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RESEARCH

Movement and Apparent Survival of Acoustically Tagged Juvenile Late-Fall Run Chinook Salmon Released Upstream of Shasta Reservoir, California

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ABSTRACT

Stakeholder interests have spurred the reintroduction of the critically endangered populations of Chinook Salmon to tributaries upstream of Shasta Dam, in northern California. We released two groups of acoustically tagged, juvenile hatchery, late-fall Chinook Salmon to determine how juvenile salmon would distribute and survive. We measured travel times to Shasta Dam, and the number of fish that moved between locations within Shasta Reservoir. We used mark-recapture methods to determine detection and apparent survival probabilities of the tagged fish as they traveled through five reaches of the Sacramento River from the McCloud River to San Francisco Bay (~590 km) over the two 3-month observation periods. After our first (February) release of 262 tagged fish, 182 fish (70%) were detected at least once at the dam, 41 (16%) were detected at least once downstream of Shasta Dam, and 3 (1%) traveled as far as San Francisco Bay. After the second (November) release of 355 tagged fish, only 4 (1%) were detected at Shasta Dam. No fish were detected below Shasta Dam, so we could not estimate survival for this second release group. The first release of fish was fortuitously exposed to exceptionally high river flows and dam discharges, which may have contributed to the more distant downstream migration and detection of these fish—though other factors such as season, diploid versus triploid, and fish maturation and size may have also contributed to release differences. The reported fish travel times as well as detection and survival rates are the first estimates of juvenile salmon emigration from locations above Shasta Dam in more than 70 years. This information should help inform resource managers about how best to assess juvenile winter-run Chinook Salmon and assist in their reintroduction to watersheds upstream of Shasta Dam.

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KEY WORDS

juvenile salmon survival; Shasta Dam; Chinook Salmon reintroduction

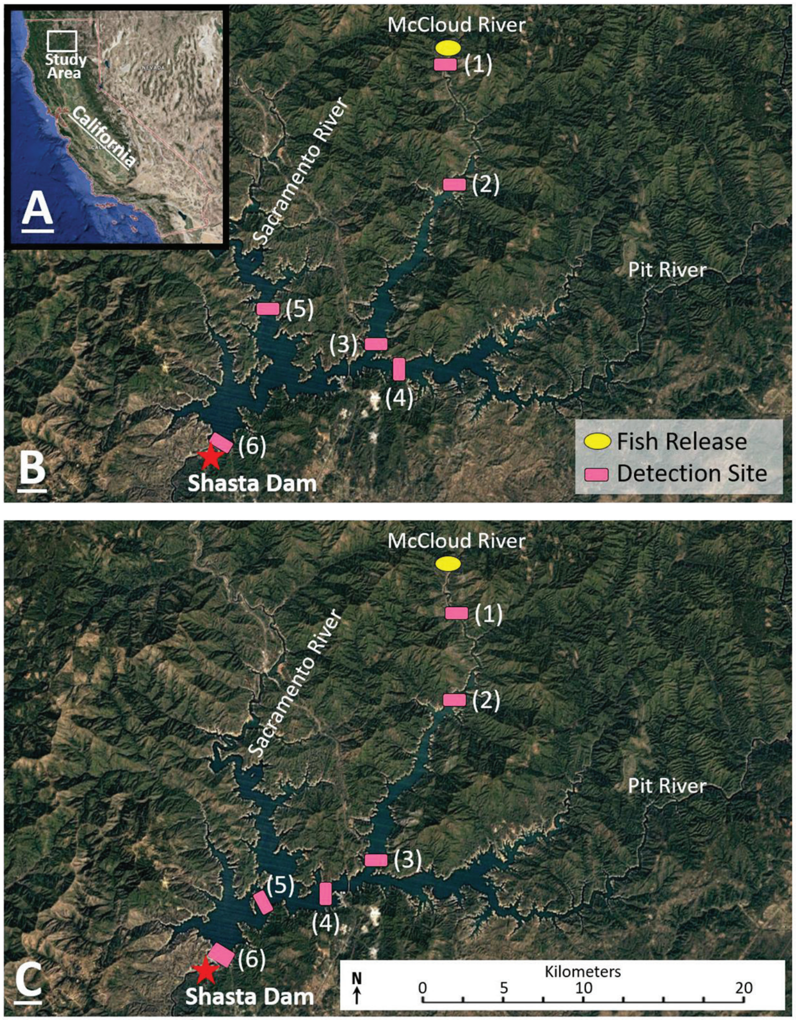
INTRODUCTION

The Shasta Dam Fish Passage Evaluation (SDFPE; Yip 2015) program was created among federal, state, tribal, and private stakeholders to determine the feasibility of reintroducing anadromous fish to tributaries above Shasta Dam, in northern California. Shasta Dam was completed in 1945, resulting in the subsequent extirpation of all anadromous fish populations upstream of the dam. The National Marine Fisheries Service (2009) determined that some dams, including Shasta Dam, were jeopardizing the continued existence of federally listed fish species and stocks, such as Sacramento River winter-run Chinook Salmon (*Oncorhynchus tshawytscha*). The 2009 determination prompted issuance of Biological Opinions that set forth a series of Reasonable and Prudent Alternatives (RPAs) that allow continued operation of Shasta Dam and Reservoir in compliance with the National Marine Fisheries Services' biological opinions (NMFS 2009, 2014).

The SDFPE program is the first attempt in over 70 years to reintroduce salmon upstream of Shasta Dam. The reintroduction of anadromous fish above Shasta Dam is not expected to be an easy task; it will require multiple years and several project stages. The general stages of the SDFPE program are to (1) assess where to best locate juvenile fish collection efforts, (2) determine fish transportation success, (3) quantify the spawning success of reintroduced adult salmon, and (4) measure the habitat used and production of the reintroduced population. Reintroduction efforts are initially focused on how best to collect juvenile salmon that are emigrating from tributaries upstream of the dam; without successful juvenile fish collection and transportation, restoring salmon populations upstream of high-head dams is difficult (Lusardi and Moyle 2017).

