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Publication Date

2022

Peer reviewed|Thesis/dissertation

Investigation of a Mortality Hotspot for Emigrating Chinook Salmon Smolts in the
California Delta

By

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THESIS

Submitted in partial satisfaction of the requirements for the degree of

MASTER OF SCIENCE

in

ANIMAL BIOLOGY

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

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2022

Acknowledgements

My husband, Quinn, thank you for your endless support, patience, and encouragement throughout my whole academic career. Without you I would not have been able to succeed in this degree. To my parents, Laurie and Gil, thank you for your persistence and support pushing me to pursue my goals in life especially with my degree. Additionally, I would like to thank Rebecca Buchanan for her extensive guidance on the statistical analysis of my thesis. Wilson Xiong for his countless hours of field help and comradery, especially on difficult days. Dennis Cocherell for his years of mentorship and selfless assistance. Gabriel Singer, Colby Hause and Scott Colborne for their assistance with the analysis and guidance through writing. David Ayers and Jesse Schroeder for providing tidal data for the study system. Trinh Nguyen for coding tips, draft reviews, friendship, and mentorship.

Abstract

Salmon are socio-ecologically important fishes distributed across the Pacific rim, and multiple ecologically significant units are declining in the Sacramento-San Joaquin River Delta of California. Available data suggests that spring-run smolt survival from the upper river in San Joaquin River restoration area (>270 rkm) to the California Delta (<160 rkm) is consistently low. Additionally, limited information from previous acoustic telemetry studies suggest that Franks Tract, a 1429 ha flooded island, is a potential mortality hotspot for outmigrating smolts. During Winter/Spring 2020, we conducted a series of targeted acoustic telemetry and tethering experiments to better understand salmon entrainment into Franks Tract as well as overall survival patterns. Telemetry studies investigating broad scale emigration patterns involved surgical tagging and release of 796 juvenile spring-run Chinook Salmon (*Oncorhynchus tshawytscha*) with JSATs acoustic transmitters. Tagged fish were distributed between three releases: an upper (n = 350) and a lower river (n = 348) release in the San Joaquin River, and an additional 98 smolts released directly into Franks Tract. The third release was conducted to investigate survival and emigration potential from the area. Provisional telemetry results suggest poor outmigration survival from all three release groups (<1% to ocean entry), but at least some (n = 2) fish released in Franks Tract did survive to Pacific Ocean entry (Benicia Bridge, 52 rkm). We also conducted a series of tethering experiments to contextualize relative predation risk of smolts within different submerged aquatic vegetation (SAV) coverage, water depth, and tidal movement in Franks Tract. Tethering results suggest that relative predation risk was moderately high over the deployment time (10.5% over 2 hours). Further, high- versus low-vegetation coverage had no effect on relative predation risk, nor did water depth. Tidal movement did have an effect on relative predation risk, with a hazard ratio for predation of 4.96 during ebb tides. Combined, our data supports the hypothesis that Franks Tract is a mortality hotspot for juvenile salmon, at least during the period studied here. Future telemetry and tethering studies may be essential for disentangling the ecology of declining salmon runs and investigating effectiveness of various management activities aimed at increasing juvenile survivorship, especially within tidal lake habitats.

Introduction

With environments rapidly changing, fishes like salmonids are unable to adapt quick enough to survive (Moyle et al. 2017, Yoshiyama et al. 2001). In spite of the portfolio effect that should protect salmonid species, there are multiple ecologically significant units (ESUs) threatened by the rapidly changing environments. Anadromous salmonids rely on freshwater as essential habitat for a significant portion of their life history (Sass et al. 2017, Kocik et al. 2022). Yet freshwater habitats, known to exhibit low resilience to rapid environmental change, quickly become unsuitable for salmon, e.g., by blocking access of adults to historical spawning habitat above dams (Yoshiyama et al. 2001), through limiting access of outmigrating juveniles to floodplains (Whipple et al. 2012), or by fundamentally altering other essential and supportive habitat types (Nobriga et al. 2005, Pringle et al. 2000).

Modified aquatic ecosystems are increasing in dominance globally, creating vast arrays of novel environments that allow invasive species to thrive, and native species to decline (Dynesius and Nilsson 1994, Vitousek et al. 1997, Carpenter et al. 2011, Cohen and Carlton 1998, Bernery et al. 2022). For example, abundance of invasive piscivores like black basses (*Micropterus spp.*) increase in human-altered environments because of their warm-water thermal niche, affinity for stable hydrologic regimes, and enhanced competitive abilities relative to native species (Brown et al. 2009a, Brown et al. 2009b, Feyrer and Healey 2002, Rahel et al. 2008). Changes in species assemblages are especially pronounced in ‘Mediterranean climates’ like California, where there is a strong pattern of species endemism linked to cold and highly variable flow regimes, alongside intense water extraction by humans and rapid climate change (Bennett and Moyle 1996, Moyle et al. 2017).

Low and declining juvenile survivorship in salmonids is a great concern in California, specifically on the San Joaquin River (hereafter, “SJR”). The completion of Friant Dam in the 1950s blocked access to critical upstream spawning habitat for spring-run Chinook Salmon (*Oncorhynchus tshawytscha*), ultimately resulting in the extirpation of the species from the San Joaquin River. Increased agricultural and municipal water demands further dried the river below the dam, leading to litigation to protect

remaining native fish populations (SJRRP 2012). The San Joaquin River Restoration Program (SJRRP) was launched in 2009 with the goals to 1) restore the river and fish populations to “good condition” and 2) “reduce impacts from water supply demands” with the hope of restoring a self-sustaining spring-run Chinook Salmon population (SJRRP 2012). Key to this reintroduction effort was understanding outmigration survival and regional mortality of juveniles through the SJR and Sacramento-San Joaquin River Delta (hereafter, “Delta”) to the Pacific Ocean.

The San Joaquin River Restoration Program has implemented multiple restoration projects throughout the upper portion of the SJR, starting below Friant dam, to improve habitat for returning adults and outmigrating juveniles. In 2013, the program assisted adult migration past impassable barriers in the SJR through trapping and transporting (SJRRP 2013, SJRRP 2014). Reintroduction of Feather River Hatchery spring-run Chinook Salmon juveniles began in 2014 and the first successful spawn occurred during 2017 in the restoration area (SJRRP 2018). To monitor outmigration success of juveniles, beginning in 2017, the program tagged spring-run smolts with coded wire tags and had a subsample (n = 700) tagged with acoustic transmitters. Tagging of juveniles with acoustic transmitters and monitoring of outmigration survival has occurred annually since (Singer 2019, Singer et al. 2019, Hause et al. 2022).

UC Davis has estimated spring-run Chinook smolt outmigration survival along the SJR from 2017-2020 using acoustic telemetry. The California Delta (hereafter, “Delta”) and San Francisco Bay represents the lowermost portion of the juvenile outmigration corridor and is a highly modified system with 1100 miles of levees constructed in 1850 to protect surrounding cities from flooding and to efficiently route water for export (Nichols et al. 1986, Hanak et al. 2007, CDWR 2022). Yet the existing levee infrastructure was only built to withstand a 100-year flood, is widely recognized as degraded (with 500 miles needing repair) and has even failed in several locations causing flooding in surrounding towns and agricultural areas (CDWR 2022, Water Education Foundation 2022a). Because some failures were too large in scope or cost to repair, large lentic water bodies influenced by tides, or “tidal lakes”, have since appeared on the landscape (CDFW 2020). These novel ecosystems are nested within the larger

Delta landscape and have created potentially dangerous habitats for outmigrating juvenile salmon. For example, tidal lakes are warmer, shallow, relatively large in area and limnetic fetch, have dense submerged aquatic vegetation (SAV) stands, and slower flow (Grossman et al. 2013). One particular tidal lake of interest is Franks Tract, a 1429 ha flooded island located in the Central Delta, which was once agricultural land but remained flooded since 1938 following multiple levee failures (CDFW 2020). Persistent levee erosion on the eastern side of Franks Tract has enabled direct connection of this habitat to Old River (Grossman et al. 2013), a migratory pathway potentially used by juvenile salmonids. Generally, entrainment points on the North and East sides of Franks Tract are the most direct routes for continued downstream migration when fish enter Franks Tract. In some scenarios, tides and pumping can combine to create reverse flows in the Central Delta waterways (Grossman 2016) and provide potentially maladaptive migratory cues.

