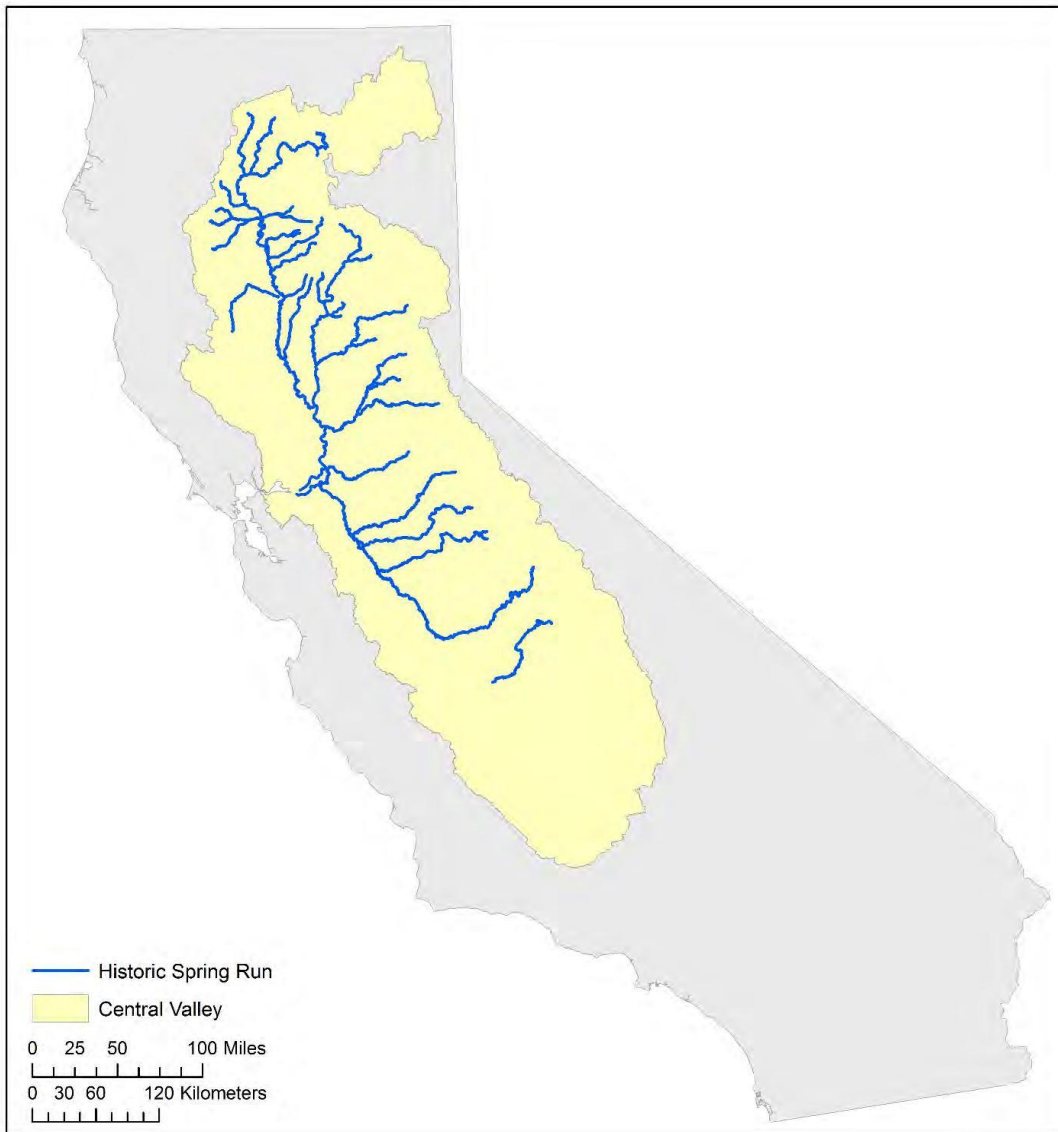




Survival and Movement Rates of wild Chinook salmon smolts from Mill Creek 2013-2016