It is currently unclear whether fish should be collected as they enter the reservoir, arrive at the dam, or both. Fish collection and survival through the reservoir to the dam was anticipated to be poor because of the reservoir's relatively slow water velocities, complex shape, and abundance of piscivorous sport fishes (e.g. Smallmouth Bass, *Micropterus dolomieu*; Rainbow Trout, *Oncorhynchus mykiss*; and others), which would decrease fish survival and the feasibility of collecting fish at the dam. Head-of-reservoir fish collection is attractive because it would eliminate fish loss in the reservoir, but operational difficulties — variable water levels and velocities, debris loads, and a need for high trap efficiencies — make it a difficult task. Consequently, information on how juvenile salmon distribute and survive as they emigrate from tributaries and through the reservoir to the dam should help inform resource managers on how and where to best locate fish collection efforts.

To better understand how juvenile Chinook Salmon may distribute and survive, we used acoustic telemetry to monitor the movements of juvenile late-fall run Chinook Salmon released into the McCloud River upstream of Shasta Dam. Biotelemetry has been successfully used to evaluate the movements and survival of juvenile salmonids in the Snake (Venditti et al. 2000; Plumb et al. 2006; Adams et al. 2014), Columbia (Beeman and Maule 2001; Skalski et al. 2002), and Sacramento–San Joaquin (Perry et al. 2010) rivers and provide information on individual fish behavior at finer space and time scales than are otherwise unattainable. Although the overall goal for the SDFPE program is to reintroduce winter-run Chinook Salmon into tributaries above Shasta Reservoir, the current population size of winter-run Chinook Salmon returning to the Sacramento River was deemed too low to be used for experimental purposes in this region (2016 phone conversation between Jim Smith and authors J. Plumb, N. Adams, J. Hannon, unreferenced, see "Notes"). So, hatchery-reared late-fall run fish were determined to be a sufficient proxy for winter-run Chinook Salmon, and so were used to obtain information on fish movements upstream of Shasta Dam and Reservoir. Resource managers wanted to know: (1) emigration rates of fish from the McCloud River into Shasta Reservoir, (2) fish distribution within the reservoir, and (3) given sufficient data, the survival rates of the tagged fish as they travel to and below Shasta Dam. Fish were released during very different river flows and dam operations, providing information on fish movement and survival rates during extreme and average river flows.



Source: Landsat 12/2012

Figure 1 Aerial views of **(A)** Shasta Dam (red star) and Reservoir and its tributaries in California: the upper Sacramento River, the McCloud River, and the Pit River. Pink markers show the locations of acoustic telemetry detection arrays that were used to estimate fish distribution and movement upriver of Shasta Dam during the February **(B)** and November **(C)** 2017 release of acoustically tagged fish. The numbers in parentheses correspond to the detection arrays and information provided in the methods.

STUDY AREA

Shasta Reservoir, created by Shasta Dam, is the largest reservoir in California, with a surface area of approximately 11,940 hectares, a volume of 550,660,000 m^3, and approximately 644 km of shoreline (U.S. Bureau of Reclamation 2015). The three major tributaries to Shasta Reservoir are the Upper Sacramento, McCloud, and Pit rivers. Many smaller tributary creeks and streams (both seasonal and perennial) flow into these major tributaries and Shasta Reservoir (Figure 1). Our study area included Shasta Reservoir and the lower portions of the McCloud River where acoustically tagged fish were released (Figure 1), but also downriver from Shasta Dam on the Sacramento River to the Golden Gate Bridge near San Francisco, California (Figure 2). In addition, there was interest by resource managers in determining if fish moved into the Sacramento and Pit rivers after they emigrated from the McCloud River and into the reservoir. To address this objective, we deployed detection arrays near the mouth of the Sacramento and Pit arms of the reservoir, and included this in our study area during the first release of acoustically tagged fish. Given our observations on the first release of acoustically tagged fish, we rearranged detection arrays in a linear orientation from the release site to Shasta Dam, and doubled the number (density) of hydrophones in the forebay area of Shasta Dam from 4 to 10 hydrophones (also see Adams et al. 2018).

METHODS

Environmental Data

To provide information on environmental conditions in the McCloud River and Shasta Reservoir during our study, we used daily

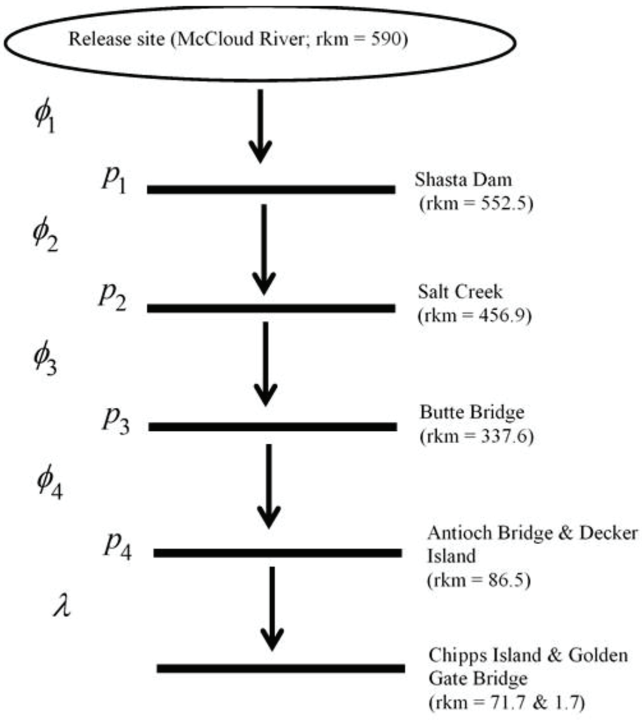


Figure 2 Schematic of the parameter structure and spatial layout of the Cormack–Jolly–Seber (CJS) model that was fit to the detection data on acoustically tagged late-fall run Chinook Salmon released into the McCloud River upstream of Shasta Dam and monitored as they traveled through these river reaches to San Francisco Bay, California, 2017.

summaries of river flow, water temperature, turbidity, and Shasta Dam operations provided by the California Department of Environmental Quality at *http://cdec.water.ca.gov/cdecstation2/*. We graphically illustrated the conditions during the periods when acoustically tagged fish were within the study area by showing the daily mean flows, temperatures, and turbidities for the McCloud River, and the daily discharges and changes in reservoir elevation at Shasta Dam.