Available data indicate that outmigration survival of juvenile Chinook salmon in the SJR is generally low, and also spatially heterogeneous (Buchanan et al. 2013, Buchanan et al. 2018, Singer et al. 2019, Hause et al. 2022). Previous acoustic telemetry tracking juvenile spring-run Chinook Salmon movements in this same system have observed low survival through the Central Delta, specifically in regions surrounding Franks Tract (Singer et al. 2019, Hause et al. 2022). Buchanan et al. (2013, 2018) also observed notably low survival of fall-run Chinook salmon throughout the lower (ie. downstream) regions of the Delta, which encompasses pathways connected to Franks Tract and other flooded islands. Extrapolating predation risk on a landscape level in the Delta, Michel et al. (2020) found that predator densities had a strong influence on risk of salmonid predation, and that the number of SAV patches impacted predator densities on finer (1-km) spatial scale. This large waterbody is shallow creating a large density of SAV (Grossman et al. 2013). This type of environment tends to proliferate rearing habitat for black bass populations (Conrad et al. 2016). Additionally, this area is known to be a strong bass fishery for fishers, with California Department of Fish and Wildlife (CDFW) tournament reports (2021, 2022) acknowledging the California Delta as one of the top for average number of participants per tournament

and total number of fish caught. BDCP Conservation Measure 15 (2013) lists Franks Tract as one of the many predatory hot spots for salmonids in the Delta. Despite the evidence highlighting Franks Tract as a potential mortality sink for outmigrating Chinook Salmon, no prior studies have specifically monitored smolt movements in this area.

Understanding salmon outmigration behavior as well as the predation pressures they face within tidal lakes represents a critical gap in our understanding towards improved conservation management of the SJR, Delta, and California's water conveyance infrastructure. For example, it is hypothesized that outmigrating juvenile salmon are entrained into tidal lakes like Franks Tract on high tides, during which fish could spend time and effort navigating towards finite exit points. Importantly, these novel environments are dense with invasive piscivores, such as black basses, which may increase the salmon's predation risk exposure (Grossman et al. 2013). Recent diet studies in the lower San Joaquin River have found native fishes, including juvenile Chinook Salmon, inside the stomachs of non-native piscivorous species (Michel et al. 2018, Grossman et al. 2013). Invasive black basses commonly have a wider range of habitat tolerances (i.e. up to 30°C) than native California species (i.e. up to 25°C) and tend to thrive in highly altered environments such as tidal lakes (Brown et al. 2009, Brown et al. 2009, Herbold et al. 1992), with optimal growth temperatures for juvenile salmonids being up to 20.5°C (Zillig et al. 2021). The Delta is indeed one of the most invaded ecosystems in the U.S. (Cohen and Carlton 1998) where habitats are rapidly shifting towards less turbid, warmer, and more vegetated states (Ferrari et al. 2014, Nobriga et al. 2005, Baxter et al. 2008). Nonetheless, little empirical research has been executed to investigate routing and survival dynamics through modified systems.

The goals of this study were to estimate 1) survival of juvenile spring-run Chinook Salmon along the full migration corridor of the SJR to the Pacific Ocean; 2) entrainment and survival of juvenile salmon within Franks Tract; and 3) relative predation risk of juvenile salmon within Franks Tract in relation to environmental covariates. These results have important implications for fisheries managers in the region

charged with restoring spring-run Chinook Salmon in the SJR, in addition to assisting water managers with providing the best possible conditions for outmigrating juvenile salmon.

Methods

Fish Tagging

Spring-run Chinook Salmon ($n = 796$) were surgically implanted with Juvenile Salmon Acoustic Telemetry System (JSATS) acoustic transmitters (ATS model SS400 injectable acoustic transmitter, Isanti, MN, USA; 216 mg, 3.38 mm x 15.0 mm, 5 sec pulse rate interval) at the Salmon Conservation and Research Facility (SCARF; Friant, CA). Fish were restricted from food 48 hours before tagging and > 24 hours after tagging was completed. Smolts were anesthetized with methanesulfonate (MS-222, 350 mg/L) and tagged at the SCARF hatchery in accordance with University of California, Davis Institutional Animal Care and Use Protocol 21614. Surgical implantations followed Singer et al. (2013) and tagged smolts ranged from 77 - 94 mm fork length (mean: 85.0 ± 4.0 mm) and 4.5 - 8.8 g (mean: 6.6 ± 0.8 g). Fish were split into three release groups: upper river ($n = 350$), Delta ($n = 348$), and Frank's Tract ($n = 98$). An additional 50 fish were tagged to estimate tag retention, battery life, and mortality. These fish were held in a separate holding tank from released fish to monitor tag battery life, shedding rates, and surgery-related mortalities over the course of the telemetry study window (March 2020 - July 2020). At the completion of the study, tag detections collected from a receiver suspended within the tank were used to analyze tag battery life. To compare shedding rates between taggers, a 2-way analysis of variance (ANOVA) was used combined with a Tukey's posthoc test.

San Joaquin River Releases Survival

The study area spanned 270 rkm starting in the SJR and extending into the Sacramento-San Joaquin River Delta and San Francisco Bay to Pacific Ocean entry (A17; Figure 1). This study included three releases of tagged fish: two in the SJR (upper river and Delta) and one as an experimental release in the Central Delta (including Franks Tract). The first release of tagged juvenile salmon ($n = 350$) occurred at the Fremont Ford State Recreation area (R1; Figure 1, Table 1). The second release ($n = 348$) of smolts

was upstream of the start of the South Delta on the SJR at Durham Ferry (R2; Table 1). The South Delta starts at the Head of Old River (HOR) where Old River (B1) diverges from the SJR. The first routing option for these releases was in the South Delta at the HOR where the Old River (B1) diverged from the SJR (A10). Here, fish could either 1) enter pumping facilities at the State Water Project (SWP; E1 and E2) or Central Valley Project (CVP; D1 and D2) or 2) circumvent water projects and enter the interior Delta by staying within Old River. Fish entrained in pumping facilities' salvage tanks would be collected and trucked downstream from the facilities to just upstream of Chipps Island (A15), bypassing the remainder of the Delta. Fish that remained within Old River continue through the system to Chipps Island. Fish that remained in the SJR at the HOR junction could continue through the South and Central Delta via the mainstem SJR or enter the interior Delta at Turner Cut, Columbia Cut, or the mouths of Middle or Old Rivers. All routes converged in the Western Delta at Chipps Island, then continued through the San Francisco Bay to Pacific Ocean entry (A17; Fig. 1).

The Delta release (R2) was conducted to ensure sufficient detections throughout the lower portion of the study area needed to derive estimates of ocean outmigration survival and detection probabilities. For both releases, fish were loaded into a 1181 L transport tank, on a trailer, with oxygen supplied by a micro-aerator connected to a 1800 psi oxygen tank. Temperature and dissolved oxygen were measured every 30 min using a YSI Professional 2030 (Yellow Springs, OH) during transport. Dissolved oxygen (DO) saturation was maintained between 80-110% and 0.15L of Stress Coat (Mars Fishcare North America Inc. Chalfont, PA) was added to reduce effects of handling stress. Upon arrival to each release location, fish were acclimated to ambient river temperatures (13.6°C at upper release and 16.1 °C at Delta release) by increasing the transport tank temperature 1°C per hour. Once the tank was within 1.5 °C of the ambient river temperature, fish were released from the transport tank.

