek
378 spring-run Chinook Salmon smolts during their out-migration to the Pacific Ocean. The acoustic
379 telemetry system used in this study had high detection probabilities greater than 85% at all
380 receiver locations. The mark-recapture models provided estimates of survival at fine spatial
381 scales during a dry and wet water year. We showed that Chinook Salmon smolts migrated
382 faster throughout their migratory corridor in 2016 (wet year) than in 2015 (dry year). This
383 difference is likely due to higher flow velocities, both in the Sutter Bypass and in the
384 Sacramento River in 2016 compared to 2015. The mean migration rate to the ocean (Golden
385 Gate Bridge) was 33.7 km d^{-1} for 2016 which is faster than total mean migration rate for
386 Sacramento River late-fall Chinook Salmon ($14.3\text{-}23.5 \text{ km d}^{-1}$, 2007-2009) reported by Michel et
387 al (2013).

388 Survival to the ocean was also higher in 2016 than in 2015 (0.7% in 2015 and 3.0% in
389 2016; Table 4). However, these survival rates are lower than most of the survival estimates
390 obtained by Michel et al. (2015) for acoustic tagged late-fall run Chinook Salmon yearlings
391 (survival per year ranged from 2.8% to 15.7%). This survival is also low in comparison to the
392 2015 and 2016 survivals found by Faulkner et al. (2016; 2017) for populations of wild
393 spring/summer Chinook Salmon from the Snake River (a tributary of the Columbia River)
394 migrating through a much longer watershed than in our study (mean survival rate of 38.3% in
395 2015 and 33.0% in 2016 through the entire 910km watershed). However, the fish tracked in
396 these two studies were larger in size than the fish tagged in the Sutter Bypass, and we have
397 shown that fish length influences out-migrating fish survival. Similar to our study, Notch (2017)
398 found very poor survival (0.3%) to the ocean for acoustic-tagged wild caught smolts from Mill
399 Creek, an upper Sacramento River tributary. This suggests that out-migration survival of spring
400 migrating wild Chinook Salmon smolts can be very low, and may be a bottleneck to recovery of
401 these populations.

402

403 In the Sutter Bypass there were two reaches with substantially lower survival than the
404 other reaches; from the release site to Butte1 during 2015, and between receivers Butte3 and
405 Butte5 in both years. These two reaches had the lowest survival per 10 km of all reaches in
406 2015, and the Butte3 – Butte5 reach had the lowest survival per 10 km of all reaches in 2016.
407 Common to both these reaches are in-river diversion weir structures; at the start of Weir2_RST
408 – Butte1 reach and in the middle of Butte3 – Butte5 reach. Studies have shown that Striped
409 Bass (*Morone saxatilis*) and Sacramento Pikeminnow (*Ptychocheilus grandis*) – both considered
410 major predators of juvenile salmon in the CCV – tend to congregate below in-river diversion
411 weir and are effective at predating on disoriented salmon smolts that pass over these
412 structures (Brown and Moyle 1981; Tucker et al. 2003; Sabal et al. 2016). Various non-native
413 salmon predator species, such as Largemouth Bass (*Micropterus salmoides*), Striped Bass,
414 Channel Catfish (*Ictalurus punctatus*), and native predators, such as Sacramento Pikeminnow
415 have been reported in the lower Butte Creek watershed (ICF Jones & Stokes. 2009). These
416 predators were also caught in the RST during this study in both years. If predators are generally
417 concentrated below these diversion weirs, and furthermore if their concentration was
418 enhanced during the low flow conditions in 2015, this may explain the lower survival of juvenile
419 Chinook Salmon in these two reaches.

420 Similarly, predation could play an important role in the Sacramento River and Delta
421 reaches as spring-run smolt out-migration timing overlaps with the Striped Bass spawning
422 season. Adult Striped Bass migrate into the San Joaquin and Sacramento Rivers in large
423 numbers in the spring to spawn and are likely to prey on juvenile outmigrants during that time
424 (Turner 1976; Tucker et al. 2003). The increase in survival observed in 2016 in the Sutter Bypass
425 and the Sacramento River corroborates with the assumption that an increase in flow induces an
426 increase of fish transport as well as a potential increase in turbidity, which could both reduce
427 spatio-temporal exposure to predation (Gregory and Levings 1998; Michel et al. 2013 and
428 references therein). The higher flow observed in the Sacramento River in comparison to the
429 Sutter Bypass could explain the relatively higher survival and faster migration rate observed in
430 this region.