Transmitters and Fish Tagging

We released fish in two separate groups that differed in tag type, fish size, and genetic type. For our first release in February 2017, we used acoustic tags manufactured by Advanced Telemetry Systems (ATS; Isanti, Minnesota) that had a mean mass in air of 0.34 g (range 0.34–0.36 g) and mean dimensions of 10.76 mm long by 5.23 mm wide by 3.61 mm deep. Expected transmitter battery life at the nominal pulse rate interval (PRI) of 10 s was about 90 d. For our second release during November 2017, the acoustic tag had a mean mass in air of 0.43 g (range 0.40–0.45 g) and was 11.75 mm long by 6.25 mm wide by 3.47 mm deep, and hydrophones were monitored for a follow-up period of 130 d from tag activation.

All tagged fish were hatchery-origin, juvenile late-fall run Chinook Salmon reared at the Coleman National Fish Hatchery in Anderson, California (Table 1). Fish were held in outdoor concrete raceways (total 2.44-m long by 12.38-m wide; 34,433 L in volume) or Canadian troughs (4.2-m by 0.99-m wide by 0.61-m deep, and 906.1 L in volume) supplied with continuously flowing water. Fish were netted into 75.7-L containers and held without access to food for an average of 24 h (range 21.7–25.1 h) before they were tagged. We tagged and released 262 fish from February 1–3, 2017, and tagged and released 355 fish from November 12–15, 2017. We surgically implanted acoustic transmitters using protocols from Liedtke et al. (2012). On average, during the first release in February, we tagged a larger and wider range in fish sizes than during the second release in November. For example, the mean tag burden for fish in the first release was 1.2%, but 2.7% for the second release (Table 1). The second release group of fish were triploid, and so differed genetically from the first release group of diploid fish.

Fish Detection Locations

We used the Juvenile Salmonid Acoustic Telemetry System receivers to collect acoustic telemetry data (JSATS; McMichael et al. 2010). We installed acoustic detection arrays upstream of Shasta Dam at different locations during the first and second fish release periods (Table 2). When the water surface depth was less than 33 m, we positioned hydrophones 1.8–4.5 m from the river bottom. We deployed hydrophones using methods described by Titzler et al. (2010). Before we released the acoustically tagged fish, we tested the autonomous hydrophones with a test set of acoustic tags to make sure they operated correctly. We retrieved the hydrophones to download data every 4 weeks, and then

Table 1 Summary statistics for the late-fall run Chinook Salmon that were acoustically tagged and released into the McCloud River during 2017. The February release group of fish were diploid, and the November release group of fish were triploid.

Release period	Fish measurement	N	Mean	Median	Range	SD	Mean tag burden (%)
February	Fork length (mm)	262	134.5	136	97–171	16.3	—
	Weight (grams)	262	28.9	28.4	10.3–62.8	10.1	1.2
November	Fork length (mm)	355	111.9	112	97–125	5.8	—
	Weight (grams)	355	15.7	15.6	10.2–21.9	2.5	2.7

Table 2 Distances in river kilometers between acoustic detection arrays and the release periods of acoustically tagged juvenile late-fall run Chinook Salmon in Shasta Reservoir and tributaries, 2017

First release (February 1–3, 2017)						
River location	**McCloud River Bridge**	**Mid-McCloud River**	**McCloud River arm**	**East Shasta Reservoir**	**Sacramento River arm**	**Shasta Dam forebay**
Release	0.8	10.3	22.1	25.4	34.1	37.4
McCloud Bridge		9.5	21.3	24.6	33.3	36.6
Mid-McCloud River			11.8	15.1	23.9	27.2
McCloud River Arm				3.3	12.1	15.4
East Shasta Reservoir					13.0	15.4
Sacramento River Arm						12.6
Second release (November 12–15, 2017)						
River location	**McCloud River Bridge**	**Mid-McCloud River**	**McCloud River arm**	**I-5 bridge**	**Below Sacramento River arm**	**Shasta Dam forebay**
Release	3.3	10.3	22.1	25.6	30.3	36.6
McCloud Bridge		7.0	18.8	22.3	27.0	33.3
Mid-McCloud River			11.8	15.3	20.0	26.3
McCloud River Arm				3.5	8.3	14.5
West of I-5 Bridge					4.7	11.0
Below Sacramento River Arm						6.3

redeployed them in their original location and checked them periodically to verify functionality.

To detect acoustically tagged fish as they migrated through the study area upstream and in the vicinity of Shasta Dam after their release on February 1–3, 2017, we deployed autonomous hydrophones at six locations:

1. one hydrophone in the McCloud River Arm at 0.8 rkm downstream of the release site at the McCloud River Bridge;
2. two hydrophones in the McCloud River about 10.3 rkm downstream of the release site;
3. four hydrophones in the McCloud River Arm about 22.1 rkm downstream of release;
4. three hydrophones in East Shasta Reservoir;
5. five hydrophones in the Sacramento River Arm located 12.6 rkm upstream of Shasta Dam; and
6. four hydrophones in the forebay about 200–400 m upstream of Shasta Dam (Figure 1).

