Contrasting the migratory behavior and stranding risk of White Sturgeon and Chinook Salmon in a modified floodplain of California

Myfanwy Johnston, Jared Frantzich, Matthew B. Espe, Pascale Goertler, Gabriel Singer, Ted Sommer & A. Peter Klimley

ONLINE FIRST

Environmental Biology of Fishes

ISSN 0378-1909

Environ Biol Fish
DOI 10.1007/s10641-020-00974-9

Environ Biol Fish
https://doi.org/10.1007/s10641-020-00974-9

Contrasting the migratory behavior and stranding risk of White Sturgeon and Chinook Salmon in a modified floodplain of California

Myfanwy Johnston · Jared Frantzich · Matthew B. Espe · Pascale Goertler · Gabriel Singer · Ted Sommer · A. Peter Klimley

Received: 6 February 2019 / Accepted: 22 April 2020

Abstract While navigating through the same migratory corridor, different species may experience differing reproductive success due the interaction of species-specific movement behavior with habitat configuration. We contrasted the migratory behavior of White Sturgeon *Acipenser transmontanus* and fall-run Chinook Salmon *Oncorhynchus tshawytscha*, two native fishes in Central Valley of California. These species co-occur in the region's Yolo Bypass floodplain seasonally, but they represent disparate reproductive strategies: White Sturgeon are iteroparous, spawning multiple times throughout their lifespan, while Chinook Salmon are semelparous, spawning only once in their lifespan. Except for brief windows when the Yolo Bypass connected to the Sacramento River during flood conditions, migrating White Sturgeon and Chinook Salmon that entered the Bypass from 2012 to 2018 had to turn around and exit it in order to complete a successful spawning migration up the Sacramento River. This "exit behavior" was critical to migratory success when the Bypass was not flooded. Between March 2012 and May 2018, the median probability of acoustically-tagged fall-run Chinook Salmon exiting the Yolo Bypass at its southern extent was estimated to be 0.74 (0.58–0.87 95% credible interval), while an individual White Sturgeon had a median exit probability of 0.99 (0.96–1.00 95% credible interval). Our results suggest that White Sturgeon successfully exit the Yolo Bypass more consistently than fall-run Chinook Salmon, indicating that fall-run Chinook Salmon are at higher risk of stranding in the Yolo Bypass. The difference in probability of exit between these two species has implications for how to manage for migratory success in altered habitats. Floodplain · Fish passage · Bayesian · Telemetry · Behavioral ecology · Movement · Stranding.

Keywords Floodplain · Fish passage · Bayesian · Telemetry · Behavioral ecology · Movement · Stranding

Introduction

While navigating through the same migratory corridor, different species may experience differing reproductive success due the interaction of species-specific movement behavior with habitat configuration (Dingle 2014; Sommer et al. 2014). In managed systems, it is important to understand how different types of migrants respond to local conditions, particularly when fish passage facilities or altered hydrology may serve as an ecological trap for one or more species (Pelicice and Agostinho 2008). The Yolo Bypass floodplain in the Central Valley of California is a highly altered, managed

M. Johnston (✉)
Cramer Fish Sciences, 13300 New Airport Rd. Ste 103, Auburn, CA 95602, USA
e-mail: Myfanwy.johnston@fishsciences.net

J. Frantzich · P. Goertler · T. Sommer
California Department of Water Resources, 3500 Industrial Blvd, West Sacramento, CA 95691-6521, USA

M. B. Espe · G. Singer · A. P. Klimley
University of California at Davis, One Shields Ave, Davis, CA 95616, USA

Published online: 07 May 2020

system through which two species of seasonal migrants navigate their spawning migrations: White Sturgeon *Acipenser transmontanus* and fall-run Chinook Salmon *Oncorhynchus tshawytscha*. Like many migratory fishes worldwide, both species belong to populations in decline (Freeman et al. 2003; Moyle et al. 2011; Yoshiyama et al. 1998). This study examines how individuals from these populations navigated the Yolo Bypass system of California during their spawning migrations in the years 2012–2018 and endeavors to contrast their species-specific behavior within a broader context of complex migratory habitat, migratory traps, and reproductive strategy.

White Sturgeon are semi-anadromous, large-bodied fish that spend the majority of their time in brackish, deep areas of estuaries with soft substrates. They migrate upriver into fresh water to spawn (Moyle 2002). White Sturgeon spawn from February to early June (Miller 1972; Kohlhorst 1976; Schaffter 1997; Jackson et al. 2016). The onset of their upstream migration is typically a response to increases in flow (Miller 1972; Kohlhorst 1976; Schaffter 1997; Jackson et al. 2016); a particularly high pulse of flow may trigger spawning itself (Kohlhorst et al. 1991). White Sturgeon are iteroparous, spawning multiple times in their long lifespans. However, only a portion of the adult population completes a spawning migration each year. Males may spawn every 1–2 years, while females will not return for 2–4 years, depending on environmental conditions (Moyle 2002). Iteroparity likely lends White Sturgeon some flexibility in assessing whether conditions are favorable or unfavorable for spawning on an annual basis (Rideout et al. 2005).

Central Valley Chinook Salmon are members of the Family Salmonidae, a large-bodied group of excellent swimmers. Chinook Salmon are semelparous: they spawn only once in their lifetimes. Mature adults in the ocean embark on their spawning migration by re-entering mainstem rivers. They may or may not display “milling” behavior (apparent meandering around the estuary, river channels, and tributaries as they switch from primarily visual and magnetic guidance to olfactory cues for navigation) before embarking on a directed path upstream, typically to their natal tributaries (Groot et al. 1975; Dittman and Quinn 1996). Vincik (2013) documented milling behavior in fall-run Chinook Salmon in the Sacramento-San Joaquin Delta specifically. The fall-run is the most abundant of the four races of Central Valley Chinook Salmon, largely through hatchery supplementation (Moyle 2002). Adult fall-run Chinook Salmon migration in the Central Valley may be triggered more by seasonal patterns (i.e. temperature and polarized solar radiation) than by particular flow-pulse cues (Williams 2006). Together with semelparity, this means that Chinook Salmon have less flexibility in timing their migration than an iteroparous species would in the same environment. Fall-run spawning peaks between mid-October and early November each year (Yoshiyama et al. 1998; Williams 2006).