Acoustic tag detection data were processed following methods in Singer et al. (2020) and Hause et al. (2022) which utilized the University of Washington Columbia Basin Research Group's filtering algorithm criteria (www.cbr.washington.edu/analysis/apps/fast). Briefly, raw detection files were filtered

to remove false-positive detections, defined as fewer than three detections of a tag on a single receiver at the estimated nominal PRI (pulse rate interval, 5 seconds) within a 60-second rolling window. Next, detections were visually examined, and records censored based on chronological sequence of detections at receiver stations used in the final model. Finally, a predator filter was applied to remove tag detections indicative of behavior suggesting that the individual was consumed by a predator (Buchanan and Whitlock 2022; Singer et al. 2020, Hause et al. 2022 in prep). For the two SJR releases, three rules were developed and weighted to remove assumed predator detections. Detections from the two SJR releases were flagged if the detection history 1) had upstream movement or movement against the flow (Perry et al. 2018, Hause et al. 2022, Buchanan and Whitlock 2022), resided within the vicinity of a site for > 36 h (excluding the first two sites downstream of each release location; Buchanan and Whitlock 2022), or 3) had a mean downstream movement rate of <1km/day (Buchanan and Whitlock 2022). Rules were weighted differently based on their relevance to indicate predator behavior. Multiple studies found movement against flow to strongly support striped bass behavior (Koo and Wilson 1972, Beland et al. 2001). Therefore, Rule 1 for all releases was weighted the heaviest (i.e. scored with a 4), while Rule 2 and 3 were not as indicative of predator behavior when examined alone (scored with a 2). A tag that received a score ≥ 4 had all detections removed downstream from the last detection assumed to be smolt movement.

A multistate release-recapture model was fit to the data following the procedures in Buchanan et al. (2013), Singer et al. (2020), and Hause et al. (2022), where model “states” represented pathways through the San Joaquin River-Delta study area. The probability of observing each detection history was estimated as a function of survival (S), receiver detection probability (P), route selection (ψ), and transition probability (ϕ). Transition probability is defined as the probability of movement into a route and survival through that route (i.e., ψS ; Buchanan et al. 2013) and was estimated where route entrainment and survival could not be estimated separately. Each SJR release was modeled separately, then combined with shared parameters between the two release groups (i.e. upper and Delta releases) at overlapping receiver locations to understand overall survival within the study system (Figure 3). Shared parameters

were sequentially added to the model and evaluated using Akaike's Information Criterion (AIC). Shared parameters were combined until AIC was lowered. In some cases, when AIC lowered or the model would not converge, detection probabilities were set to 0% or 100% depending on detections downstream of the site.

Franks Tract Release Survival and Movement

For this study, the Central Delta is described as the section of the Delta starting at Turner Cut and extending to Jersey Point (A14). Franks Tract is a large 1429 ha flooded island located in the middle of the Central Delta (Figure 2). Franks Tract is unique in that it oscillates between fresh and slightly saline conditions with water movement dissimilar to unidirectional flow or tidally influenced rivers, and thus functions as a tidal lake (Young et al. 2018).

A third release group (R3) included 98 tagged fish released directly into Franks Tract. Fish were released in Franks Tract within 4 days of when SJR released fish were detected entering the Central Delta at Durham Ferry (A7). Fish were transported to the release location in two large coolers (R3, Table 2, 127 L) with electric aerators and temperature and dissolved oxygen levels recorded every 30 minutes during transport. Fish were transported by boat in coolers to the direct center of Franks Tract and acclimated before release (Figure 2) following the same protocols described for the SJR releases. Immediately prior to release, all fish were scanned with a portable receiver to verify surgically implanted tags remained functional.

Acoustic telemetry data were processed as described above, with the exception of the predations filtering rules, which were adjusted to account for a difference in habitat features within Franks Tract. For fish released in Franks Tract, predation was inferred based on 1) movement against the flow (Perry et al. 2018; Hause et al. 2020 in prep; Buchanan and Whitlock 2022), 2) residence within the vicinity of a site for >36 h (Buchanan and Whitlock 2022), not including the first site of detection, and 3) movement time between two sites within Franks Tract > 9 h. The 9 h gap between detections was selected to allow for a 3

h buffer between a full tidal change (6 h) for fish to reorient. Rules were weighted in the same manner as above and detections scoring ≥ 4 were removed.

A separate multistate release-recapture model was fit to Franks Tract data following methods described above (Figure 4). For the model to converge, multiple locations had their survival fixed to 0 or 1, which was determined by examining detection counts at each site.

Franks Tract Relative Predation

In March 2020, substrate surveys of Franks Tract were conducted to measure relative coverage of SAV in the water column. GPS sonar-based surveys of SAV were conducted using Lowrance DownScan Imaging on a Lowrance Elite Ti2 GPS from January 21st – 23rd, 2020. The sonar ran at a frequency of 455 kHz. Transects were performed at 8 km h⁻¹, perpendicular to the longest axis across Franks Tract, with 200m spacing between transects. To ensure adequate shoreline coverage, transects ran parallel to the banks inside and outside of Franks Tract. Data were uploaded into BioBase software (BioBase Corporation, Beverly, MA USA) for spatial quantification and visualization of vegetation coverage within the water column and bathymetry. Results from bathymetric mapping were then used to determine potential locations for tethering experiments.

Relative predation risk was estimated between vegetated and non-vegetated sites within Franks Tract using predation event recorders (PERs; Demetras et al. 2016; Appendix Figure 1). PERs were modified to remain stationary during trials and allow comparison between habitat types (Demetras et al. 2016; Cyril Michel, National Oceanic and Atmospheric Administration, personal communication). Habitat type was determined by the spatial distribution of SAV coverage and informed the locations of PER deployments. Areas within Franks Tract that displayed > 50% plant coverage within the water column were identified as “high vegetation” sites, and < 50% coverage was considered “low vegetation” sites. I then used a stratified random sampling design to select PER deployment locations within each strata. PERs were released throughout Franks Tract covering both high (n = 69) and low vegetation (n = 92) locations.

Juvenile fall-run Chinook Salmon (mean fork length = 75 ± 4 mm) were attached to PERs by threading a 2 lb test monofilament fishing line through the fish's gills and mouth in accordance with University of California, Davis Institutional Animal Care and Use Protocol 21614 (Demetras et al. 2016). Fishing line was then attached to a 25 lb test braided line tied through a magnet on the bottom of the PER. When separated from the PER, the magnet activated a reed switch that began a timer. Magnet separation was assumed to reflect predation events on the salmon, and the time recorded upon PER retrieval represented time elapsed since the predation event. Underwater cameras were affixed to some PERs to confirm predation events were in fact a result of predators versus equipment malfunction. Five PERs were simultaneously deployed at each site for 1 - 2 hours before retrieval.

Trials in which tethered salmon became entangled on vegetation mats collided with the PER were excluded from further analyses. Predation events were then coded as 1 (predation event) or 0 (non-predation). The relationship between time to predation and environmental variables (vegetation, depth, and tidal stage) was modeled using Cox Proportional-Hazards Regression analysis (Demetras et al. 2016) via the `coxph` function in R (R Core Team 2022) package `survival` (Therneau 2015). Vegetation and tidal movement were examined as categorical variables, while depth at the time of PER deployment were treated as continuous variables. If the model's covariates were estimated to be statistically significant ($P \leq 0.05$), hazard ratios were also analyzed. A hazard ratio (HR) estimates the ratio of the threatened treatment group's hazard rate over the control group. If a hazard ratio is > 1 demonstrates a covariate is positively associated with the event (i.e. predation or decreased survival) occurring, and negatively associated with survival time. $HR < 1$ reveals a negative association with the event (i.e. improved survival), while an $HR = 1$ implied no association.

Results

Fish Tagging

Fish held back for the tag effects study ($n = 50$) had a mean fork length of 81 ± 4.1 mm and mass of 5.7 ± 0.88 g. There were no post-tagging mortalities throughout this study. The receiver used to

monitor the battery life of tags that died prematurely. However, all tags were active during the 71 day period that the receiver was functional. Released fish were ultimately detected in the system for 86 days post-release, and therefore we are confident that the majority of the tags remained active during the study period. We observed an overall tag shedding rate of 40.7% overall. A 2-way ANOVA followed by a Tukey posthoc test found there was no significant difference in migration distance by different taggers per release ($P = 0.27$, Appendix Figure 3). At the end of the study, fish were necropsied to investigate the high shedding rate. We found multiple tags were enlarged by developing a bubble inside the tag. It is unclear what caused the bubble, but it may be due to tag battery issues.