To detect acoustically tagged fish as they migrated through the McCloud River and Shasta Reservoir after their release on November 12–15, 2017 (Table 2), we deployed autonomous hydrophones at six locations that differed from the locations of the February release:

1. one hydrophone in the McCloud River Arm at 3.3 rkm downstream of the release site at the McCloud River Bridge;
2. two hydrophones in the McCloud River about 10.3 rkm downstream of the release site;
3. four hydrophones in the McCloud River Arm about 22.1 rkm downstream of the release site;
4. five hydrophones 1.2 rkm west of the I-5 Bay Bridge;
5. six hydrophones downstream of the Sacramento River Arm; and
6. five hydrophones in the forebay about 320–400 m upstream of Shasta Dam and five hydrophones mounted on the upstream face of Shasta Dam.

We processed data from the hydrophones to remove false-positive records before analysis. False-positive records indicate detection of a transmitter when the transmitter was not present, and are common in most active telemetry systems (Beeman and Perry 2012). We used the procedures developed by the Pacific Northwest National Laboratory (2010 written communication from M. Weiland, Pacific Northwest National Laboratory, to J. Beeman, unreferenced, see "Notes") to remove false-positive records. The steps include removing three types of records: (1) records from tag codes not released, (2) records suspected of being from reflections of valid tag signals (multi-path), and (3) records that were not close to a multiple of the tag pulse interval (McMichael et al. 2010).

Travel Times and Movements Upstream of Shasta Dam

We defined travel times for each fish as the difference in time between two locations. We provided summary statistics for the fish travel times (d) and rates (km/d) from release location to the other detection locations. We provided information on travel rates to each location because travel rates may be directly compared to juvenile salmon travel rates from other studies. To provide information about fish movements within Shasta Reservoir, we tabulated the fraction of fish detected at each tributary arm of Shasta Reservoir, as well as the number of trips by fish to other locations after being detected at a previous location.

Fish Survival and Detection

We used additional acoustic tag detections from both release groups at and below Shasta Dam to estimate survival and detection parameters under a Cormack–Jolly–Seber model framework (CJS; Cormack 1964; Jolly 1965; Seber 1965). This modeling approach has been used for decades to estimate the survival and detection of tagged juvenile salmon (Skalski et al. 1998; Perry et al. 2010, 2012), and it enabled us to estimate survival and detection probabilities for fish traveling from the McCloud River to the Golden Gate Bridge — 590 km (Figures 1 and 2). Acoustic detection data obtained at sites downriver of Shasta Dam came from hydrophones deployed and maintained by the National Marine Fisheries Service (Arnold Ammann; Santa Cruz, California). Because there were few detections below Shasta Dam, we pooled detection sites that were relatively close to each other to represent a single detection array for that approximate location (Figure 2). This ensured that the distance over which fish were detected was relatively short compared to the distance over which survival was to be estimated. We chose five locations to provide estimates of survival over pre-defined reaches (Figure 2), such that survival estimates represented the result of all survival processes and routes between each of the locations. The distances between locations varied from 37 to 250 km, so we also provided estimates of fish survival that are standardized by the distance of the reach. The relatively long distance (590 km) and small sample size (< 355 fish) resulted in sparse detection data downriver of Shasta Dam. As a result, using maximum likelihood methods to estimate survival and detection would have been unreliable (Gelman et al. 2014). To overcome this, we used Bayesian methods and Markov Chain Monte Carlo (MCMC) optimization (Gibbs sampler) to solve for detection and survival parameters following the statistical (multinomial) structure of the CJS model that has been applied to migrating juvenile salmon (Skalski et al. 1998; Perry et al. 2010, 2012).

To estimate survival and detection under the CJS model, we assigned each fish to one of 32 possible detection history codes, indicating whether fish were or were not detected at the monitoring sites. Thus, we assumed that counts of fish over the set of possible detection history codes followed a multinomial distribution, where we then derived the probability of observing the i^{th} detection history, π_i , from the following underlying probabilities: (1) ϕ_k, apparent survival probability from k to the $k+1$ detection location, (2) p_k, the probability of detection at the kth detection location, and (3) λ, the joint probability of surviving and being detected within the last downstream detection site. For example, the probability of observing the detection history of fish that survived and were detected at all but the last detection site may be expressed as:

$$\pi = s_1 \cdot p_1 \cdot s_2 \cdot p_2 \cdot s_3 \cdot p_3 \cdot s_4 \cdot p_4 \cdot (1 - \lambda).$$

Following the recommendations of Kéry and Schaub (2012), we used uniform prior distributions to estimate the posterior distributions of the parameters. We used R software (R Core Team, 2017) and the ‘rjags’ package (see supplemental information) to perform analyses and fit the model.

RESULTS

Environmental Conditions

McCloud River flows were an order of magnitude greater during the first release of acoustically tagged fish (February) than during the second release (November). McCloud River flows after the February release of fish peaked at 992.8 m^3s^{-1} (Figure 3), whereas flows after the November release of fish peaked at 30.1 m^3s^{-1}. Mean daily flows in the McCloud River were 117.3 m^3s^{-1} and peaked on February 21, about 19 d after the first release of tagged fish. Turbidity in the McCloud River peaked when river flows peaked in February, and ranged from 0.5–396.3 nephelometric units (NTU; Figure 3). After the first release of tagged fish, water temperatures steadily increased, as expected with the progression of spring. Water temperatures in the McCloud River during the February release ranged from 6.2 °C to 13.9 °C. November water temperatures in the McCloud River ranged from 3.2 °C to 10.3 °C.

Discharge at Shasta Dam varied by an order of magnitude between the February and November release periods of acoustically tagged fish (Figure 3). Total daily outflow peaked in mid- to late-February and had a small increase in late April. Outflow ranged from 463.6 to 2,112.6 m^3s^{-1} in February, 137.2 to 1,833.9 m^3s^{-1} in March, 203.3 to 855.7 m^3s^{-1} in April, and 110.7 to 285.5 m^3s^{-1} during May 1–10. In contrast, total daily outflow after the November release of acoustically tagged fish was consistently lower, and ranged from 62.7 to 146.5 m^3s^{-1} during November 12, 2017 to March 11, 2018 (mean 106.7 m^3s^{-1}). The Shasta Dam outflow was higher during the first release period than during the second, and the river outlets at Shasta Dam (which can pass juvenile salmon) were used daily from February 1–March 8, 2017, and discharged a mean of 705.6 m^3s^{-1}. In contrast, the river outlets were not used at all after the November release of acoustically tagged fish.