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

440
441 It is important to note that our study focused on a single rearing and out-migration life
442 history strategy where spring- and fall-run juveniles leave the tributaries as smolts. The results
443 of this study might not be representative of other life history strategies where juveniles out-
444 migrate as fry, parr and yearlings. Smolts evolved to out-migrate with spring snowmelt freshets
445 during April and May, however, various human-induced and environmental constraints such as
446 the homogenization of the hydrology due to dams, elevated water temperature associated with
447 dams, and water diversions in the Delta peaking during the spring are now likely diminishing
448 the benefits of this life history strategy and leading to lower out-migration survival. Given these
449 constraints, earlier out-migration life histories (fry/parr) might exhibit higher relative survival.
450 However, due to their small size, which precludes acoustic tagging, very little is known about
451 these life histories. Studies that aim to quantify the proportion of returning adults with the
452 different out-migration life histories (such as in Sturrock et al. (2015)) would be needed to put
453 the smolt out-migration life history studied here in broader context.

454
455 Our results have strong implications for the management of threatened CCV spring-run
456 Chinook Salmon populations. Butte Creek currently supports the most abundant population of
457 spring-run Chinook Salmon in the CCV and is a key component for the diversity and viability of
458 the spring-run stock. The Sutter Bypass has been designated by NOAA Fisheries as a critical
459 habitat for CCV spring-run Chinook Salmon and is considered an important rearing habitat and

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

471

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Table 1. Study reach location, distance from Golden Gate (rkm) and length (km).

Region	Reach	Distance from ocean (rkm)	Reach length (km)	Region length (km)
Sutter Bypass	Weir2_RST – Butte1	249.54 – 249.05	0.49	43.06
Sutter Bypass	Butte1 – Butte2	249.05 – 238.46	10.59	
Sutter Bypass	Butte2 – Butte3	238.46 – 226.46	12.00	
Sutter Bypass	Butte3 – Butte5	226.46 – 216.98	9.48	
Sutter Bypass	Butte5 – Butte6	216.98 – 206.48	10.50	
Sacramento River	Butte6 – I80 Bridge	206.48 – 170.74	35.74	54.05
Sacramento River	I80 Bridge - Freeport	170.74 – 152.43	18.31	
Delta	Freeport – Benicia	152.43 – 52.04	100.39	100.39
Bay	Benicia – Golden Gate	52.04 – 0.80	51.24	51.24

Table 2. Weight (g) and Fork length (mm) of juvenile Chinook Salmon captured, tagged and released at the Sutter Bypass RST in 2015 and 2016. Group assignment is shown only for fish with genetic stock assignment posterior probability exceeding 75%. n = sample size; SD = standard deviation.

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

Table 3. Comparison of $\sim reach + year$ survival model versus models including *reach* and individual/environmental covariates (fish length, condition factor (*K*), Sutter Bypass flow and water temperature at release). The detection probability (p) is constant for each model. Npar = number of model parameters; AICc = AIC score corrected for small sample size; $\Delta AICc$ = distance from the most parsimonious model; w = Akaike weights. Models are ordered from lowest to highest AICc. Lower AICc scores indicate greater relative model parsimony. β parameter estimates are shown for the two covariate models with substantial support over the reach only model.

Model	Npar	AICc	$\Delta AICc$	β coefficient
$\phi(\sim reach + year) p(\sim 1)$	11	1394.074	0	
$\phi(\sim reach + ReleaseFlow) p(\sim 1)$	11	1396.929	2.85	0.24
$\phi(\sim reach + Fish Length) p(\sim 1)$	11	1402.226	8.15	0.17
$\phi(\sim reach + ReleaseTemp) p(\sim 1)$	11	1404.477	10.40	
$\phi(\sim reach) p(\sim 1)$	10	1405.719	11.64	
$\phi(\sim reach + K) p(\sim 1)$	11	1406.765	12.69	

Table 4. Overall and per region percent survival, mean migration rate (km d^{-1}) and mean migration time (d), along with their standard error (SE) and standard deviation (SD), for juvenile Chinook Salmon tagged each year. NA = Not Applicable.