Both White Sturgeon and Chinook Salmon are key components of a species assemblage that benefits from a functioning floodplain, including managed floodplain systems such as the Yolo Bypass (Fig. 1) in the Central Valley of California (Opperman 2008; Moyle et al. 2013). Historically, the Yolo Bypass was a large, natural floodplain (the Yolo Basin) that inundated at least partially in all years, increasing connectivity throughout the river channels and tidal sloughs of the northern Sacramento-San Joaquin Delta (Whipple et al. 2012). This provides a context for why individuals of both species enter the present-day Yolo Bypass each year during spawning periods; however, the role of the managed Yolo Bypass in the spawning life stage of these species is not well understood. With the exception of providing access to Putah Creek (Fig. 1), which offers some spawning habitat for Chinook Salmon when it is accessible (Chapman et al. 2018), the Yolo Bypass does not contain suitable spawning substrate for either species. Additionally, a lack of consistent fish passage through the Yolo Bypass has resulted in stranding and mortality of adult White Sturgeon, Green Sturgeon, and Chinook Salmon since the 1980s, especially in wet years after floodwaters begin to recede (Williams 2006; Thomas et al. 2013; Heublein et al. 2017). Prior to 2019, the Yolo Bypass provided unimpaired fish passage to the Sacramento River only during flood conditions, when Sacramento River unimpaired runoff was greater than 9.62×10^9 m^3 (7.8 million acre-feet) and/or river stage is greater than 9.8 m (32 ft. NADV88), the stage at which floodwaters overtop the Fremont Weir (Fig. 1) and flow into the Yolo Bypass. Historically, these conditions have occurred in roughly 60% of years (Harrell and Sommer 2003); relative to this study, these conditions occurred for 3 days in December of 2014, less than 1 day in January of 2016, 15 days in March of 2016, 4 days in December of 2016, and intermittently for approximately 100 days in January–April of 2017 (https://cdec.ca.water.gov). Recently implemented fish passage improvements (including modifications to the fish ladder at Fremont Weir and the Wallace Weir Fish Rescue Facility downstream) have begun to address barriers to Chinook Salmon and White Sturgeon passage in the Yolo Bypass (California Department of Water Resources 2020). Prior to the completion of these projects, there was no passage to the Sacramento River at Fremont Weir in the absence of floodwaters. Migrating adult White Sturgeon and Chinook Salmon that entered the base of the system via the Toe Drain canal (Fig. 1) had to turn around and exit before they could migrate up the Sacramento River. As a result, this "exit behavior" from the system was critical to the migratory success of these species when the Yolo Bypass was not flooded.

Especially because of the stranding risk it still poses in most years (Thomas et al. 2013; Sommer et al. 2014), understanding how Chinook Salmon and White Sturgeon navigate the Yolo Bypass is key to managing for their migratory success going forward, and has implications for many other systems where unintended consequences arising from complexity of either natural or altered hydrology and fish passage facilities will disproportionately affect migratory fishes (Pelicice and Agostinho 2008; McLaughlin et al. 2013). The goal of this multi-year study was to examine differences in migratory behavior and to estimate each species' probability of exiting the Yolo Bypass during their peak migratory periods, while accounting for tag shedding or mortality events.

Methods

Study area

The Yolo Bypass system is a 240 km^2 (59,000-acre) managed floodplain in the Central Valley of California that occupies the lower portion of the region's historical flood basin (Sommer et al. 2001a; Fig. 1). The partially-leveed system has been modified to divert floodwaters from the Sacramento River and its tributaries around the city of Sacramento and surrounding metropolitan areas. The hydrology of the system is complex, with inputs from smaller west-side streams (Putah Creek, Cache Creek, Knights Landing Ridge Cut; Fig. 1) as well as seasonal inundation from Sacramento Valley floodwaters via two weirs, Fremont Weir and Sacramento Weir (Fig. 1). The Toe Drain Canal, which runs along the eastern edge of the Yolo Bypass, is the only perennially-navigable water channel within the Yolo Bypass. During drier periods, when Sacramento River discharge at Knight's Landing is less than approximately 2000 m^{3}s^{-1} and the Fremont Weir is *not* overtopping, the Toe Drain functions as a tidal slough as far north as Interstate-80, receiving tidal flows from the Cache Slough complex (which lies just north of the mouth of the Sacramento River; Fig. 1). The extent of the area monitored in this study spanned approximately 60 km, from Wallace Weir (River Kilometer 166 at the base of Ridge Cut, measured from the Golden Gate Bridge in the San Francisco Bay) downstream to the Cache Slough complex (River Kilometer 106). The Toe Drain itself terminates within the Yolo Bypass north of the Cache Slough complex, at approximately River Kilometer 114.

Tagging

White sturgeon White Sturgeon were captured in an eight-meter long, three-chambered fyke trap, located in the Toe Drain and maintained by the California Department of Water Resources (CDWR) (Sommer et al. 2014). A sturgeon caught in the fyke trap was placed in a two-meter fish cradle rested between two sawhorses, with the sturgeon in an inverted position and water pumped from the Toe Drain flowing over its gills. As White Sturgeon can be caught by fishermen and consumed following their release, no anesthetic was used, but all other surgical and histological sampling procedures followed Heublein et al. (2009). White Sturgeon were implanted with an acoustic transmitter (Vemco, Inc. V16-H) 16 mm in diameter, 90 mm long weighing 14 g, battery life between 1 and 10 years (tags used in 2012 had shorter battery life than tags used in 2014). For White Sturgeon tagged in 2014, a blood sample (~3 mL or less) was also collected from the caudal vein, posterior to the anal fin via hypodermic needle and stored in a vacutainer. The blood samples were later centrifuged and the plasma extracted and assayed in order to validate the sex determination of the histological analysis. In all cases, sturgeon recovered quickly from surgery and were released immediately following at the site of capture. No known mortalities were associated with the tagging procedure, which took 3–4 min for each fish. Only fish larger than 80 cm were tagged.