Fish Travel Times and Movements Upstream of Shasta Dam

During the first release of juvenile salmon in February, the fish moved downstream relatively quickly, with most fish detected just downstream of the release site (0.8 rkm) on the day of the release (Table 3; Figure 4). Median travel time for tagged fish arriving at the mid-McCloud River detection site was 2.56 d; median travel time to the McCloud River Arm detection site was 22.34 d. Less than 50% of the fish were detected at East Shasta Reservoir and the Sacramento River Arm. The first fish arrived at the east Shasta Reservoir detection site 8 d after release, and the median travel time for the 53 fish detected there was 29.89 d (Table 3). The median travel time to the Sacramento River Arm was 55.69 d. A total of 182 fish (70%) were detected at least once at the Shasta Dam forebay, and the median time it took

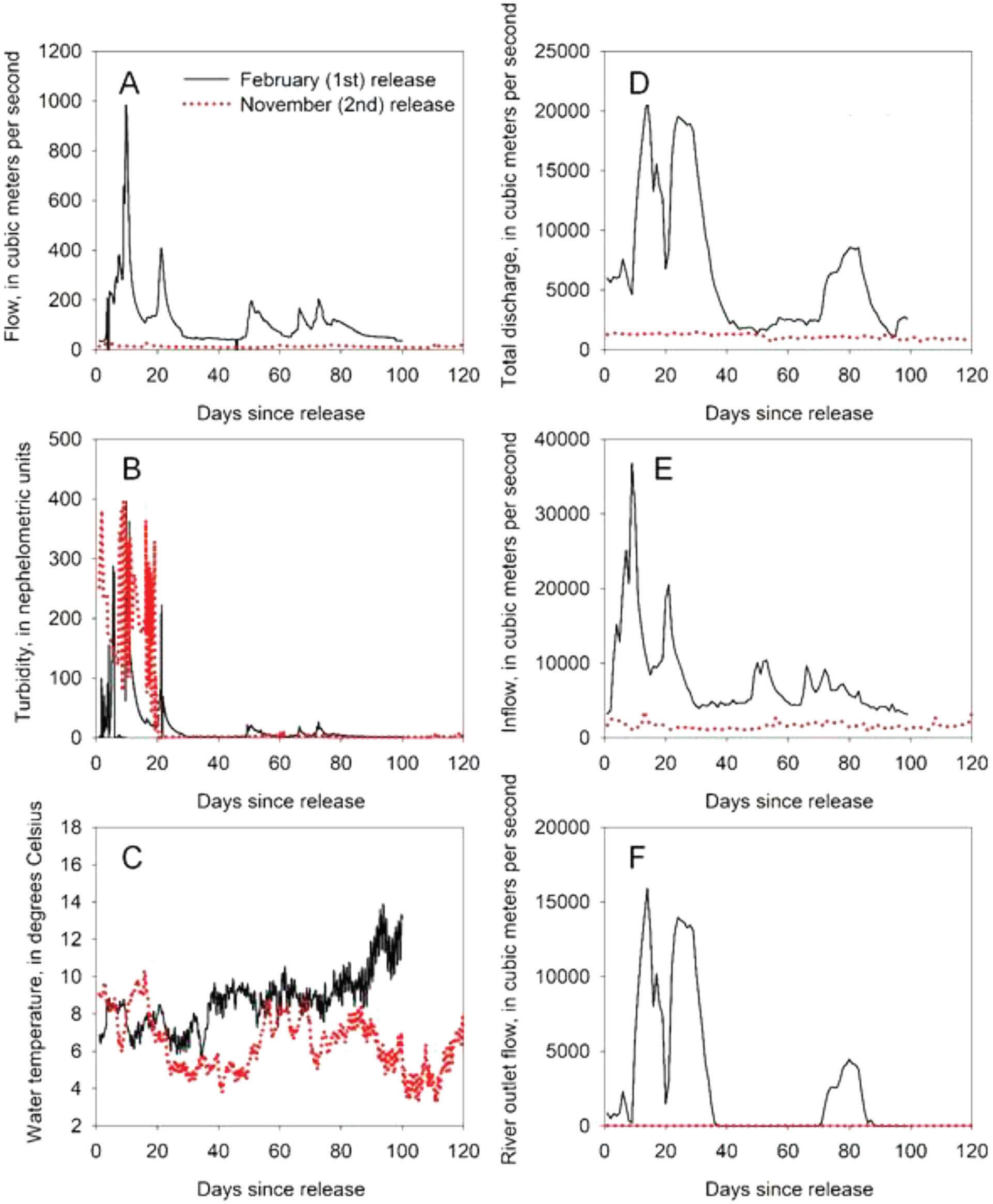


Figure 3 Plot of daily total discharge, turbidity, and water temperature in the McCloud River (*panels* **A**, **B**, and **C**) and total discharge, inflow, and river outflow at Shasta Dam (*panels* **D**, **E**, and **F**), California during the first release (February 1–May 10, 2017) and second release (November 12, 2017–March 11, 2018) groups of acoustically tagged juvenile late-fall run Chinook Salmon.

Table 3 Summary statistics for travel times (days) of acoustically tagged juvenile late-fall run Chinook Salmon from their release location on the McCloud River 0.8 km upstream of Shasta Reservoir. Note that detection locations and effort were not identical between the February and November release periods.