Year	Region	% Survival \pm SE	Mean migration rate (km d^{-1}) \pm SD	Mean migration time (d) \pm SD
2015	All	0.7 \pm 0.7	NA	NA
	Sutter Bypass	19.1 \pm 3.3	10.24 \pm 4.61	5.75 \pm 4.28
	Sacramento River	51.8 \pm 9.6	33.21 \pm 14.31	1.88 \pm 0.73
	Delta	7.1 \pm 6.9	NA	NA
2016	All	3.0 \pm 1.2	33.69 \pm 15.32	18.44 \pm 3.93
	Sutter Bypass	35.5 \pm 3.4	22.13 \pm 6.21	2.15 \pm 0.81
	Sacramento River	69.0 \pm 5.5	56.83 \pm 16.26	1.09 \pm 0.57

1 Figure captions

2

3 Figure 1. Map of the California's Central Valley showing the different regions considered in the
4 study, the release and receivers location.

5

6 Figure 2. A. Mean daily flow in April of 2015 and 2016 from the Sacramento River (Verona
7 station: http://cdec.water.ca.gov/cgi-progs/stationInfo?station_id=VON), and Sutter Bypass
8 (BSL station: http://cdec.water.ca.gov/cgi-progs/staMeta?station_id=BSL). B. Mean daily water
9 temperature during April 2015 and 2016 from the Sacramento River (Verona station:
10 http://cdec.water.ca.gov/cgi-progs/stationInfo?station_id=VON), and Sutter Bypass (Butte1
11 site, ATS receiver thermistor). The shaded rectangles indicate tagging and release time period in
12 Sutter Bypass for 2015 in red and 2016 in blue.

13

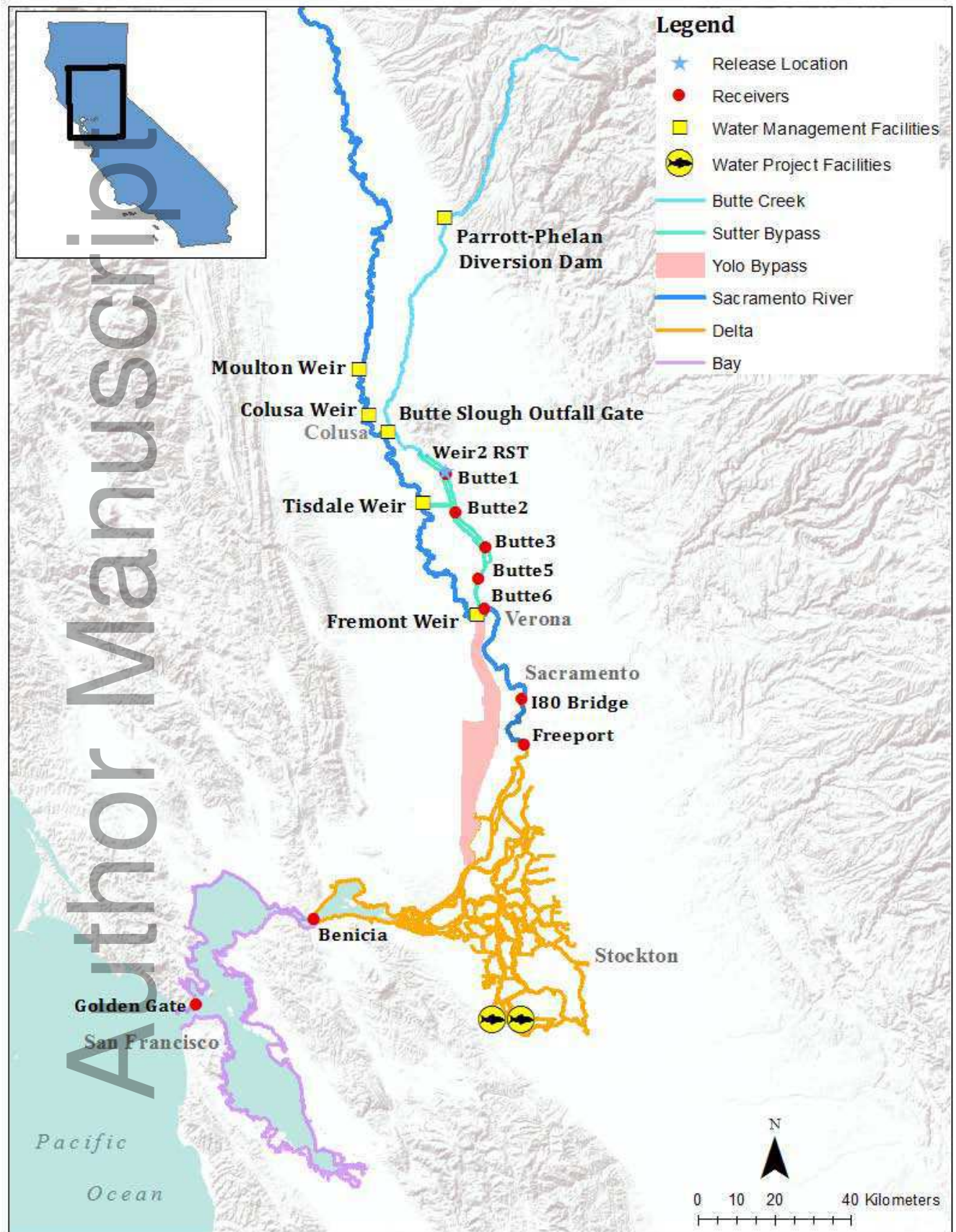
14 Figure 3. Boxplot of per year region movement rates (km d^{-1}). The horizontal bold line
15 represents the median value and the vertical whiskers represent the 95% percentiles. The dots
16 are extreme values.