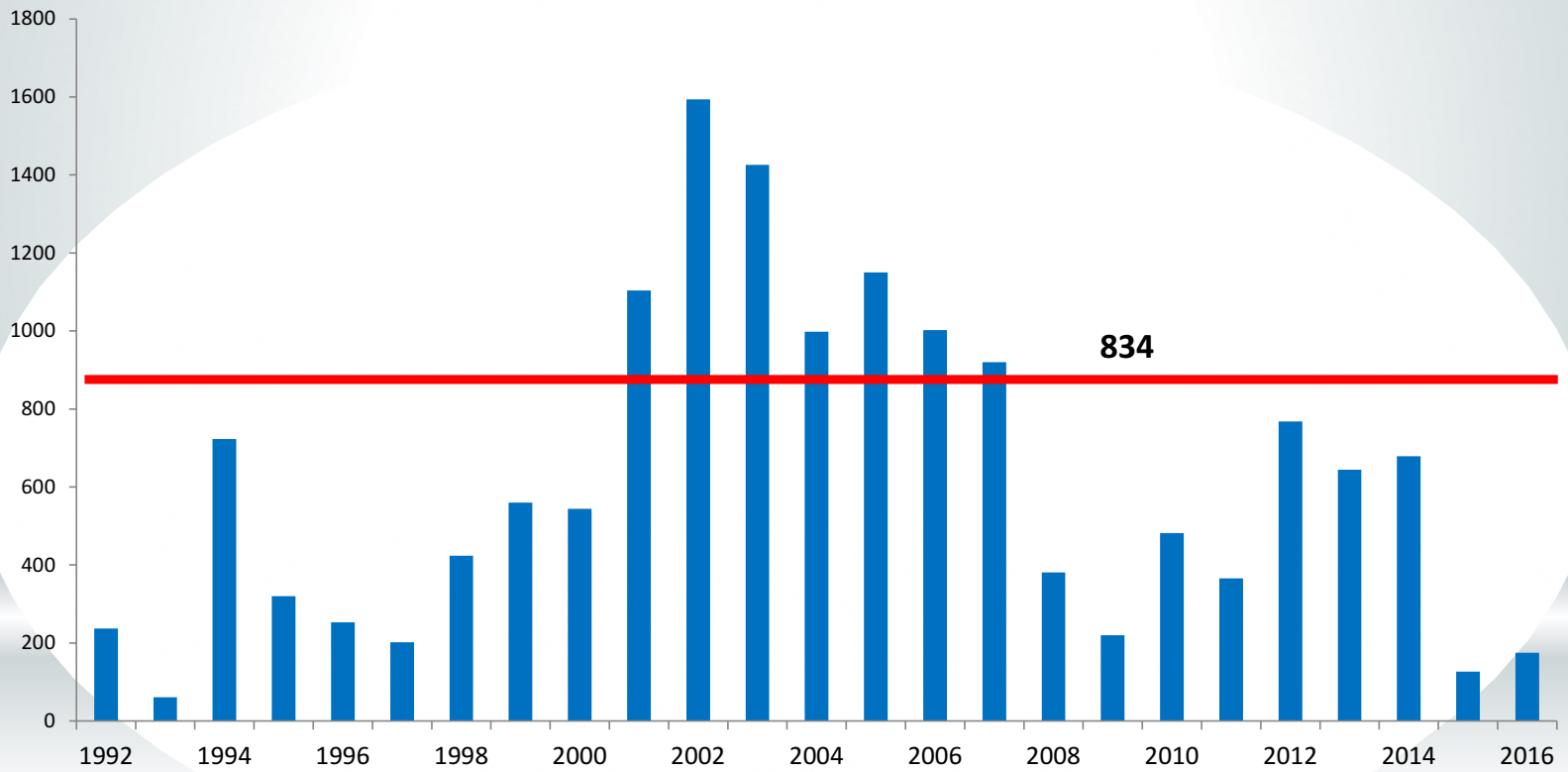


Jeremy Notch, Flora Cordoleani, Arnold Ammann, Matt Johnson, Alex McHuron

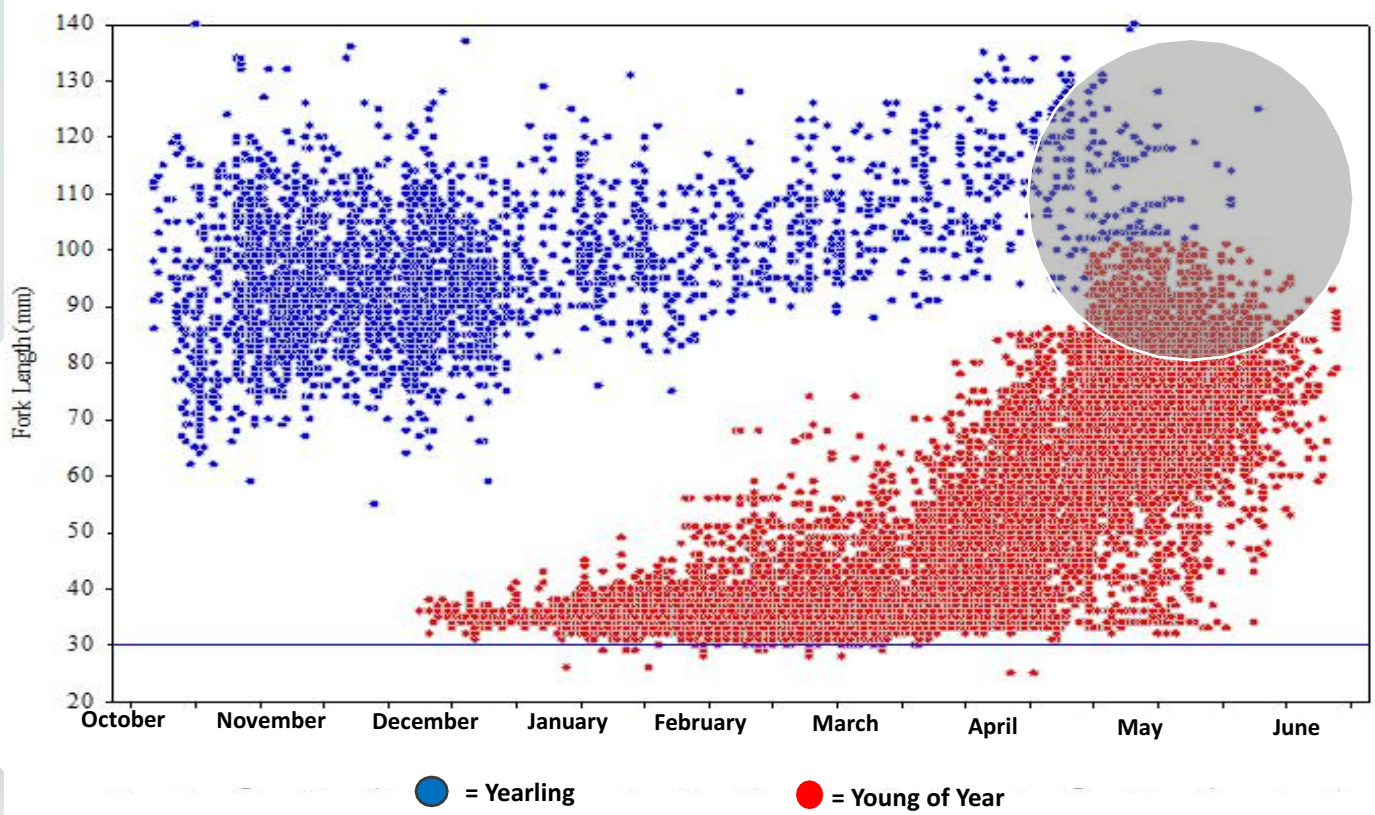