			Travel time (d)					
Location	**Distance (rkm)**	**N**	**Min**	**25th**	**Median**	**75th**	**Max**	**Median rate (km d^{-1})**
February release 2017								
McCloud Bridge	0.8	257	0.01	0.05	0.09	0.12	2.06	8.89
Mid-McCloud River	10.3	215	1.21	2.09	2.56	3.40	19.01	4.02
McCloud River Arm	22.1	202	6.34	12.00	22.34	39.00	92.55	0.99
East Shasta Reservoir	25.4	53	8.47	15.88	29.89	39.81	94.32	0.85
Sacramento River Arm	34.1	57	18.11	45.21	55.69	70.10	92.72	0.61
Shasta Dam Forebay	37.4	182	17.82	40.08	54.18	70.42	94.97	0.69
November release 2017								
McCloud Bridge	3.3	311	0.11	0.31	0.37	0.47	11.97	8.92
Mid-McCloud River	10.3	98	1.28	1.95	2.71	3.86	54.05	3.80
McCloud River Arm	22.1	18	7.51	13.37	16.02	18.43	80.38	1.38
West of I-5 Bridge	25.6	9	10.88	15.59	19.71	25.26	81.41	1.30
Sacramento River Arm	30.3	7	16.87	19.60	21.03	30.20	81.75	1.44
Shasta Dam Forebay	36.6	4	23.76	24.29	30.88	60.19	83.45	1.19

to get there was 54 d. The first fish arrived at Shasta Dam 17 d after release, and continued to arrive at the Shasta Dam until the end of the study period. Overall, there was an increase in travel time, and decrease in travel rate as fish approached Shasta Dam. Fish were also observed making multiple trips to some of the detection sites (Table 4). For example, one tagged fish had a sequence of detections that totaled 79.2 rkm between detection locations.

The acoustically tagged fish released in the second group during the following November had a very different pattern of detection and travel time than those released in February. Of the November-released fish that were detected in the study area, most were detected 3.3 rkm downstream of the release location within the first 3 days after their release (Figure 4). Between day 3 and 10, fish arrived steadily at the mid-McCloud River array, but few fish were detected after day 10. Perhaps most significantly, few fish were detected outside of the McCloud River Arm, and only four fish were detected at Shasta Dam. These four fish were detected at each of the detection arrays in sequential order (upstream to downriver) with no upstream movement (Table 4). Also, the November-released fish had fewer trips among the detection arrays than the February-released fish — despite lower river flows, less spread-out detection arrays, and larger sample size of fish during the November release.

Fish Survival and Detection

Under the CJS modeling framework, fish detection and survival probabilities could be estimated at and between our five primary detection locations (Figure 2). Detection probabilities for the February release of acoustically tagged fish varied from 0.331 to 0.608 downstream of Shasta Dam (Table 5). Detection probability was highest at Shasta Dam ($p_1 = 0.971$, SD = 0.0279; Table 5), which might be expected, given the relatively slow water velocities upstream of the dam, the number of hydrophones that were located there, and the extra time needed for fish to locate a passage through the dam. Of the February-released fish, 0.710 (SD = 0.0340) survived the reservoir and arrived at Shasta Dam. Our estimates of fish survival were lowest in the reach just downstream of Shasta Dam ($\phi_2 = 0.222$, SD = 0.0404), where mortality associated with