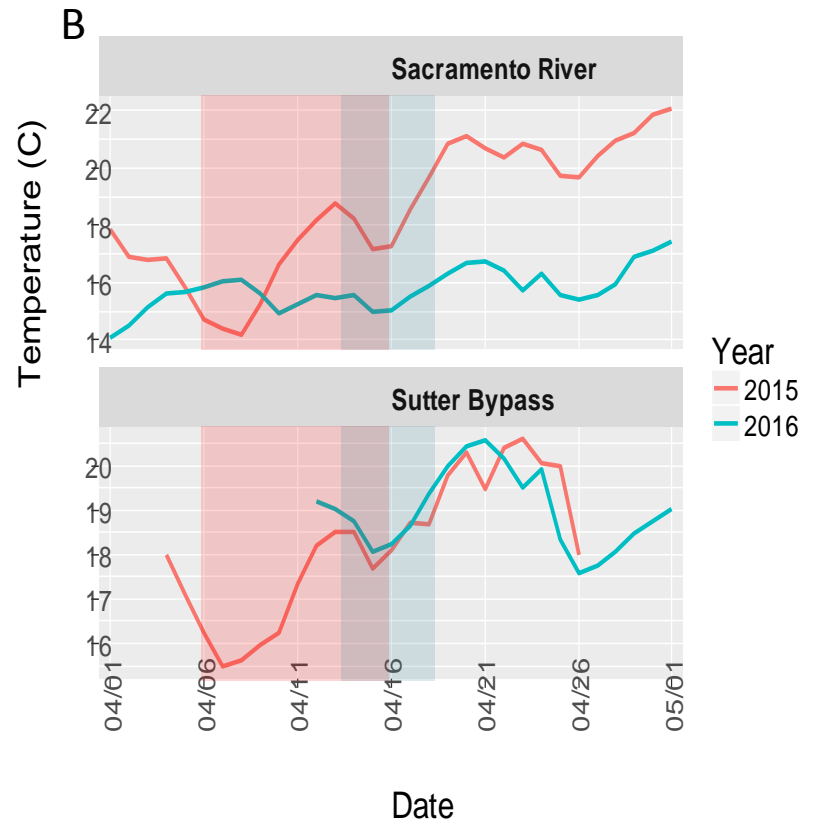
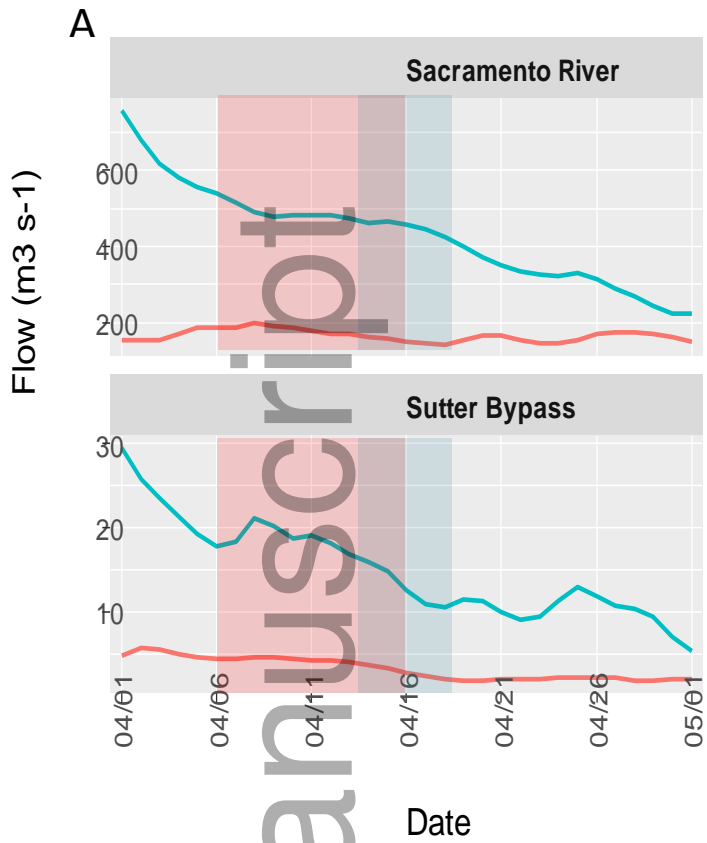
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