San Joaquin River Releases Survival

Of all the fish released in the SJR, only a single fish successfully completed their migration to the Pacific Ocean. Insufficient detections at Benicia Bridge (A16) and the Golden Gate (A17; $n < 5$) prevented our ability to derive meaningful estimates of survival and detection probability in these reaches. Therefore, the model was truncated to conclude at Chipps Island, approximately 71 rkm upstream from the Pacific Ocean entrance at the Golden Gate Bridge (A17). Additionally, we observed no fish utilizing Turner Cut as a migration pathway and subsequently did not include this route in the final model.

Overall, survival to Chipps Island (A15), the last location before reaching the San Francisco Bay, was low ($n = 3$). Survival through the mainstem SJR, from release (A1) to Mossdale (A9), was higher than through-Delta survival (from A9 to A15; Table 5). As fish entered the Delta at HOR, over 80% routed down Old River (Table 4). Most fish were entrained at the CVP (D1, D2, Table 4) and SWP (E1, E2, Table 4), with transition probabilities to each location estimated at 0.330 (+/- 0.050), 0.149 (+/- 0.037) respectively. Survival from the CVP and SWP to Chipps Island (A15) was 0.019 (+/- 0.014) and 0.010 (+/- 0.010) respectively. Survival through the mainstem SJR, starting at A10, was lower than through the Old River route to Chipps Island. With sparse data, we found that zero fish were detected at Chipps Island from the SJR route (starting at A10) and 2.9% from Old River. Entrainment in Franks Tract was high ($n = 2$) considering very few fish survived through regions that had access to Frank Tract ($n = 6$).

Outmigrating smolts could enter Franks Tract via pathways through the interior Delta or from the mainstem SJR at East Inlet (H1) or False River (G2; Figure 2). Fish were observed to use both of these pathways into Franks Tract, with one fish detected at Holland Cut (B4) from Old River Hwy4 (C1) and two fish at the East Inlet (H1) entrance from MacDonald Island (A13).

Franks Tract Release Survival and Movement

Of the 98 released fish, 64% ($n = 63$) were never detected again following release. Of the smolts detected after release ($n = 35$), it took an average of 63.5 h (range 6 to 204.5 h) to reach an exit in Franks Tract. Fish were detected at all receiver locations (with the exception of Fisherman's Cut) and there were no dominating patterns in movement after release. No tagged fish used Fisherman's Cut (F1) or Taylor Slough (H1) as exit points from Franks Tract. Of the five remaining routing options, transition probability was highest at Holland Cut (B5; 0.13 ± 0.03), followed by False River (I1; 0.09 ± 0.03), Old River Quimby (J1; 0.06 ± 0.02), East Inlet (G1; 0.04 ± 0.2), and Sand Mound Slough (K1; 0.03 ± 0.02) (Figure 2, Table 6). False river was the only site where fish successfully exited Franks Tract and were detected downstream at Chipps Island ($sI2 = 0.2 \pm 0.14$; Table 6). Few fish from the Franks Tract release were detected at Benicia Bridge and Golden Gate Bridge ($n = 2$ and $n = 0$, respectively).

Franks Tract Relative Predation

Overall, 10.5% ($n = 17$) of fish were predated on during the study. Using a Cox Proportional-Hazards Regression model, we predicted survival of tethered salmon as a function of vegetation coverage, tidal movement and water depth. We did not find a significant effect of vegetation ($Z = 1.04$, $P = 0.29$) or depth ($Z = 0.65$, $P = 0.51$) on relative predation risk (Table 7). However, tidal effects were significant, with descending tides almost 4 times more hazardous than ascending tides ($HR = 4.96$, $Z = 2.09$, $P = 0.04$; Table 7, Figure 5).

Discussion

We estimated that, in 2020, outmigration survival of spring-run Chinook salmon smolts from release in the SJR to the ocean was again very low ($n = 1$ or 0.001%). This observation is comparable to

previous estimates of survival in this same study area from 2017 - 2019 (<1% - 5%, Singer et al. 2020; Hause et al. 2022), and was not unexpected given the dry conditions during the study period. (CDWR 2022). Results from prior studies on the SJR (Singer 2019) show overall outmigration survival estimates for juvenile Chinook Salmon estimating < 1% in dry years. Wet years in contrast have overall survival values of 5.0% (Singer 2019, Hause et al. 2022). Specifically, Delta survival for both SJR and Sacramento River smolts ranging from 0.0 - 53.0% and 2.0 - 70.0% for dry and wet years (Buchanan et al. 2013, Buchanan et al. 2018, Michel et al. 2015, Perry et al. 2010, Singer et al. 2020), respectively. Therefore, wet years are consistently recruiting the largest year classes of salmon into the ocean population while dry years result in lower salmon production. These results mirror numerous studies highlighting the importance of flow to periodic years of high salmon recruitment (Michel et al. 2015, Jager and Rose 2003, Michel et al. 2021, Singer et al. 2020). Furthermore, these results call attention to the vulnerability of salmon to effects of climate change. Columbia River Basin research suggests that Chinook salmon smolt-to-adult ratios (SARs) need to be ~ 0.02 for a self-sustaining population (NPCC 2014). Given that juvenile outmigration survival in the SJR is already below this ratio in years like 2020, it is extremely unlikely that a self-sustaining population of Chinook salmon can exist in the SJR if consecutive drought years like 2020 persist over the 3 - 5 year life-cycle of Chinook salmon. Given that climate change is making the intensity and duration of droughts longer (Mukherjee et al. 2018), this will result in longer periods of poor-to-nominal recruitment in many California watersheds. And in watersheds that are already marginally productive, such as the SJR, effects of climate change will likely be intense (Moyle et al. 2017, Crozier et al. 2021), further highlighting the need for adaptive solutions to boosting juvenile salmon survivorship, especially during drought years.

Survival was highest through the upper reaches of the mainstem SJR ($S = 9.5\%$) until Head of Old River with most fish routing down Old River ($\psi = 81.7\%$), which is much higher than previous studies during a dry water year (Buchanan et al. 2013, Singer 2019, Hause et al. 2022). Although survival to Chipps Island through salvage at the facilities along the Old River route was higher (CVP 1.9%, SWP < 1%, and Old River route < 1%) than fish that remained in the SJR route through the Delta (0.0%), we

do not believe the pumping facilities are a beneficial route for smolts overall. Higher survival through the CVP has been observed previously in telemetry studies during dry water years (Buchanan et al. 2013, Buchanan et al. 2018, Singer et al. 2019, Hause et al. 2020). During normal-to-wet years, survival and routing selection was much higher in the SJR versus fish salvaged by the pumping facilities (i.e. 2017; Singer et al. 2019). Higher survival through salvage during dry years may result from reduced travel distances for salvaged smolts and less a beneficial effect of the facilities. Total survival continued to be low in this dry water year with only one fish surviving to Pacific Ocean entry (< 1%).

Previous studies have revealed that juvenile survivorship through the Central Delta is consistently low. Furthermore, tidal lake habitats inside the Delta like Franks Tract are hypothesized to be mortality hotspots, in part because of presumed high predation risk due to abundant thermally tolerant predators. Franks Tract, and similar tidal lakes, appear to be major habitats that contribute to reduced juvenile salmon survival overall. In total, 33% (n = 2) of salmon released upstream survived to the entry points of Franks Tract (n = 6) and were entrained in the tidal lake without escaping. Given that studies of this kind are rare, it is difficult to assess the degree to which such an entrainment rate is high, low or average. However, that some fish were entrained into the tidal lake lends credence to the notion that these habitats are used regularly enough in salmon migrations that they may need to be included in future telemetry models and studies. Results of the experimental release of 98 salmon inside Franks Tract mirrored these patterns but contextualized them further. Fish released in Franks Tract were confirmed to have low escapement survival (2%) with all detected escapements occurring through the False River route only. The majority (n = 63) of these fish were never detected again following release. The fate of these fish is unknown. Fish could have died, been predated on, stayed within the area, or passed receivers undetected. For the surviving salmon, it took an average of 63.5 h (6 - 204.5 h) to exit Franks Tract or not be detected again (5 rkm). Results contrast to typically much faster downriver migration rates which average < 25 to > 100 km^d⁻¹ for juvenile spring-run Chinook Salmon in the San Joaquin River and Delta in previous years (2017-2018; Singer et al. 2019). Therefore, migrating through Franks Tract is likely slowing outmigration progress for salmon that enter this region, and increasing the time available to interact with a predator in

Franks Tract. Furthermore, the finding that fish were detected at almost all receiver locations in Franks Tract suggests that there was not a clear outmigration path for salmon, and that fish were, to an extent, searching for an exit point. Similar patterns are likely to apply in other tidal lakes. We also observed multiple occurrences of fish egressing Franks Tract, reaching Chipps Island or Benicia Bridge, only to turn around and return to Franks Tract (i.e., were ingested by a predator that used Franks Tract regularly as habitat).