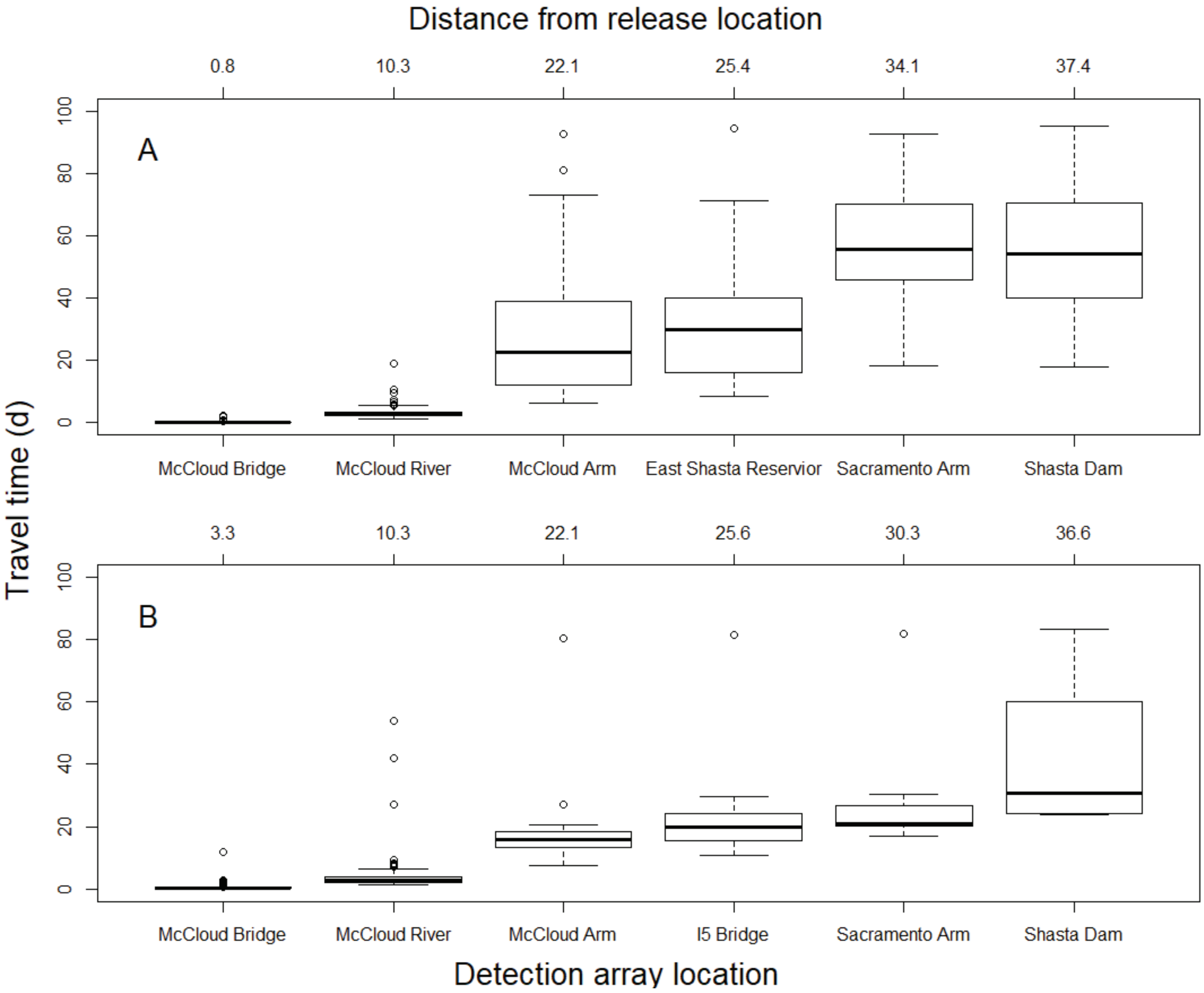


Figure 4 Box and whisker plots showing the travel time distributions for acoustically tagged juvenile late-fall run Chinook Salmon traveling between release at the McCloud River Bridge and detection arrays in Shasta Reservoir and tributaries, California, for our first release of acoustically tagged fish in February (**A**) and November (**B**), 2017. The thick line denotes the median, the extent of boxes identify the interquartile range, the extent of whiskers is the 2.5 and 97.5 percentiles, and circles signify outlying data points.

passing Shasta Dam should contribute to a lower estimate of fish survival in this reach. Fish survival was relatively high (>0.84) in reaches farther downstream, especially considering the amount of time (>100 d) and distance (>119 km) the fish had to travel. Only four tagged fish (1%) from the November release group were detected at Shasta Dam, and no fish were detected at our arrays below Shasta Dam for estimating survival. Survival and detection probabilities could not be estimated for the November-released fish because of the paucity of detections below the McCloud River Arm. Given the higher density of hydrophones at the dam during the November release period, fish survival was likely extremely poor for this release group.

DISCUSSION

It has been more than 70 years since juvenile salmon have emigrated from tributaries above Shasta Dam, and this study provides the first estimates about juvenile Chinook Salmon movements and survival after release into a major tributary upstream of Shasta Dam and Reservoir. Fortuitously, the acoustically tagged

Table 4 Summary statistics for the numbers of acoustically tagged juvenile late-fall run Chinook Salmon that made trips to each detection site after being released at the McCloud River Bridge

	Number of trips to each detection site					
Detection site	**1**	**2**	**3**	**4**	**5**	**6**
	First release February 2017					
Below McCloud River bridge (0.8 rkm)	256	1	0	0	0	0
Mid-McCloud River	206	8	0	1	0	0
McCloud River arm	165	32	3	1	0	1
East Shasta Reservoir	42	10	1	0	0	0
Sacramento River arm	63	3	1	0	0	0
Shasta Dam forebay	170	12	0	0	0	0
	Second release November 2017					
Below McCloud River Bridge (3.3 rkm)	311	0	0	0	0	0
Mid-McCloud River	97	1	0	0	0	0
McCloud River arm	17	1	0	0	0	0
West of I-5 Bridge	8	1	0	0	0	0
Sacramento River arm	5	1	0	0	0	0
Shasta Dam forebay	4	0	0	0	0	0

Table 5 Summary statistics of the posterior distributions for each Cormack–Jolly–Seber model parameter for river reach i (1) detection probability, p_i, (2) apparent survival probability, ϕ_i, (3) the joint probability of detection and survival, λ_i, and for comparison (4) the corresponding derived estimates of apparent survival provided on a per-100 kilometer basis, ϕkm_i. We obtained parameters estimates were obtained by fitting the survival model to the acoustic detection data on tagged late-fall run Chinook Salmon released during February 2017. For the second release of fish in November 2017, there were too few detections to allow us to estimate parameters.

Parameter	Reach or location	Mean	Standard deviation	2.5%	50%	97.5%
ϕ_1	McCloud R to Shasta Dam	0.710	0.034	0.647	0.709	0.782
ϕ_2	Shasta Dam to Salt Cr	0.222	0.040	0.152	0.219	0.310
ϕ_3	Salt Cr to Butte Br	0.912	0.078	0.711	0.933	0.997
ϕ_4	Butte Br to Antioch	0.841	0.116	0.578	0.862	0.994
p_1	Shasta Dam	0.971	0.028	0.897	0.980	0.999
p_2	Salt Cr	0.331	0.079	0.187	0.328	0.497
p_3	Butte Br	0.608	0.091	0.426	0.610	0.778
p_4	Antioch	0.563	0.113	0.357	0.558	0.796
λ	Antioch to Golden Gate	0.119	0.058	0.033	0.111	0.255
ϕkm_1	Rel to Shasta Dam	0.400	0.045	0.311	0.401	0.521
ϕkm_2	Shasta Dam to Salt Cr	0.204	0.033	0.140	0.203	0.293
ϕkm_3	Salt Cr to Butte Br	0.922	0.085	0.756	0.942	1.000
ϕkm_4	Butte Br to Antioch	0.929	0.065	0.802	0.970	1.000

fish were released during two periods that had very different river flows, reservoir conditions and dam operations. River flows in the McCloud River and Shasta Dam differed by an order of magnitude between the two release periods of acoustically tagged fish. River flows were historically high during the February release, but flows during the November release were similar to 10-yr average river flows (see *http://cdec.water.ca.gov/cdecstation2/*). Temperatures and water turbidities were not as markedly different between the release periods (Figure 3). Consequently, this study measures juvenile Chinook Salmon behavior during different seasons and over a wide range of river flows, which may help inform resource managers about where to best implement a trap-and-haul program when they reintroduce anadromous fish into tributaries upstream of Shasta Dam.