Mill Creek Spring-Run Escapement 1992 - 2016



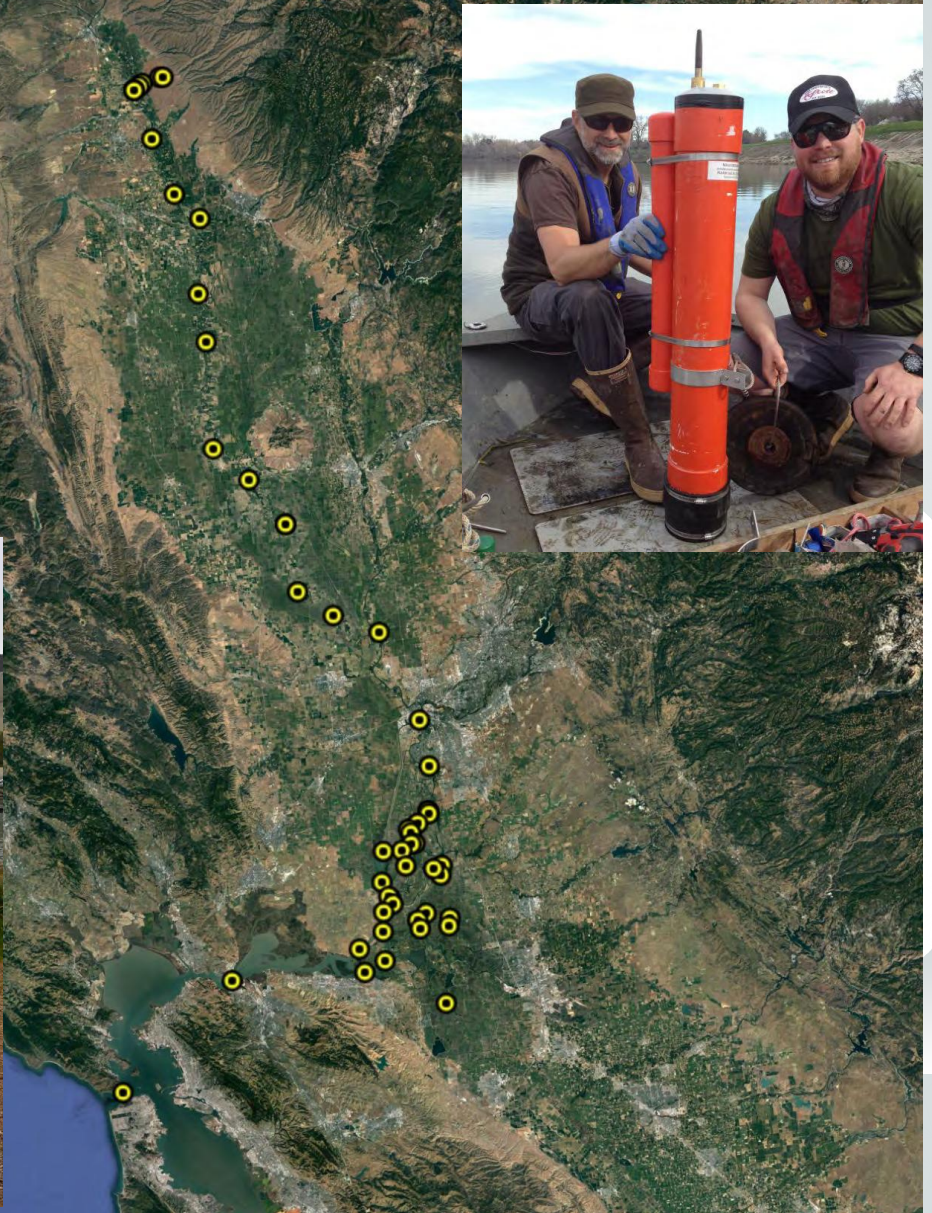
1995 – 2010 Mill Creek Rotary Screw Trap Data