Understanding drivers and consequences of varying predation rates has a long and important history in fisheries ecology (Sass et al. 2006, Camp et al. 2011, Rozas and Odum 1998). However, marine ecologists in particular have investigated the critical importance of tides and water depth in driving fish predation risk (McIvor and Odum 1988, Baker and Sheaves 2007, Rypel et al. 2007, Nobriga and Feyrer 2007, Kimerei et al. 2013). Many of the factors identified in previous studies (e.g., habitat, depth, tide) are also factors that could be important in mediating the predation risk to juvenile salmon in tidal lake habitats of the Sacramento-San Joaquin River Delta. In this study, we examined three discrete parameters that might influence relative predation rates: vegetation, depth, and tidal movement. However, only tidal movement was found to be a significant covariate in the Cox Proportional-Hazards Regression Model. This finding indicates that juvenile salmon face the highest relative predation risk in deeper waters on descending tides. At first glance, results appear to contradict previous studies, e.g., the depth refugia hypothesis (Grol et al. 2014, Paterson and Whitfield 2000) and work on refugia benefits of SAV (Heck and Thoman 1981, Dibble et al. 1997). Rypel et al. (2007) provided data on tethered prey fish that showed a critical depth threshold for predation at ~ 30 - 60 cm in tidally driven Bahamian creeks. Alternatively, Baker and Sheaves (2007) found no significant effect of depth on predation in an Australian tropical estuary. Although depth was not found to have a significant impact on predation hazard in this study a water depth threshold nonetheless remains plausible in these habitats. Due to accessibility constraints, we excluded the shallowest depths (< 1 m) and ultimately lack data on potential predation refugia occurring at those depths. Therefore, these results are best interpreted as predation risk of juvenile salmon in deeper water habitats (> 1 m). Future research could expand on this work by more closely testing the depth

refugia hypothesis (Baker and Sheaves 2007) within estuaries of the San Francisco Bay and Delta. Similarly while vegetation was not a driver of relative predation risk in deeper habitats, aquatic vegetation could be an important habitat variable at shallower depths, especially at contact zones with deeper water or transitional zone habitats. As for tides, there exists abundant evidence that predator behavior and abundance is strongly linked with tides (Krumme 2004, Stevens et al. 2006, Gibson 2003, Colombano et al. 2020). In a newly restored tidal wetland in the Delta, it was found that predation on Chinook smolts was highest at the mid-descending and low tidal phases (David Ayers, University of California, Davis, personal communication). For riverine environments, Demetras et al. (2016) observed highest predation rates on an outgoing tide in a tidally influenced section of the San Joaquin River. Additionally, a study in Maine concluded that striped bass moved throughout the system independent of tide while Atlantic smolts moved with the tide (Beland et al. 2001). Further research is needed to determine how broadly applicable these results are to other habitats in the Delta or estuarine habitats more generally.

There are also major limitations to all tethering experiments (e.g., Kneib and Scheele 2000; Aronson 2001). For example, tethered smolts may face a higher risk of predation than free swimming smolts due to their inability to escape, potentially leading to higher predation rates in experiments. However, relative predation rates in this study were not extremely high. The primary assumption of any tethering experiment is that a functional relationship exists between loss of tethered prey and true ecological predation rates (Kneib and Scheele 2000). As such, data from tethering experiments are best viewed as a comparative examination of covariates effects on predation risk (i.e., relative predation risk). Nonetheless, tethering remains one of few methods available for empirically testing critical predation risk questions (Aronson and Heck 1995, Sass et al. 2006), and serves as our best measure for understanding relative predation rates in ecologically complex habitats such as Franks Tract.

Overall, Franks Tract appears to serve as a challenging habitat for outmigrating salmonids than riverine pathways. Survival rates of telemetered fish from any of the release groups was low, and those fish that did survive appeared to struggle to locate critical exit points. Results from tethering suggest that tidal flows may be driving much of the predator-prey dynamic within Franks Tract. Furthermore, this

particular tidal lake is densely covered with SAV, even during winter and spring outmigration windows for salmon. Other studies in the Delta have linked high levels of SAV to increased populations of non-natives, especially largemouth bass (Nobriga et al. 2005, Conrad et al. 2016). During spring-run outmigration, SAV occurs in the littoral shallow water areas of Franks Tract, with some vegetation growing into the limnetic center. Later in the year however, Franks Tract is completely overgrown with vegetation. Largemouth bass are commonly found in lentic waters that include dense layers of SAV. In contrast, smallmouth bass are found in hard bottom, unvegetated sites, and tolerate velocities slightly faster than largemouth bass (Brown et al. 2009). Thus, both species of black bass cover the variety of substrate habitat available in Franks Tract, which may limit predation refugia, except perhaps in the shallowest zones (Rypel et al. 2007).

Another challenge seen from these results is the plight to manage for fishes and municipal water supply. Our results showed there was only one viable exit in 2020, False River. In 2021 and 2022, an impassible rock barrier was installed to block salt water from intruding into Franks Tract and ultimately into Old River (CDWR 2021). The SJR, Old River, and Franks Tract has been known to experience reverse flows in the Central Delta, especially in dry years, because of water export from the state and federal water pumping facilities (SWP and CVP) which supply most of the agricultural and municipal water for the state especially Southern California (Water Education Foundation 2022b; BOR 2022). These reverse flows and dry water years bring salt water deep into the Central Delta and towards the pumping facilities off Old River, causing flow to be unusable (Grossman et al. 2013, Buchanan et al. 2013). With this barrier in place, the risk of mortality for outmigrating salmonids entrained into Franks Tract may be exacerbated.

The results of this research are applicable to conservation management of fisheries. For example, a variety of other novel tidal lakes resulting from levee failure or land subsidence that occur in the Sacramento-San Joaquin River Delta, including Mildred Island and Sherman Island (Grossman 2016, Thompson 2006, Lund 2011). The ecological architecture of each tidal lake differs, but they share key characteristics, such as shallow depths, large limnetic fetch, dense amounts of SAV, and high abundances

of non-native piscivorous fishes (Grossman et al 2013, Feyrer and Healey 2003). In short, similar factors that render Franks Tract challenging habitat for outmigrating Chinook Salmon smolts would also be applicable to other tidal lakes. Furthermore, levee infrastructure repairs have become such a concern that the Central Valley Flood Protection Plan Update (2022) estimated \$315 to \$385 million per year for necessary repairs and improvements. As levees age, managers will have to repair hundreds of miles of damaged and aging levees or manage increased numbers of large tidal lakes that would undoubtedly resemble Franks Tract. Additional research is needed to examine Chinook Salmon survivability in Franks Tract (or other tidal lakes) across multiple water years. If these habitats, even in wet years, continue to yield high mortality, water managers might explore options for preventing access of migratory native fishes to these habitats, at least through commonly routed locations during winter and spring. However, blocking the only survivable pathway out of Franks Tract with a barrier, as seen in 2021 and 2022, could further exacerbate high mortality (CDWR 2021). Another management option might involve rehabilitating tidal lakes into tidal marshes or managed wetlands to better support native species overall (Aha et al. 2021, Baker et al. 2020, Colombano et al. 2021). Thus supporting initiatives like Franks Tract Futures (CDFW 2020) could help to restore tidal marshes and improve natural habitat cues needed for Chinook Salmon outmigration success.

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Footnotes

none

Tables

Table 1: List of acoustic receiver locations used in study.