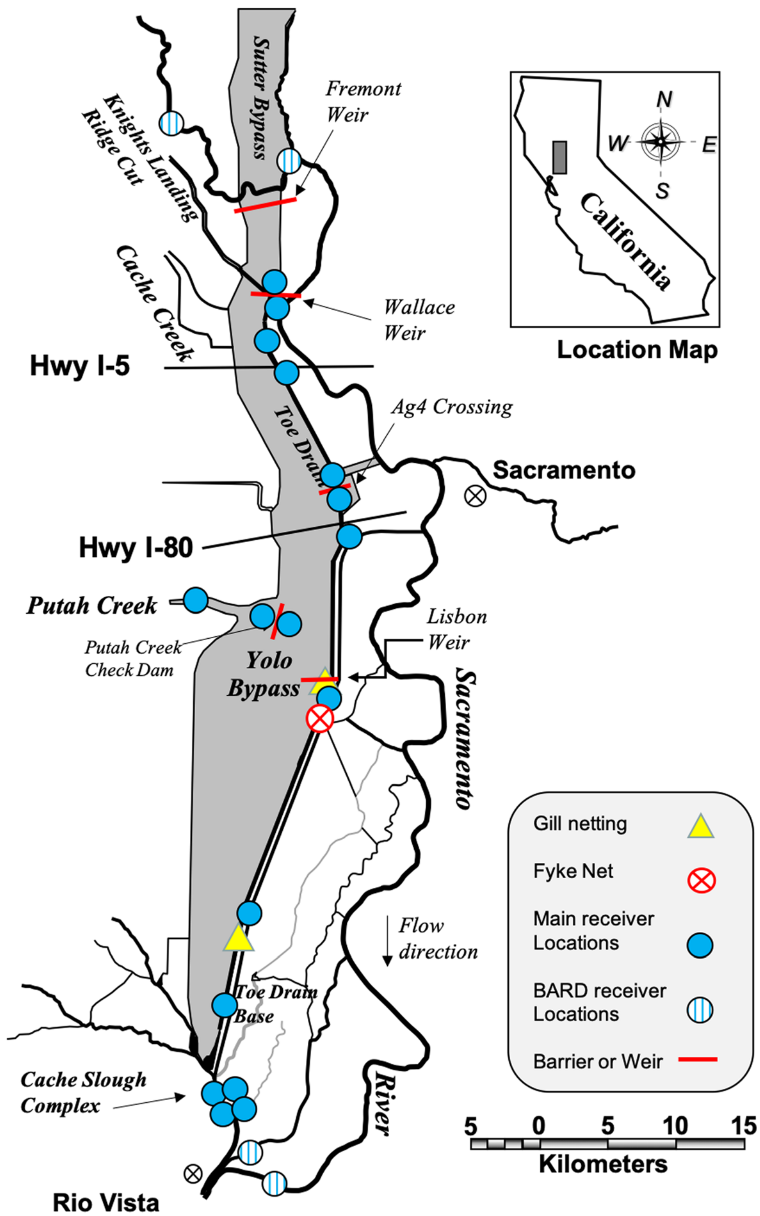

Fig. 1 Study area, tagging locations (Chinook Salmon were sampled at both the Fyke Net and the gill netting sites; White Sturgeon were sampled only at the Fyke Net), primary Yolo Bypass receiver locations, selected BARD receiver locations, and passage barriers throughout the study area

Chinook salmon Chinook Salmon were sampled via the same CDWR fyke trap, or by trammel and/or gill netting. Netting took place either on the downstream side of Lisbon Weir, or approximately 1.0 km downstream of the CDWR Rotary Screw Trap in the Toe Drain (Fig. 1). Chinook Salmon sampled from the fyke trap were transported in a two-meter fish cradle to a specially-constructed fish surgery cradle. The upright, 1 m-long wooden cradle was lined with foam and coated with aquarium water conditioner to avoid disturbing the mucus layer on the salmon. A damp cloth was placed over the salmon's head to protect the eyes. A tube was inserted into the mouth of the salmon to maintain a gentle flow of water passing over the gills. Once the fish was securely in place, a V9 acoustic tag (9 mm in diameter, 21–45 mm length, weighing 1.6–3.3 g; Vemco, Inc.) was attached to the base of its dorsal fin. This involved passing two 3.5-inch, 17-gauge needles completely through the tissue at the base of the dorsal fin so that they protruded on the opposite side of the puncture point. The two ends of a 10-inch, 26-gauge stainless steel wire, with a V9 tag shrink-wrapped to the middle of it, was threaded through the needles so that both ends of the wire were on the same side of the dorsal fin. The needles were then removed, and the wire gently pulled to cinch down the tag at the base of the dorsal fin. The wires were then twisted together tightly (10–15 twists), securing the tag in place. Excess wire was cut off and the ends of the remaining wire were pushed close to the fish and coated with wax to prevent snagging. Fish tagged after 2014 also had external Floy® tags affixed to the dorsal side of their bodies, opposite and offset from the external acoustic tag. After the tagging procedure was complete (approximately 2 min), the salmon was placed in an oxygenated recovery tank and observed until orientation returned (1–4 min), after which it was carefully released back to the Toe Drain.

In 2012 and 2013, some adult Chinook Salmon were sedated prior to tagging using carbon dioxide (CO_2). If a fish could not be adequately restrained during collection, it was placed in a temporary holding tank (>100-liter capacity). Compressed CO_2 from a small cylinder was released into the water bath at a rate such that it did not displace air by more than 20% of the chamber volume per minute, following IACUC dosage recommendations (Borski and Hodson 2003). When loss of equilibrium was achieved, the fish was removed and placed on the surgical table for the procedure. Because we noticed increased recovery and handling time in some fish, we discontinued the use of CO_2 after 2013.

Fish caught using a gill-net or trammel net followed the same procedures, except that they were transferred from the net into a CDWR boat for transport to shore. The boat was equipped with a holding tank (>100-l capacity) for fish transport before surgery (transport to shore took less than 1 min). In order to prevent recapture in the gill net, fish tagged below the rotary screw trap were released slightly upstream (approximately 0.5 km) of where they were caught; fish tagged at Lisbon Weir were released approximately 50 m away from the gill netting site, on the downstream side of the weir. A summary of tagged fish across years is given in Table 1.

Acoustic receiver Array

The presence or absence of the released fish was recorded with an array of 69khz-sensitive acoustic receivers (VEMCO Ltd., VR2W) placed throughout the Yolo Bypass (Fig. 1). The acoustic array consisted of single, autonomous receivers in most locations. At the base of the Cache Slough complex where the width of the river exceeded expected detection range of a single receiver, at least two receivers were deployed. Fig. 1 displays the receiver locations that were used consistently across years of the study, however, the spatial organization of individual reaches and number of receivers differed slightly between years. The acoustic receiver array data were downloaded approximately quarterly.

Analysis

Data included for analysis begin in March of 2012 and end in April of 2018. For easier reference to migration periods of both White Sturgeon and fall-run Chinook Salmon within a single analysis unit, acoustic detections of tagged fish were grouped by "detection year." A detection year begins on July 1st and extends through June 30th of the following year (Table 2). Thus, the detection data (March 2012–April 2018) spans seven detection years: 2011–2017 (Table 2). The raw data from the Yolo Bypass receiver array was first processed with the software program VUE (Version 2.4, Vemco, Inc), and then with the statistical programming software R (Version 3.6.2, The R Core Team 2020). All detections were corrected in VUE for the time-drift that occurred in the receivers during deployment. False detections were identified using VUE's screening tool, where single detections of a fish are flagged for review; the detection was discarded as false if it was inconsistent with the spatiotemporal context of the rest of the fish's detections.