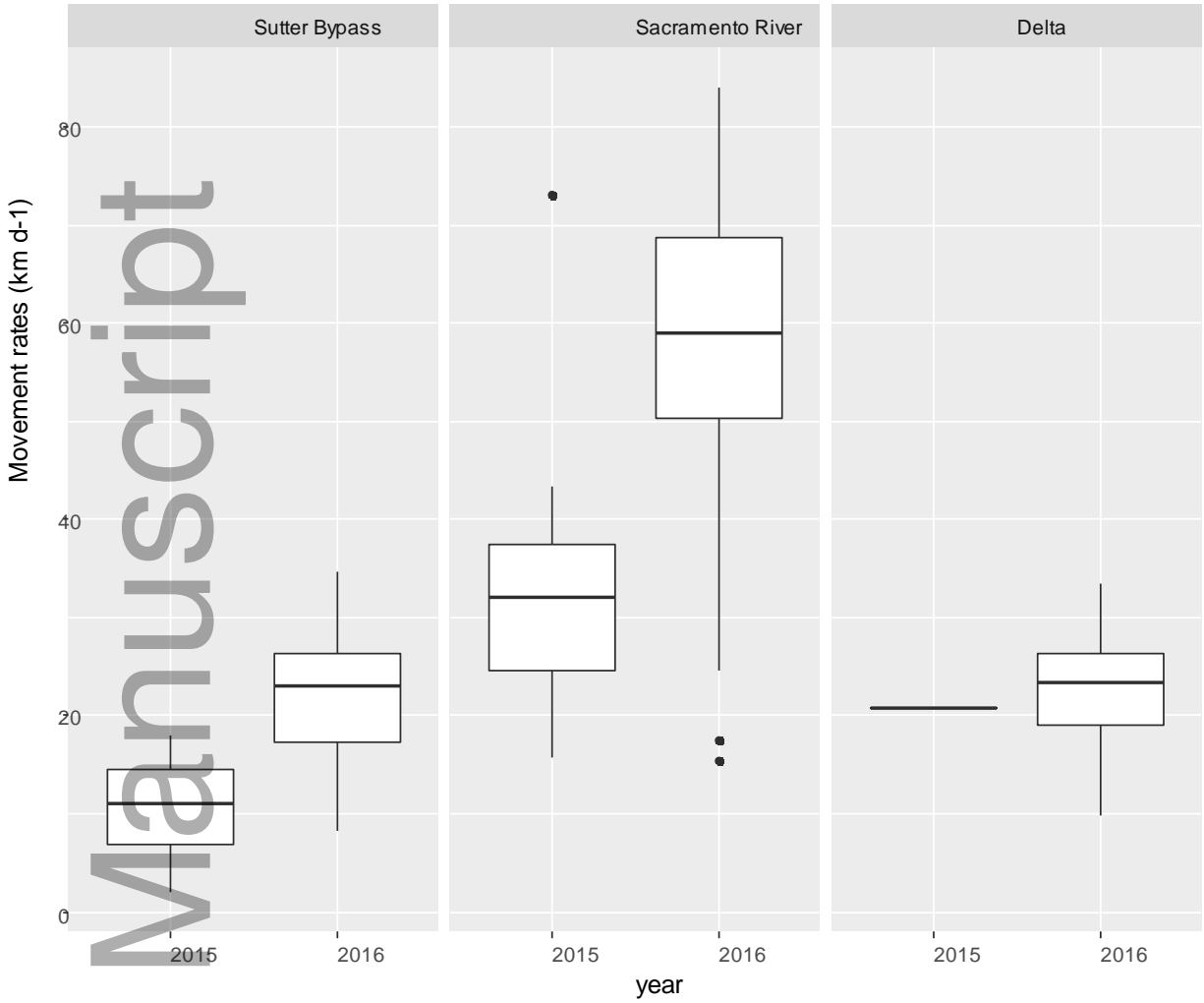
18 Figure 4. 2015 and 2016 region survival rates with their lower and upper 95% confidence limits.