Receiver code	Location name	rkm	Route
R1	Upper River release	278	Release
A1	Below Upper Release	277	San Joaquin River
A3	Newman	268	San Joaquin River
A4	Hills Ferry	265	San Joaquin River
A5	Crows Landing	246	San Joaquin River
A6	Grayson	215	San Joaquin River
R2	Delta Release	187	Release
A7	Durham Ferry	185	San Joaquin River
A8	BCA	175	San Joaquin River
A9	Mossdale	166	San Joaquin River
A10	SJ ¹ Head of Old River	161	San Joaquin River
B1	OR ¹ Head of Old River	158	Old River
B2	OR Middle River	152	Old River
A11	Howard	151	San Joaquin River
A12	SJG (SJ Garwood)	144	San Joaquin River
D1	CVP (Central Valley Project)	135	Old River
D2	CVP tanks	135	Old River

E1	SWP (State Water Project) Forebay	134	Old River
E2	SWP interior channel	132	Old River
A13	MacDonald Island	126	San Joaquin River
B3	OR Hwy4	125	Old River
A14	Jersey Point	97	San Joaquin River
A15	Chipps Island	71	All routes
A16	Benicia Bridge	52	All routes
A17	Golden Gate Bridge	1	All routes

¹: SJ represents San Joaquin River and OR represents Old River.

Table 2: Receiver codes and metadata for experimental release in Franks Tract.

Receiver code	Location name	rkm
R3	Franks Tract Release	105
K1	Sand Mound Slough	109
B5	Holland Cut	109
J1	Old River Quimby	109
G1	East Inlet	110
I1	False River	101
F1	Fisherman's Cut	102
H1	Taylor Slough	102
A14	Jersey Point	97
A15	Chipps Island	71
A16	Benicia	52
A17	Golden Gate	1

Table 3: Sample sizes and mean sizes (fork length and weight) \pm 1 SD for tagged fish.

Release group	N	Mean FL (mm)	Mean weight (g)	Release date
Upper River Release	350	80.9 \pm 3.8	5.8 \pm 0.8	March 16 th , 2020
Delta Release	348	81.6 \pm 4.1	5.8 \pm 0.9	March 24 th , 2020
Franks Tract Release	98	81.5 \pm 4.0	5.7 \pm 0.9	March 24 th , 2020

Table 4: Transition probability (ϕ) and route selection (ψ) from multi-state mark-recapture model of San Joaquin River releases. Table shows the estimate \pm 1 SE per transition probability and routing selection. Note that ψ parameters sum to 1, but ϕ parameters do not, because they jointly estimate survival and route selection.

Parameter	Route	Estimate	SE
ψ A1	SJR at HOR Junction	0.1825	0.0344
ψ B1	Old River at HOR Junction	0.8175	0.0344
ϕ B2E1	Transition to SWP from B2	0.1496	0.0369
ϕ B2D1	Transition to CVP from B2	0.3304	0.0503
ϕ B2B3	Continuing on Old River from B2	0.0432	0.0211

Table 5: Reach-specific survival for larger pathways along the migration route to the Pacific Ocean +/- 1 SE. Estimate is survival per reach with lower and upper bounds of the 95% confidence interval.

Reach	Estimate	SE
Upper release to Mossdale	0.0950	0.0157
Old River route to Chipps	0.0291	0.0166
San Joaquin River route to Chipps	0	-
Old River through CVP	0.0194	0.0136
Old River through SWP	0.0097	0.0097
Old River through Hwy4	0.0097	0.0097

Table 6: Transition probability (ϕ) and route survival (S) estimates +/- 1 SE from multi-state mark-recapture model for the Franks Tract experimental release.

Parameter	Route	Estimate	SE
ϕ_{RI1}	Transition to False River from FT Release	0.0918	0.0292
ϕ_{RK1}	Transition to Sand Mound from FT Release	0.0306	0.0174
ϕ_{RB5}	Transition to Holland Cut from FT Release	0.1326	0.0343
ϕ_{RJ1}	Transition to OR Quimby from FT Release	0.0612	0.0242
ϕ_{RG1}	Transition to East Inlet from FT Release	0.0408	0.0199
sI2	Survival from False River to Chipps	0.2222	0.1386
sK2	Survival from Sand Mound to Chipps	0*	-
sB6	Survival from Holland Cut to Chipps	0*	-
sJ2	Survival from OR Quimby to Chipps	0*	-
sG2	Survival from East Inlet to Chipps	0*	-
sA16	Survival from Chipps to Benicia Bridge	1*	-
	Overall survival out of Franks Tract to Chipps	0.2	-

*Based on observed data, these values were fixed to allow the model to converge.

Table 7: Results from Cox Proportional Hazard model. CI refers to lower and upper bound 95% confidence intervals. HR denotes the hazard ratio.

Predictor	HR	95% CI	p-value
Habitat			
Non-vegetated	-	-	
Vegetated	1.80	0.60, 5.40	0.29
Depth	1.12	0.79, 1.60	0.51
Tidal Movement			
Ascending	-	-	
Descending	4.96	1.10, 22.30	0.04

Figures

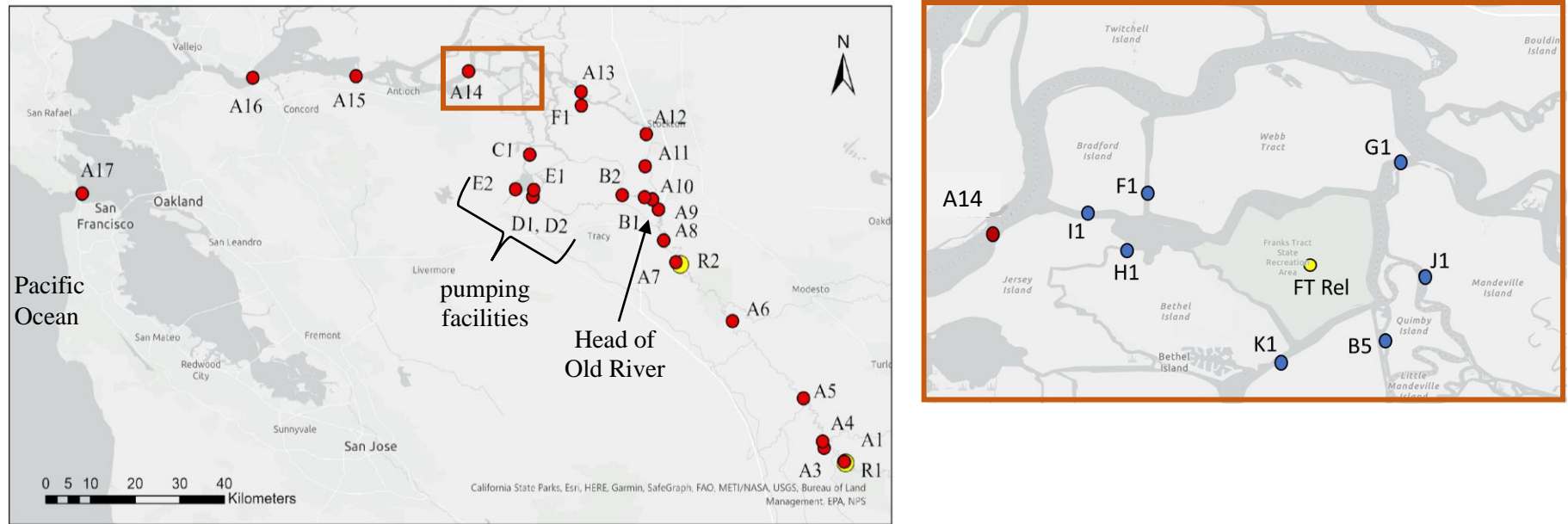


Figure 1: Map of acoustic receiver locations (from Table 1) in study area. Red circles denote receiver locations and yellow circles indicate release locations. The side panel (orange outline) shows Franks Tract receiver locations (blue dots), experimental release location (yellow dot), external receiver locations (red dot)