Tag "shedding" events were identified either as: any tag that remained in a single location with continuous detection for at least 7 days (i.e., no gaps in detections greater than 1 h during the 7-day period at a single location), or as a fish subsequently recovered (by anglers or researchers) without its acoustic tag present. The latter occurred for three Chinook Salmon: two in detection year 2014 (fish were recovered in the Wallace Weir fyke trap with wires present but no acoustic tags), and one in detection year 2015 (fish recovered in the Wallace Weir fyke trap with Floy® tag intact but not acoustic tag present). The two fish recovered in the Wallace Weir fyke trap 2014 were individually identified through recorded fork length at tagging and re-capture and by their detection histories relative to the time of re-capture.

Table 1 Tagging summaries for White Sturgeon and fall-run Chinook Salmon monitored in this study. Year tagged refers to the calendar year in which the fish were tagged

Year Tagged	Species	Total Tagged	Fork Length Range (mm)	Mean Fork Length in mm (SD)	Number of Males	Number of Females	Number of Unknown Sex
2013	Chinook	49	600–998	809 (93)	21	23	5
2014	Chinook	35	618–960	750 (89)	15	15	5
2015	Chinook	30	556–955	743 (91)	17	11	2
2016	Chinook	51	552–919	701 (93)	15	14	22
2017	Chinook	50	555–925	695 (94)	31	18	1
2012	White Sturgeon	67	960–1900	1462 (235)	42	4	21
2014	White Sturgeon	25	980–1900	1438 (256)	23	1	1

Table 2 White Sturgeon returns, Chinook Salmon detection summaries, and recorded exit status for both White Sturgeon and Chinook Salmon by detection year

Detection year	Calendar date range	Number of White Sturgeon detected	Number of White Sturgeon exited	Number of White Sturgeon that did not exit	Number of Chinook Salmon detected	Number of Chinook Salmon exited	Chinook Salmon that did not exit	Chinook Salmon with confirmed shed tags within the Yolo Bypass
2011	2011-07-01 – 2012-06-30	67	63	4	NA	NA	NA	NA
2012	2012-07-01 – 2013-06-30	10	10	0	NA	NA	NA	NA
2013	2013-07-01 – 2014-06-30	35	35	0	49	44	5	0
2014	2014-07-01 – 2015-06-30	18	18	0	35	22	11	2
2015	2015-07-01 – 2016-06-30	22	21	1	30	19	10	1
2016	2016-07-01 – 2017-06-30	22	22	0	51	42	9	0
2017	2017-07-01 – 2018-06-30	8	8	0	50	32	18	0

No White Sturgeon had confirmed shed tag events. Chinook Salmon exit counts include fish detected upstream of the Putah Creek check dam. White Sturgeon tagging took place in March of 2012 and 2014 (detection years 2011 and 2013, respectively); Chinook Salmon tagging for the fish analyzed in this study occurred every year until 2017, beginning in fall 2013 (detection year 2012)

After analyzing for false detections, the remaining detections in the database were processed into individual detection histories and analyzed for assignment to one of three "exit" categories according to pre-defined criteria: 1) a successful exit, 2) an unsuccessful exit (i.e. an unconfirmed shed tag or mortality event within the Yolo Bypass), or 3) a confirmed shed tag event. A successful exit was defined as a fish which, after being observed as moving directionally downstream (i.e., the progression of its detection history moved downstream within the Yolo Bypass), was detected at either the Base of the Toe Drain or the Cache Slough Complex (Fig. 1) and then was not detected in the Yolo Bypass again upstream of the Cache Slough Complex in the Yolo Bypass array within the same detection year. Because detection probability was not perfect at any individual receiver, the receivers at the base of the Toe Drain and in the Cache Slough Complex were grouped for the purpose of defining an exit or the lack of one. For Chinook Salmon, a successful exit was also recorded if its final detection location was above the Putah Creek check dam (Fig. 1), under the assumption that having passed above the check dam, these fish had the potential to access suitable spawning habitat in Putah Creek and did not need to exit the Yolo Bypass again in order to complete a successful migration. An *unsuccessful* exit (category 2) was then defined as a fish with a final detection location somewhere within the Yolo Bypass array upstream of the Cache Slough Complex and/or the Base of the Toe Drain, and that was also not detected anywhere outside of the Yolo Bypass array after its final detection within the Yolo Bypass. The only fish assigned to exit category 3 were the three re-captured Chinook Salmon described above.

To support these exit category definitions, a data query on the Biotelemetry Autonomous and Real-time Database (BARD; http://cftc.metro.ucdavis/BARD/) was run on the tag IDs from this study so that detection histories for each fish could be cross-checked with those from the Yolo Bypass array. The BARD database (formerly the core array of the California Fish Tracking Consortium) included receivers in place throughout the Sacramento-San Joaquin Delta during the entirety of our study period. The majority of BARD receivers were deployed and maintained by researchers involved in this study; as deployment methods and maintenance were similar, the probability of detection and detection range would have been comparable to the Yolo Bypass receivers. Some relevant locations of BARD receivers are indicated in Fig. 1, including those just beyond the upstream and downstream extent of the Yolo Bypass receiver array; details on the full extent of the array in place during this study are available in the analysis repository at https://github.com/Myfanwy/Johnstonetal2019_EBF.

The Fremont Weir did overtop several times during this study period, particularly in late 2014, 2016, and early 2017 (detection year 2016). The BARD receivers located upstream and downstream of Fremont Weir (at Knights Landing and near the junction with the Feather River, respectively) did not reveal any detection histories of tagged fish consistent with having passed over Fremont Weir during overtopping events, and only one tagged Chinook Salmon (in 2014) was detected in the upper reaches of the Bypass just prior to an overtopping event; the fish was not subsequently detected again. Our receiver array did not provide full coverage of the weir, however, and detection probabilities at acoustic receivers are lower during high flow events (Steel et al. 2014) so we cannot be certain that tagged fish did *not* pass over Fremont Weir while it was overtopping. However, the total coverage of the Yolo Bypass and BARD arrays before and after overtopping events, the near-complete detection record for tagged White Sturgeon during these events, and the lack of tagged Chinook Salmon detected at receivers leading upstream to the Fremont Weir in the Toe Drain prior to overtopping events make it unlikely that this occurred with any significant consequences to the results of this analysis.