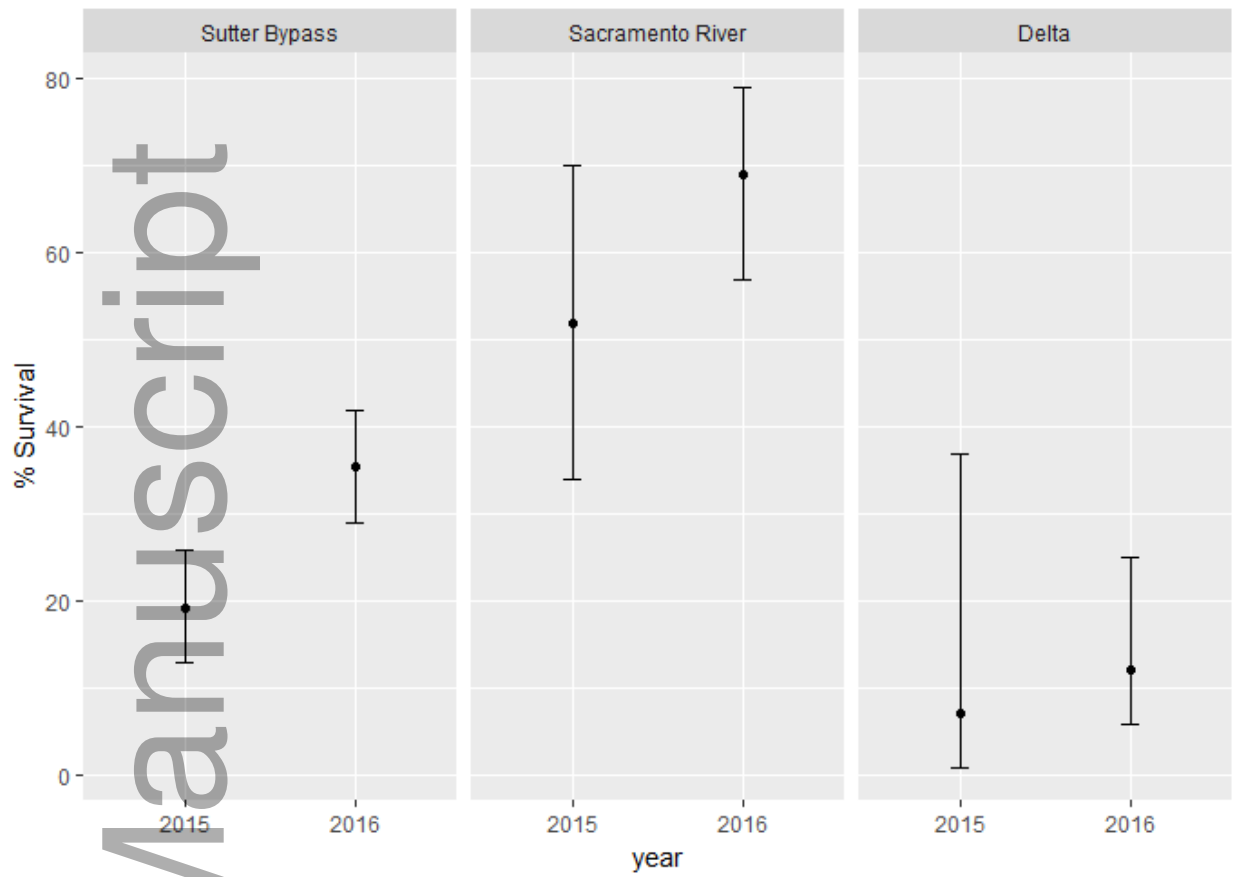
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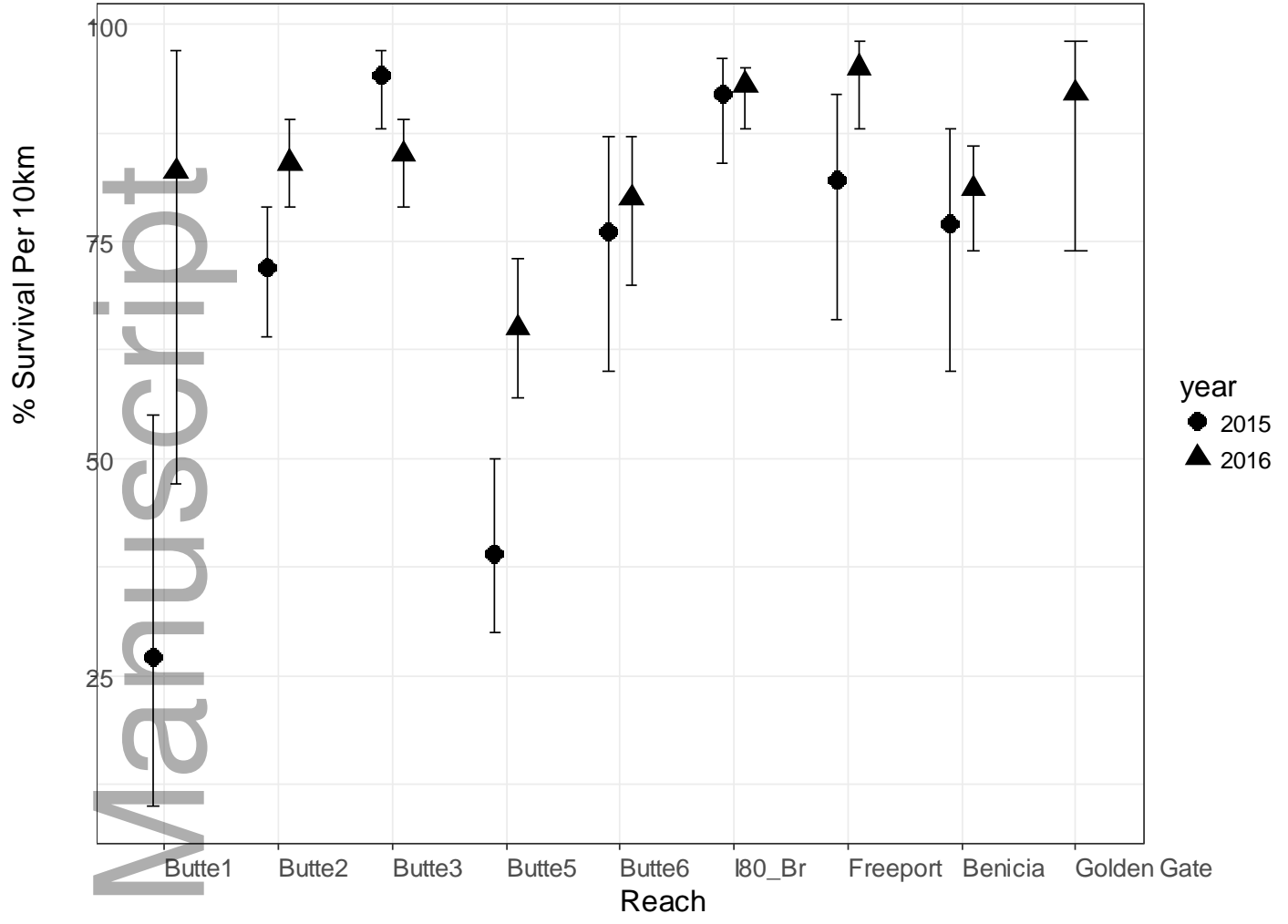
20 Figure 5. 2015 and 2016 reach specific per 10km survival rate estimates along with their lower
21 and upper 95% confidence limits.











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