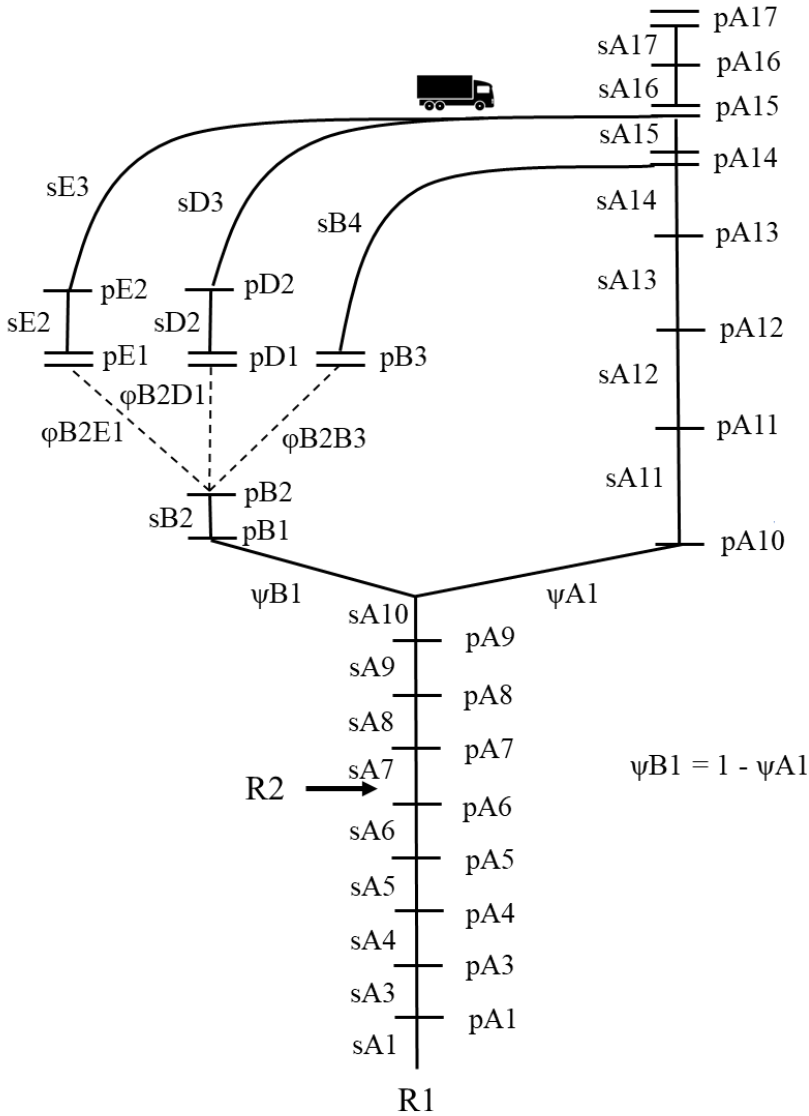


Figure 3: Schematic of mark-recapture model estimating survival (s), detection probability (p), route selection (ψ), and transition probability (ϕ) for the San Joaquin River (R1 = release 1 and R2 = release 2). Routes are labeled as follows: San Joaquin River (A), Old River (B), federal pumping facility (Central Valley Project; D), and state pumping facility (State Water Project; E). The truck icon represents fish being transported from both salvage facilities to the release location upstream of Chipps Island (A15).

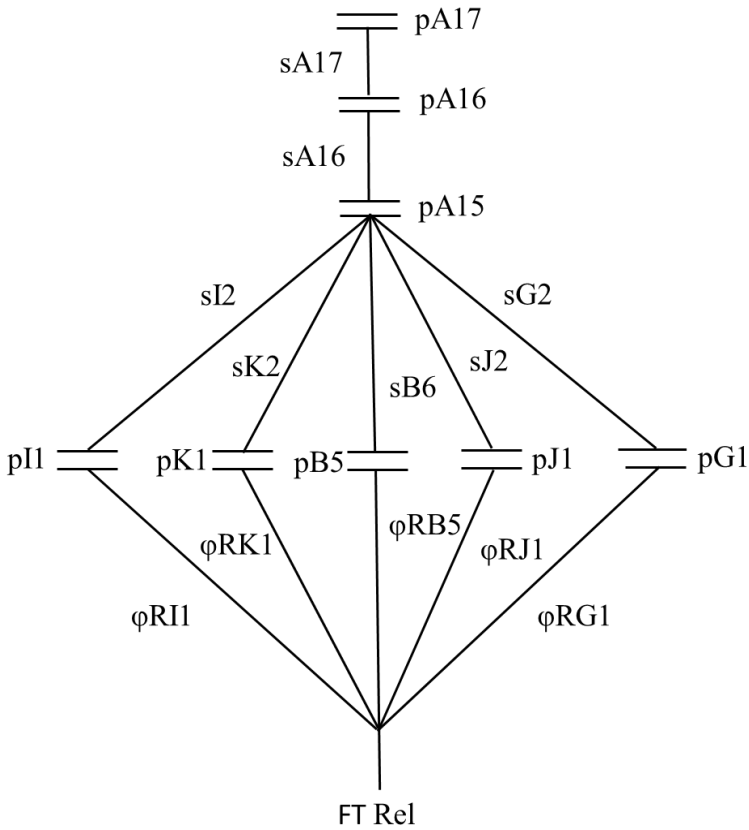


Figure 4: Schematic of mark-recapture model estimating survival (s), detection probability (p), and route selection (ψ) for Franks Tract Release (FT REL). Vertical lines represent pathways to receiver locations, see Table 2 for receiver/routing definitions.

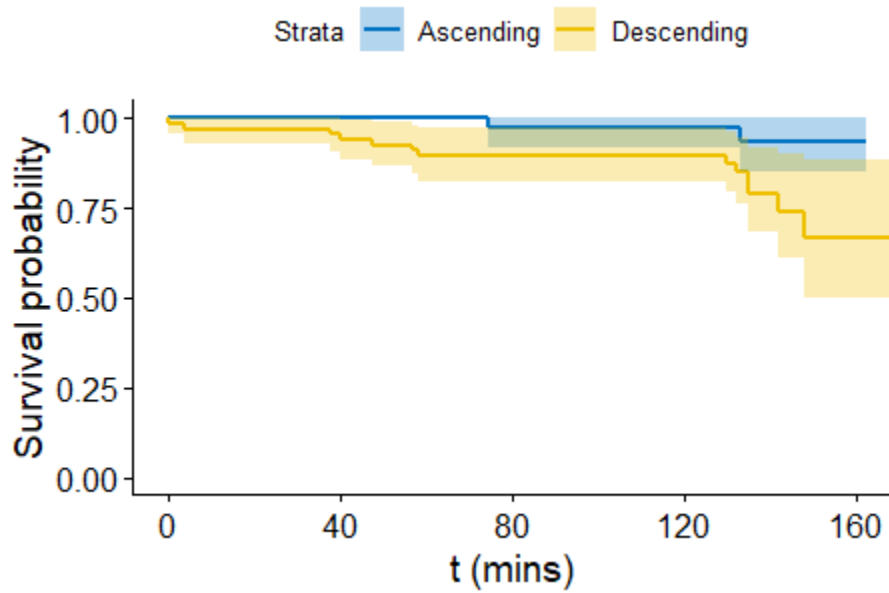
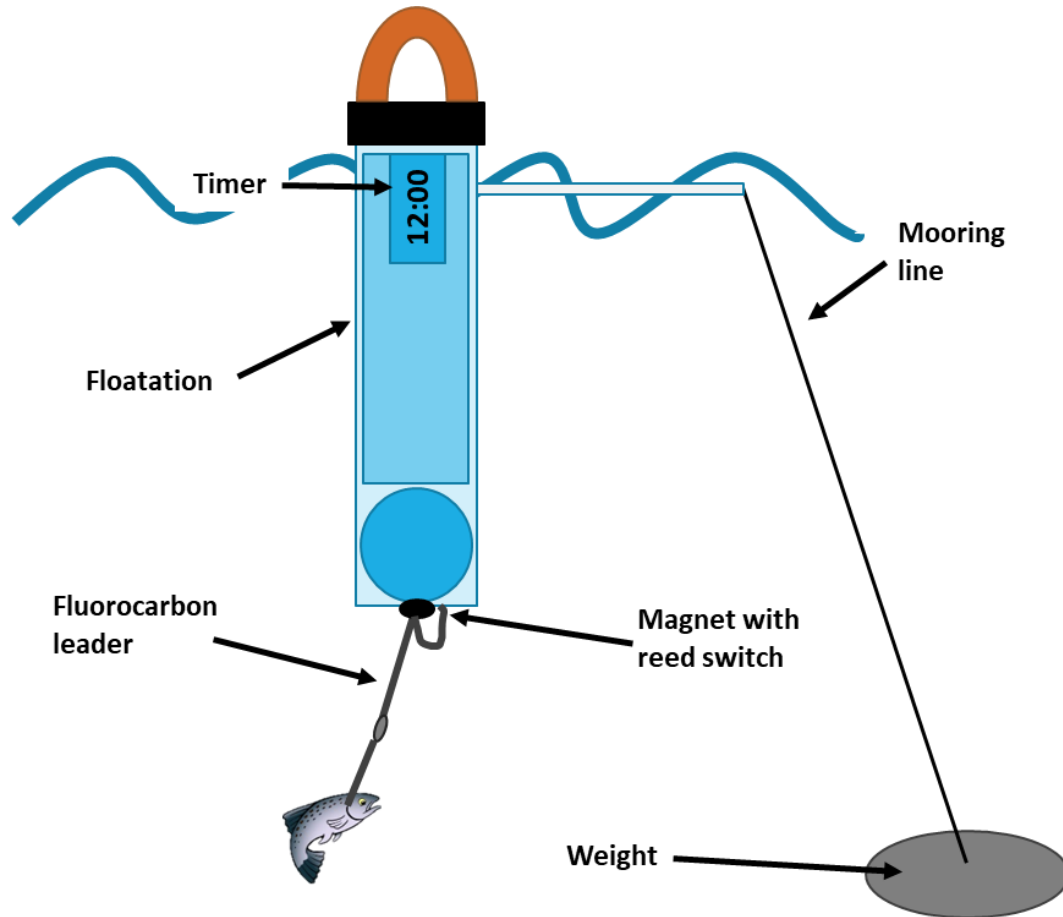