Modeling

A multi-logistic regression model (sometimes called a categorical logistic regression model) was written in Stan and fit in R using the *rstan* package (Stan Development Team 2018) to estimate the probability of a categorical outcome y, one of K possible categories, determined by θ. Our model allowed for three possible values of the outcome y, corresponding to the exit categories defined above: *1:* exiting the Yolo Bypass; *2:* not exiting the Yolo Bypass (i.e. a possible mortality or shed tag); or *3:* confirmed shedding of a tag. θ is then a simplex of probabilities of length K, one for each outcome, which sum to 1.0:

$$y_i \sim Categorical(\theta_i)$$

In turn, θ_i is determined by a linear regression with a softmax link function:

$$\theta_i = Softmax(X_i * \beta + U_i)$$

where X_i is a vector of predictors, β is a matrix of predictors with K columns (one per outcome) and D rows (one per predictor). The term U_i is a vector of random effects for observation i of length K, one for each outcome. The softmax link function ensures that the vector θ_i is between 0 and 1 (similar to the logistic link function) and that it sums to 1.

The design was unbalanced: both species were not observed or tagged in all detection years and many individual White Sturgeon returned in multiple detection years (Table 2). Hence their observations could not be considered independent, and we first fit a model with random effects (varying intercepts) for both tag identification number (tag ID) and detection year. However, due to the small amount of information on individual effects, the variance parameter for tag ID was estimated to included zero. Because the proportion of Chinook Salmon categorized as 2 (shed tag/mortality) varied with year (ranging from 0.10–0.36), we also fit a model incorporating a year-species interaction with random effects; the interaction did not have a consistent predictive effect on exit category (all credible intervals included zero. Finally, we fit a model with random effects on detection year only. We compared the three models using Widely-Available Information Criteria (WAIC, a Bayesian information criteria method comparable with AIC in frequentist statistics) with the *loo* package (Vehtari et al. 2019). WAIC determined no substantial difference in fit between the three models (incorporating the interaction and tag ID effects increased uncertainty without improving model fit), so in service of parsimony we present the simplest model of the three. The final model structure was then:

$$y_i \sim Categorical(\theta_i)$$

$$\theta_i = \alpha + \beta_{Species_i} + U_{DetectionYear_i}$$

where exit status y for the observation of fish i was equal to 1, 2, or 3 according to the three exit categories described above. The *ggplot2* package (Wickham 2016) was used for data visualization. The analysis code including all candidate models and data is available at www.github.com/Myfanwy/Johnstonetal2019_EBF.

Results

Fish observations

A total of 215 Chinook Salmon and 92 White Sturgeon were tagged and monitored over the course of the study (Table 1). Blood samples were not available for the 67 White Sturgeon tagged in 2012, but steroid profiles of blood samples taken from White Sturgeon tagged in 2014 confirmed that the sex ratio of the 25 individuals tagged was heavily male-biased (23 were male one was female, and one was indeterminate). Field morphometrics used in the field estimated the sex ratio of Chinook Salmon to be more balanced (1.2 male:female average). Returning tagged White Sturgeon were detected exiting the Yolo Bypass more consistently across years than Chinook Salmon and had no confirmed shed tag events (Table 2). Individual residence time was not modeled, but across detection years (2011–2017), White Sturgeon were detected within the Yolo Bypass in all months of the year except July. Some individuals were detected at the base of the Cache Slough complex in October of each calendar year and did not exit the Yolo Bypass array until January–April of the following calendar year. We were unable to verify the passage of any individual tagged fish over the Fremont Weir in flooded conditions, but we did note that the wettest conditions experienced with respect to fall-run Chinook Salmon (detection year 2016) was associated with the highest recorded number of fish detected in Putah Creek across all the years monitored (11 fish in 2016, vs. 2 fish in 2013, 0 fish in 2015 and 5 fish in 2017).

Model results

An individual Chinook Salmon had an estimated median probability of 0.74 of successfully exiting the Yolo Bypass (0.58–0.87 95% credible interval, defined as the interval that includes 95% of the mass of the posterior distribution as computed by the quantile method), while an individual White Sturgeon had a median exit probability of 0.99 (0.96–1.00 95% credible interval) (Table 3). The median difference in probability of exit between White Sturgeon and Chinook Salmon was 0.24 (0.12–0.40 95% CI).

Discussion

Relative to fall-run Chinook Salmon, the White Sturgeon in this study had a much higher probability of exiting the Yolo Bypass across years (Fig. 2). The disparate reproductive strategies of White Sturgeon and Chinook Salmon may offer some insight into these results. As an iteroparous species, White Sturgeon may be predisposed to abandon a migratory path when conditions do not appear to be favorable to spawning (Moyle 2002). As a White Sturgeon proceeds northward in the Yolo Bypass in a dry year, the Toe Drain becomes narrower and shallower with an absence of suitable spawning substrate. White Sturgeon attuned to these local cues may actively turn around and exit in response. Alternately, White Sturgeon in the Yolo Bypass may not have embarked on a directional spawning migration at all; since their spawning migrations are intermittent, we do not know if an individual movement path in the Yolo Bypass is in pursuit of spawning, or if it is for a different ecological function altogether. In contrast, fall-run Chinook Salmon have a single opportunity to spawn in their lifetime, are unlikely to enter the Delta as adults during their spawning period for any other reason, and are not likely to turn around once embarking on a directional path (Dingle 2014; Quinn 2018). Thus, in the absence of connectivity to the Sacramento River, Chinook Salmon may be more susceptible to experiencing the Yolo Bypass as a migratory trap than White Sturgeon.

The Yolo Bypass has often been cast in one of two contrary ecological roles. The first role is as a native fish refuge and management success story. When flooding occurs, the Yolo Bypass represents some of the most important seasonal habitat available for native fish in the region (Sommer et al. 2001a, b, 2004, 2008; Jeffres et al. 2008; Feyrer et al. 2006). Juvenile Chinook Salmon reared in floodplain habitat have exhibited greater growth and survival than those reared in the mainstem river (Kjelson et al. 1982; Sommer et al. 2001a; Jeffres 2017). Sacramento splittail (*Pogonichthys macrolepidotus*) produce their strongest year classes when the Yolo Bypass experiences extended flood conditions (Sommer et al. 1997). In addition to the increased rearing area present during floodplain inundation, food supply is increased through enhanced populations of fish and invertebrates on the floodplain (Feyrer et al. 2006; Jeffres 2017). Even in dry years, juvenile Chinook released in the Toe Drain have exhibited relatively high survival (Johnston et al. 2018). Finally, the Yolo Bypass supports numerous human demands in the form of flood control, agriculture, and recreation.