Acoustically tagged fish were detected throughout Shasta Reservoir—from the Pit River mouth to the mouth of the upper Sacramento River, indicating that juvenile salmon can disperse throughout Shasta Reservoir. Some fish during the February release were recorded making multiple trips between locations in the reservoir despite (1) the historically high river flows, (2) the wider spatial arrangement of the detection arrays, (3) fewer tagged fish being released, and (4) fewer hydrophones at Shasta Dam than for the November-released fish. February-released fish also exhibited greater average travel times to Shasta Dam, and were detected as far downriver as San Francisco Bay. In contrast, the November-released fish were exposed to average river flows for the time of year, a less disperse arrangement of detection locations from the release site to Shasta Dam, and a higher density of hydrophones at Shasta Dam. Yet, November-released fish were detected at a much lower proportion, had shorter (faster) and less variable travel times to the dam, and had fewer trips measured among the detection sites. The low survival and detection during the November release period is possibly related to the faster travel times that were observed for this release group. Shorter travel times and faster travel rates to the dam could arise because slow-traveling fish may have been more likely to die and succumb to predation, but this is uncertain because we could not observe these fish. We do not know the ultimate fates of undetected fish from the second release group. Fish could have died, or emigrated out of the reservoir undetected beyond the battery life of the transmitter, and some unknown fraction of fish detections could have been predators that had eaten a tagged juvenile salmon. Inadvertent predator detections can be removed from the record, but currently we have no information on the movements of tagged predators in Shasta Reservoir that could be used to filter out detections of predators from detections of juvenile salmon (e.g., see Romine et al. 2014). Given what is known about juvenile salmonids upstream of dams, as river flows and water velocities decrease (Venditti et al. 2000; Plumb et al. 2006; Tiffan et al. 2009), the historic differences in river flows and atypical dam operations likely contributed to the observed differences in fish detection (and apparent survival) among the release groups.

Our study can make few statements about differences in survival between the release groups because the second release group was so poorly detected that we could not estimate their survival. Several factors likely contributed to this result. First, the groups of fish were released in different seasons. All fish were Sacramento River late-fall run Chinook Salmon that were released within their natural time for downstream migration (e.g. see *http://www.cbr.washington.edu/sacramento/data/query_redbluff_graph.html*); however, migration phenology differentiates the life stages of salmon (Groot and Margolis 1991), and juvenile fall-run Chinook Salmon in other river systems have been shown to out-migrate over a protracted period that extends from outmigration at age 0+ to 1+ (Connor et al. 2004). Thus, the differences in fish detection, movement, and survival that we observed between the two release groups could have resulted from differences in season and migratory disposition of the fish. Second, the release groups also differed by age, with younger, smaller fish comprising most of the November release. On average, the smaller fish in the November release group had higher tag burdens—though all tag burdens in this study were well within a range reported to minimally affect swimming ability (Perry et al. 2013) and survival (Geist et al. 2018) of juvenile Chinook Salmon. Nonetheless, higher survival for larger juvenile salmon has been documented (Muir et al. 2011), and this could have contributed to the differences among these release groups. Lastly, the release groups differed genetically, with diploid fish released in February, and triploid fish released in November. These genetic differences could also have contributed to the observed differences among the release groups (O'Flynn et al. 1997; Garner et al. 2008).

The detection of acoustically tagged fish as far downriver as San Francisco Bay was unexpected. Before this study, the professional judgement of resource managers was that juvenile salmon survival would be very poor through Shasta Reservoir. Under the very high flows during the February release, survival was higher than expected, and similar to that measured at large run-of-the-river dams and reservoirs on the Snake and Columbia rivers (Plumb et al. 2012; Skalski et al. 2016). Under average river flows in November; however, the a priori expectation of poor fish survival to Shasta Dam was supported. We do not know the extent to which detection-array arrangement, high flows, season, fish age and size, and genetic type contributed to the results of this study. However, the rapid decline in fish detection to Shasta Reservoir for the November-released fish under average flow conditions suggests that locating fish-collection efforts to capture fish over a protracted out-migration period at Shasta Dam appears ill advised. Further, the large size of Shasta Reservoir and the expected poor performance of fish collection structures in such a large forebay as Shasta Dam supports this conclusion (Kock et al. 2019). Although we do not know the effectiveness of collecting juvenile salmon at Shasta Dam, they may best be trapped using in-river or head-of-reservoir fish traps to collect and transport them to locations below Shasta Dam; however, the efficacy of these types of traps upriver of Shasta Dam is also unknown.

CONCLUSIONS

Our results for survival should be interpreted cautiously and with several caveats in mind. First and foremost, our estimates do not account for the expiration of the transmitter's battery, which was about 100 d. The median travel time from release in the McCloud River to Shasta Dam (for fish that were detected) was about 31 to 55 d, indicating that the transmitter had used about one-third to one-half of its expected battery life by the time the fish had arrived at Shasta Dam, so some fish arrived at Shasta Dam and points downriver after the transmitter's expected battery life. Consequently, our detection and survival estimates are likely biased toward faster-traveling fish (Townsend et al. 2006). Slower-traveling fish would be more likely to have their transmitters expire by the time they arrived at the downriver sites, which could explain the relatively high (per 100 km) survival rates in the two farthest-downriver reaches of our study area. Acoustically tagged fish that traveled relatively slowly would be unlikely to be detected (because of battery failure), but faster-traveling fish would be more likely to be detected, leading to biased survival estimates. Nonetheless, Eicher et al. (1987) showed mean survival estimates through Shasta Dam from test releases of Chinook Salmon during the early 1960s that ranged from 53 to 71%, so our fish survival estimates in the reach just upriver and downriver of Shasta Dam are not outside expectations, given the distances involved. Other researchers have used acoustic telemetry to estimate juvenile salmon survival and found generally high apparent survival rates for juvenile salmon that travel through reaches of the lower Sacramento River (Perry et al. 2010), providing support for our apparent survival rates in the lower Sacramento River. Because our survival estimates may be biased by long fish travel times beyond the transmitter's battery life, our study's survival estimates are perhaps best used as a guideline (e.g., precision, sample size, or transmitter battery life considerations) for future studies that aim to estimate fish survival through and below Shasta Dam on the Sacramento River, as well as at other high-head dams and river systems.

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NOTES

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