Figure 5: Predicted survival probability for tidal movement from Cox proportional hazard model, with blue (top line) representing ascending tide and yellow (bottom line) representing descending tide. Each solid line represents estimated survival probability at time t, with shading signifying the 95% confidence interval.

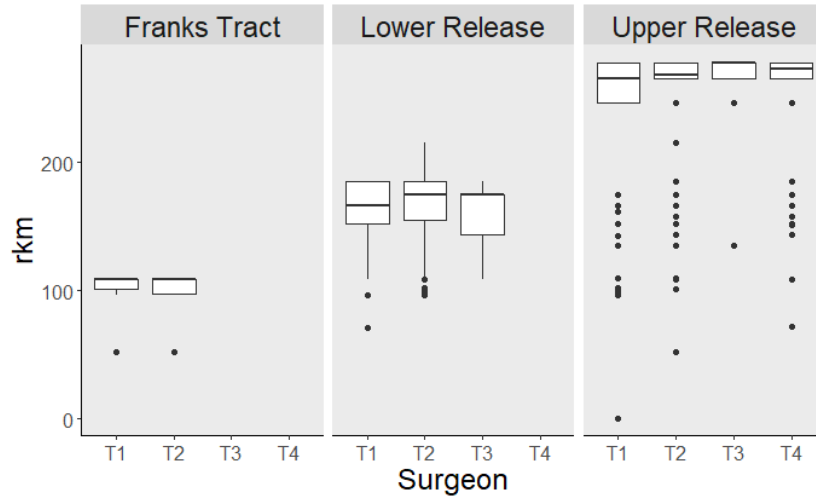
Mathematical and statistical expressions

None

Appendices and supplements



Appendix Figure 1. Schematic of a stationary predation event recorder (PER). When a fish is predated, the fluorocarbon leader attached to the fish and magnet will pull the magnet, triggering a timer. In the description above, trials ended when the tethered salmon was predated upon 12 min prior to experiment initiation.



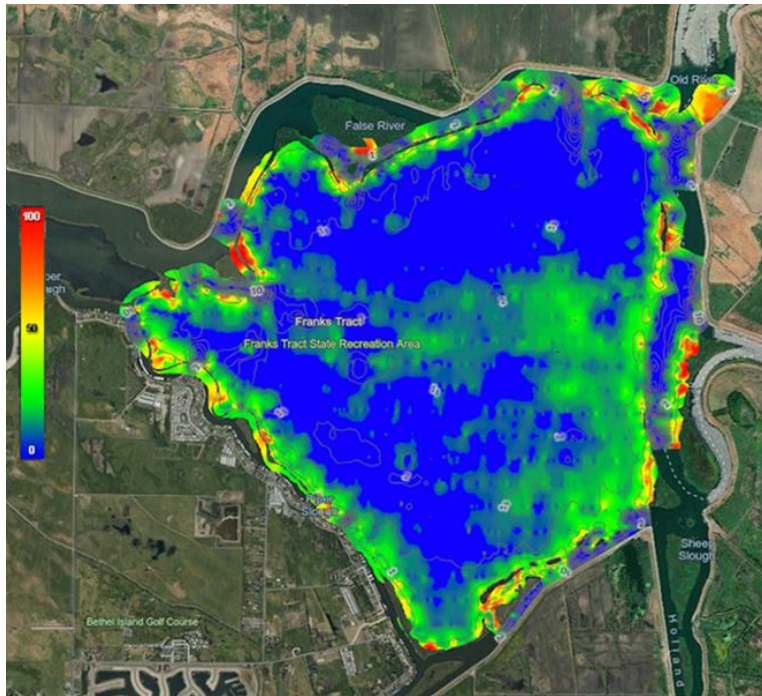
Appendix Figure 2: Maximum distance traveled by tagged fish as a function of four independent taggers. The x-axis displays the four taggers within the study and y-axis shows the distance (rkm) of fish tagged by each tagger. Boxes represent the median and interquartile ranges. There was no significant difference in distance traveled as a function of tagger (2-way ANOVA, $F = 1.304$, $P = 0.272$).

Appendix Table 1: Reach specific survival (S), detection probability (P), and transition probability (ϕ) from multi-state mark-recapture model of San Joaquin River releases. Estimates are for each parameter with standard error (+/- 1 SE). Sites A10 and downstream are combined estimates for both the upper and Delta releases. Sites A9 and upstream are estimates only for the upstream release.

Parameter	Estimate	SE
sA15	0*	-
sA14	0.5000	0.3536
sA13	0.5000	0.2500
sA12	0.4000	0.1549
sA11	0.4348	0.1034
sB4	0.2464	0.2146
sD3	0.3333	0.1925
sD2	0.1932	0.0713
sE3	0.3333	0.2722
sE2	0.2133	0.1093
ϕ B2E1	0.1496	0.0369
ϕ B2D1	0.3304	0.0504
ϕ B2B3	0.0432	0.0212
sB2	0.9126	0.0278
sA10	0.7973	0.0330
sA9	0.8797	0.0557
sA8	0.9211	0.0437
sA7	0.9595	0.0327

sA6	0.6324	0.0585
sA5	0.4306	0.0413
sA4	0.8620	0.0355
sA3	0.5328	0.0270
sA1	0.9768	0.0088
pA15a	1*	-
pA15b	1*	-
pA14a	1*	-
pA14b	1*	-
pA13	1*	-
pA12	1*	-
pA11	1*	-
pA10	1*	-
pB3a	0.8625	0.1337
pB3b	0.8625	0.1337
pD2	1*	-
pD1a	0.6761	0.0884
pD1b	0.8692	0.0701
pE2	1.0000	-
pE1a	0.9244	0.0529
pE1b	0.9244	0.0529
pB2	1*	-
pB1	1*	-
pA9	0.9365	0.0217
pA8	1*	-
pA7	0.9211	0.0437
pA6	1*	-
pA5	1*	-
pA4	0.9118	0.0344
pA3	0.9933	0.0066
pA1	0.9945	0.0055

*Based on observed data, these values were fixed to allow the model to converge.



Appendix Figure 3: Map of vegetation coverage in Franks Tract estimated using Lowrance DownScan imaging. Transects, 200 m apart, were conducted parallel to the longest section of Franks Tract. Blue indicates no vegetation and red indicates 100% vegetation coverage.