The second role in which the Yolo Bypass is cast is as a migratory trap for adult native fishes (Thomas et al. 2013; Sommer et al. 2014); a designation shared by many other altered migratory corridors worldwide (Pelicice and Agostinho 2008; Jeffres and Moyle 2012; McLaughlin et al. 2013). Even when the Fremont Weir is not overtopping, the flows in the Cache Slough complex are typically stronger than in the mainstem of the Sacramento River because of tidal effects. Flow increases as small as 40 m^3s^{-1} have triggered upstream movement and spawning in White Sturgeon in the Sacramento River (Schaffter 1997), and attraction to channels of greater relative velocity has been demonstrated in salmon species (Smith et al. 1997). As a result, White Sturgeon and Chinook Salmon may be drawn into the Toe Drain by the higher flows in the Cache Slough complex relative to those at the entrance of the Sacramento River (Sommer et al. 2014). As they migrate up the Toe Drain, migrants use finite bioenergetic resources in their attempt to reach spawning grounds that are not accessible to them. Delays in upstream movement can occur at numerous partial barriers to passage, including Lisbon Weir, the Swanston ("Ag4") agricultural crossing just north of the I-80 Bridge in the Toe Drain, and Wallace Weir (Fig. 1). When the Yolo Bypass does flood, the temporal connection between the floodplain and the Sacramento River is much briefer than it would have been historically (Whipple et al. 2012). In this condition, threatened and endangered species (including green sturgeon and winter-run Chinook Salmon) can become stranded, and thus vulnerable to poaching (Thomas et al. 2013; Heublein et al. 2017). Adult migrants can also succumb to low oxygen conditions and high temperatures (Vincik and Johnson 2013), removing them from the spawning population.

The results of this study suggest that for adult White Sturgeon and fall-run Chinook Salmon, the Yolo Bypass represents a mixture of both roles. There are overarching differences in seasonal residence and migratory behavior in the Yolo Bypass between the two species. White Sturgeon in particular have a much longer seasonal residence period than previously thought; after leaving the Yolo Bypass in mid-April – June each year, many returning individuals from this study were consistently detected within the Yolo Bypass again beginning in September or October (Cramer Fish Sciences MASL

Table 3 Estimated marginal probability of each of three exit categories by species. Estimates presented are medians, with 95% Credible Intervals in parentheses

Species	Probability of non-exit/shed tag/mortality	Probability of exit	Probability of confirmed shed tag event
White Sturgeon	0.01 (0.00–0.04)	0.99 (0.96–1.00)	5.98e-05 (7.65e-04 - 5.69e-03)
Chinook Salmon	0.25 (0.13–0.41)	0.74 (0.58–0.87)	3.66e-03 (3.93e-04 – 0.02)

2019). Since White Sturgeon spawning peaks between February and April, the arrival of White Sturgeon in the Yolo Bypass well before this time signifies that White Sturgeon may be “staging” ahead of their migration (Klimley et al. 2015; Heublein et al. 2017) or utilizing the Bypass for some other essential function (i.e., feeding). If White Sturgeon benefit from the Yolo Bypass outside of their spawning period, support may be added to the role of the Yolo Bypass as beneficial habitat to adult native California fishes even under low-flow conditions, even for those species to which it poses significant risks under other conditions (e.g., Thomas et al. 2013). Additionally, 13 of the tagged fall-run Chinook Salmon in detection years 2016 and 2017 reached spawning habitat in Putah Creek (Fig. 1), confirmed by detection histories and/or carcass surveys. Under low-flow conditions, the Toe Drain represents the only migratory route currently available for Chinook Salmon to enter Putah Creek, providing tremendous reproductive benefit to individuals of that species. However, our results suggest that for most fall-run Chinook Salmon, the Yolo Bypass represents a potential energetic and/or migratory trap during their spawning migration. Relative to White Sturgeon, the tagged fall-run Chinook Salmon in this study were much less likely to exit the Yolo Bypass, exposing them to a higher risk of stranding.

This study contrasted the two species within the contexts of reproductive strategy and individual behavior, but there are many factors apart from these that would influence the movement of these two species. While their residence in the Yolo Bypass does overlap, White Sturgeon and fall-run Chinook Salmon migrate during different times of the year. As a result, they may

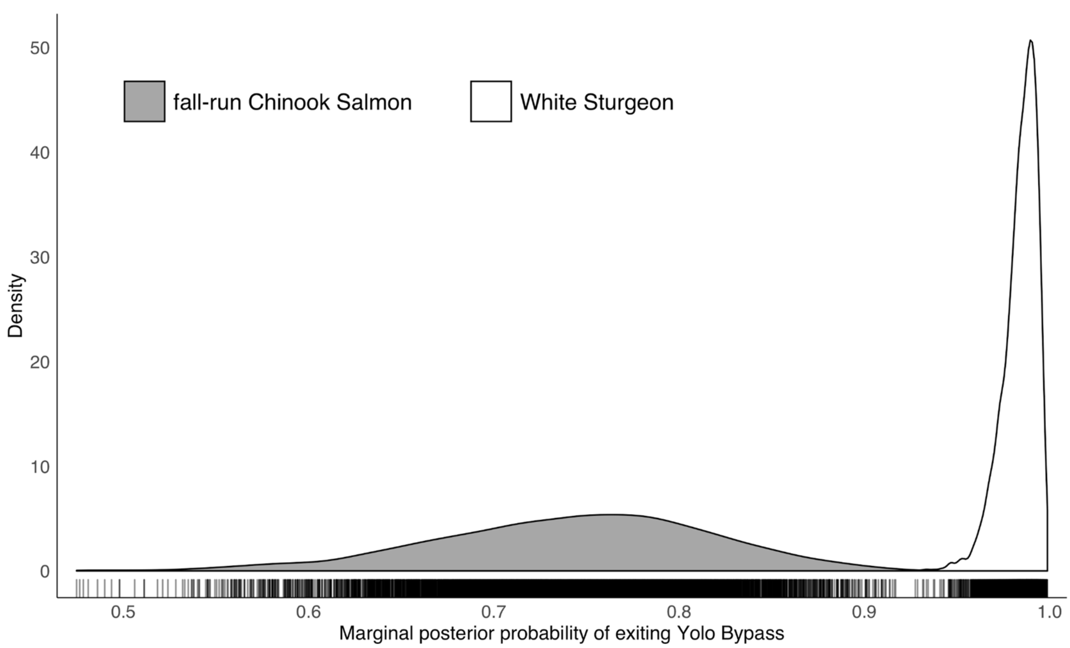

Fig. 2 Density of the distributions for each species' estimated probability of exiting the Yolo Bypass, averaged over the variability in detection years. The 95% credible interval for each marginal distribution is plotted (0.58–0.88 for Chinook Salmon, 0.96–0.99 for White Sturgeon). Rug marks representing posterior samples have been added at 50% transparency to aid in visual assessment of the tails of the distributions

experience very different hydrological conditions, affecting their relative likelihoods of turning around and exiting the Bypass in any given year. It is also important to note that Chinook Salmon may be fully capable of exiting unsuitable habitat if they receive signals along the migratory corridor that conditions are impassable or unsuitable for spawning, but that these signals were unavailable as a consequence of this system's altered hydrology. Finally, it is difficult to compare tagging effects between two different species and attachment methods. We chose external tagging methods because a recent study had found the risk of mortality was lower than for gastrointestinal tags, and because external tags were well-suited to short-term deployments (Corbett et al. 2012; Thorstad et al. 2013), but it is possible that Chinook Salmon in this study were more affected by the tagging process than White Sturgeon.

There are still many unknowns in what the Yolo Bypass represents to adult migrating native fishes. For White Sturgeon that successfully exit the Yolo Bypass and complete a migration up the Sacramento River in the same year, it is unknown whether the time spent in the Yolo Bypass is beneficial or harmful to their spawning success. The tendency of fall-run Chinook Salmon to exit with lower probability than White Sturgeon indicates that a portion of the population entering the Yolo Bypass each year is exposed to a higher risk of stranding. However, the Toe Drain also represents the only migratory route available for Chinook Salmon to reach the spawning habitat in Putah Creek under low-flow conditions. These mixed costs and benefits to individuals of both species indicate that the role of the Yolo Bypass during the adult life stage of White Sturgeon is more complex than we currently understand and that management of adult Chinook Salmon passage throughout the Yolo Bypass requires recognition of the risks and benefits it provides to the species across a range of conditions.

Conclusions

The difference in what the Yolo Bypass represents to these two native species has implications for how we should manage their migratory passage and presents a case study for similarly altered migratory systems worldwide. White Sturgeon very successfully enter and exit the Yolo Bypass in consecutive years and may be utilizing it for something other than a migratory corridor. For at least a portion of migrating fall-run Chinook Salmon, the Yolo Bypass may represent a migratory trap, especially in drier years and as the migration season advances. Fish passage improvements at Fremont Weir and the newly-operational (January 2019) Wallace Weir Fish Rescue Facility have been designed to help mitigate stranding, and ongoing data collection from tagged fish will help managers assess exit behavior before and after these projects are completed. Chinook Salmon passage to spawning habitat in Putah Creek should be maintained and improved. The large difference found in the movement behavior and resultant exposure to stranding risk in the same migratory corridor (albeit at different times of year) provides context for studies of migratory behavior in other altered systems where passage and/or exposure to risk of stranding may be species-specific.

Acknowledgements We thank all persons who generously offered their time, expertise, and resources assisting this study and analysis, especially Matthew Pagel, Naoaki Ikemiyagi, Lynn Takata, Lauren Miele, Sheena Holley, James Newcomb, Mike Thomas, John Brennan, Jacob Katz, Michelle Stone, Philip Sandstrom, and Ryan Battleson. The manuscript was greatly improved by the constructive comments of two anonymous reviewers. This work was originally funded by the Department of Fish and Wildlife Ecological Restoration Program and approved by the UC Davis Protocol for Animal Care and Use Committee.

References

Borski RJ, Hodson RG (2003) Fish research and the institutional animal care and use committee. ILAR J 44(4):286–294

California Department of Water Resources (2020) Yolo bypass habitat restoration projects. Yolo Bypass Projects. https://water.ca.gov/Programs/Environmental-Services/Restoration-Mitigation-Compliance/Yolo-Bypass-Projects. Accessed 2 Dec 2020

Chapman E, Jacinto E, Singer G, Willmes M, Hobbs J, Moyle P (2018) Restoration on Putah Creek Provides Home for Chinook Salmon. Oral Presentation. Bay Delta Science Conference, Sacramento, California, September 12

Corbett SC, Moser ML, Dittman AH (2012) Experimental evaluation of adult spring Chinook salmon radio-tagged during the late stages of spawning migration. N Am J Fish Manag 32(5): 853–858

Dingle H (2014) Migration: the biology of life on the move, 2nd edn. Oxford University Press, New York

Dittman A, Quinn T (1996) Homing in Pacific salmon: mechanisms and ecological basis. J Exp Biol 199(1):83–91

Feyrer F, Sommer T, Harrell W (2006) Managing floodplain inundation for native fish: production dynamics of age-0 splittail in California's Yolo bypass. Hydrobiologia 573:213–226

Freeman MC, Pringle CM, Greathouse EA, Freeman BJ (2003) Ecosystem-level consequences of migratory faunal depletion caused by dams. Am Fish Soc Symp 35:255–266

Groot C, Simpson K, Todd I, Murray PD, Buxton GA (1975) Movements of sockeye salmon (Oncorhynchus nerka) in the Skeena estuary as revealed by ultrasonic tracking. J. Fish Res Board Can 32:233–242

Harrell WC, Sommer TR (2003) Patterns of Adult Fish Use on California's Yolo Bypass Floodplain. In: Faber PM (ed) *California riparian systems: Processes and floodplain management, ecology, and restoration*, 2001 Riparian habitat and floodplains conference proceedings. Riparian Habitat Joint Venture, Sacramento, pp 88–93

Heublein JC, Kelly JT, Crocker CE, Klimley AP, Lindley ST (2009) Migration of green sturgeon, Acipenser medirostris, in the Sacramento River. Environ Biol Fishes 84(3):245–258. https://doi.org/10.1007/s10641-008-9432-9

Heublein J, Bellmer R, Chase RD, Doukakis P, Gingras M, Hampton D, Israel JA, Jackson ZJ, Johnson RC, Langness OP, Luis S, Mora E, Moser ML, Rohrbach L, Seesholtz AM, Sommer T, Stuart JS (2017) Life history and current monitoring inventory of San Francisco estuary sturgeon. U.S. Department of Commerce, NOAA technical memorandum NMFS-SWFSC-589. https://doi.org/10.1007/s10641-008-9432-9

Jackson ZJ, Gruber JJ, Van Eenennaam JP (2016) White sturgeon spawning in the San Joaquin River, California, and effects of water management. J Fish Wildl Manag 7(1):171–180

Jeffres CA (2017) From Subduction to Salmon: *Understanding Physical Process and Ecosystem Function in Aquatic Ecosystems*. Diss. University of California, Davis

Jeffres C, Moyle P (2012) When good fish make bad decisions: coho salmon in an ecological trap. N Am J Fish Manag 32(1):87–92

Jeffres CA, Opperman JJ, Moyle PB (2008) Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook Salmon in a California river. Environ Biol Fish 83(4):449–458

John G. Williams, (2006) Central Valley Salmon: A Perspective on Chinook and Steelhead in the Central Valley of California. San Francisco Estuary and Watershed Science 4 (3)

Johnston ME, Steel AE, Espe M, Sommer T, Klimley AP, Sandstrom P, Smith D (2018) Survival of juvenile Chinook salmon in the Yolo bypass and the lower Sacramento River, California. San Francisco Estuary Watershed Sci 16(2)

Kjelson MA, Raquel PF, Fisher FW (1982) Life history of fall-run juvenile Chinook Salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin estuary, California

Klimley AP, Chapman ED, Cech JJ Jr, Cocherell DE, Fangue NA, Gingras M, Jackson Z, Miller EA, Mora EA, Poletto JB, Schreier AM, Seesholtz A, Sulak KJ, Thomas MJ, Woodbury D, Wyman MT (2015) Sturgeon in the Sacramento–San Joaquin watershed: new insights to support conservation and management. San Franc Estuary Watershed Sci 13(4). https://doi.org/10.15447/sfews.2015v13iss4art1

Kohlhorst DW (1976) Sturgeon spawning in the Sacramento River in 1973, as determined by distribution of larvae. Calif Fish Game 62(1):32–40

Kohlhorst DW, Botsford LW, Brennan JS, Caillet GM (1991) Aspects of the structure and dynamics of an exploited Central California population of white sturgeon (*Acispenser transmontanus*). In: Williot P (ed) Acipenser. Cemagref Publishers, Bordeaux, pp 277–293

McLaughlin RL, Smyth ER, Castro-Santos T, Jones ML, Koops MA, Pratt TC, Vélez-Espino LA (2013) Unintended consequences and trade-offs of fish passage. Fish Fish 14(4):580–604

Miller LW (1972) Migrations of sturgeon tagged in the Sacramento-San Joaquin Estuary. Calif Fish Game 58(2):102–106

Moyle PB (2002) Inland fishes of California. Univ of California Press

Moyle PB (2013) Novel aquatic ecosystems: the new reality for streams in California and other Mediterranean climate regions. River Res Appl

Moyle PB, Katz JV, Quiñones RM (2011) Rapid decline of California's native inland fishes: a status assessment. Biol Conserv 144(10):2414–2423

Opperman J (2008). Floodplain conceptual model. Sacramento (CA). Delta Regional Ecosystem Restoration Implementation Plan. http://www.science.calwater.ca.gov/pdf/drerip/DRERIP_floodplain_conceptual_model_final_012208.pdf

Pelicice FM, Agostinho AA (2008) Fish-passage facilities as ecological traps in large neotropical rivers. Conserv Biol 22(1):180–188

Quinn TP (2018) The behavior and ecology of Pacific salmon and trout. University of Washington Press

Rideout RM, Rose GA, Burton MP (2005) Skipped spawning in female iteroparous fishes. Fish Fish 6(1):50–72

Schaffter RG (1997) White sturgeon spawning migrations and location of spawning habitat in the Sacramento River, California. Calif Fish Game 83:1–20

Smith IP, Johnstone ADF, Smith GW (1997) Upstream migration of adult Atlantic salmon past a fish counter weir in the Aberdeenshire Dee, Scotland. J Fish Biol 51(2):266–174

Sommer T, Baxter R, Herbold B (1997) Resilience of splittail the the Sacramento-San Joaquin estuary. Trans Am Fish Soc 126:961–976

Sommer TR, Harrell WC, Nobriga ML, Brown R, Moyle PB, Kimmerer WJ, Schemel L (2001a) California's Yolo bypass: evidence that flood control can be compatible with fisheries, wetlands, wildlife, and agriculture. Fisheries 26:6–16

Sommer TR, Nobriga ML, Harrell WC, Batham W, Kimmerer WJ (2001b) Floodplain rearing of juvenile Chinook Salmon: evidence of enhanced growth and survival. Can J Fish Aquat Sci 58:325–333

Sommer TR, Harrell WC, Solger AM, Tom B, Kimmerer W (2004) Effects of flow variation on channel and floodplain biota and habitats of the Sacramento River, California, USA. Aquat Conserv: Mar Freshw Ecosyst 14(3):247–261

Sommer T, Harrell B, Matica Z, Feyrer F (2008) Habitat associations and behavior of adult and juvenile splittail (Cyprinidae: *Pogonichthys macrolepidotus*) in a managed floodplain wetland. San Francisco Estuary Watershed Sci 6 (2), article 3. [online serial]

Sommer TR, Harrell WC, Feyrer F (2014) Large-bodied fish migration and residency in a flood basin of the Sacramento River, California, USA. Ecol Freshw Fish 23(3):414–423

Stan Development Team (2018) RStan: the R interface to Stan. R package version 2.19.2. http://mc-stan.org

Steel AE, Coates JH, Hearn AR, Klimley AP (2014) Performance of an ultrasonic telemetry positioning system under varied environmental conditions. Anim Biotelemetry 2(1):15

The R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna https://www.r-project.org/

Thomas MJ, Peterson ML, Friedenberg N, Van Eenennaam JP, Johnson JR, Hoover JJ, Klimley AP (2013) Stranding of spawning run green sturgeon in the Sacramento River: post-rescue movements and potential population-level effects. N Am J Fish Manag 33(2):287–297

Thorstad EB, Rikardsen AH, Alp A, Økland F (2013) The use of electronic tags in fish research–an overview of fish telemetry methods. Turk J Fish Aquat Sci 13(5):881–896

Vehtari A, Gabry J, Magnusson M, Yao Y, Gelman A (2019) "loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models." R package version 2.2.0, https://mc-stan.org/loo

Vincik RF (2013) Multi-year monitoring to facilitate adult salmon passage through a temperate tidal marsh. Environ Biol Fish 96(2–3):203–214

Vincik RF, Johnson J (2013) A report on fish rescue operations at Sacramento and Delavan NWR areas April 24 through June 5, 2013 Colusa Basin Stranding Meeting, July 2013

Whipple AA, Grossinger RM, Rankin D, Stanford B, Askevold RA (2012) Sacramento-san Joaquin Delta historical ecology investigation: exploring pattern and process. San Francisco Estuary Institute-Aquatic Science Center, Richmond

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer-Verlag, New York

Williams JG (2006) Central Valley Salmon: A perspective on Chinook and Steelhead in the Central Valley of California. San Franc Estuary Watershed Sci 4(3). https://doi.org/10.15447/sfews.2006v4iss3art2

Yoshiyama RM, Fisher FW, Moyle PB (1998) Historical abundance and decline of Chinook Salmon in the Central Valley region of California. N Am J Fish Manag 18(3):487–521