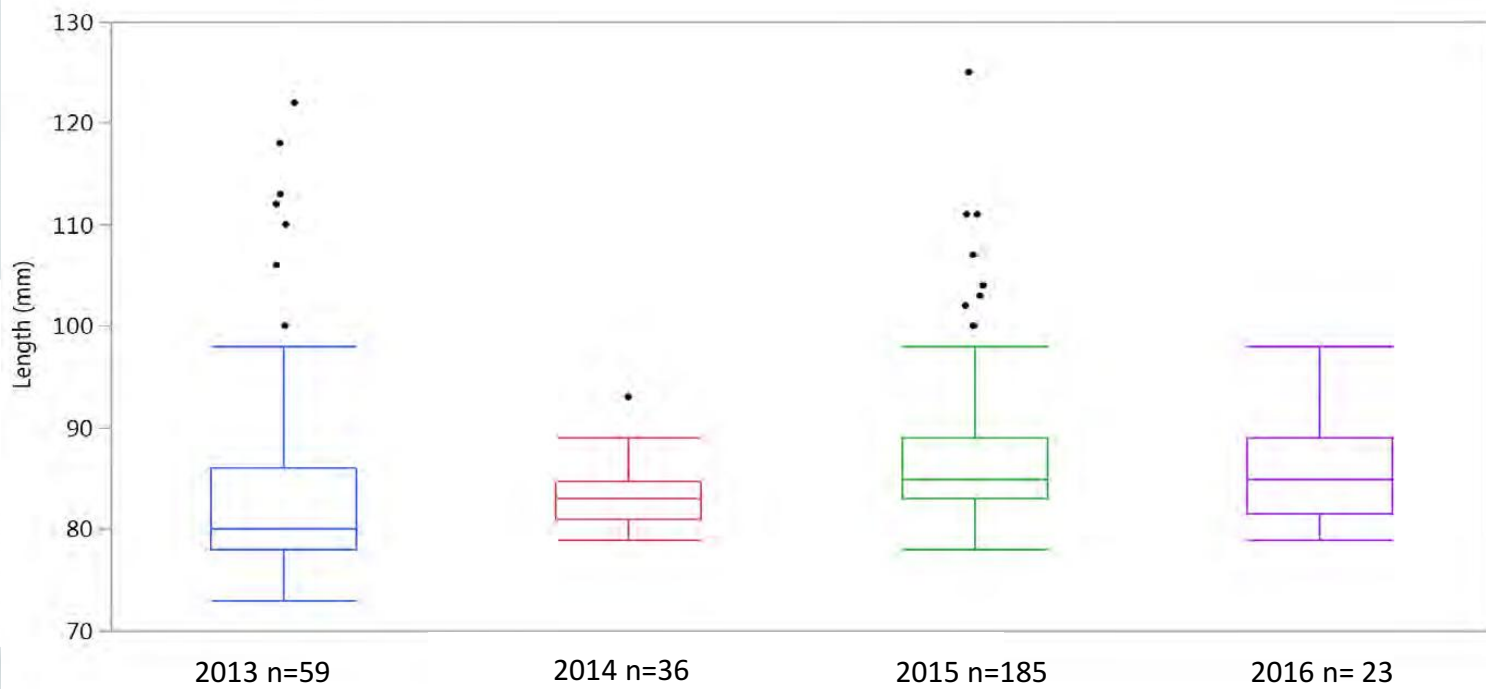
Fish Collection and Tagging

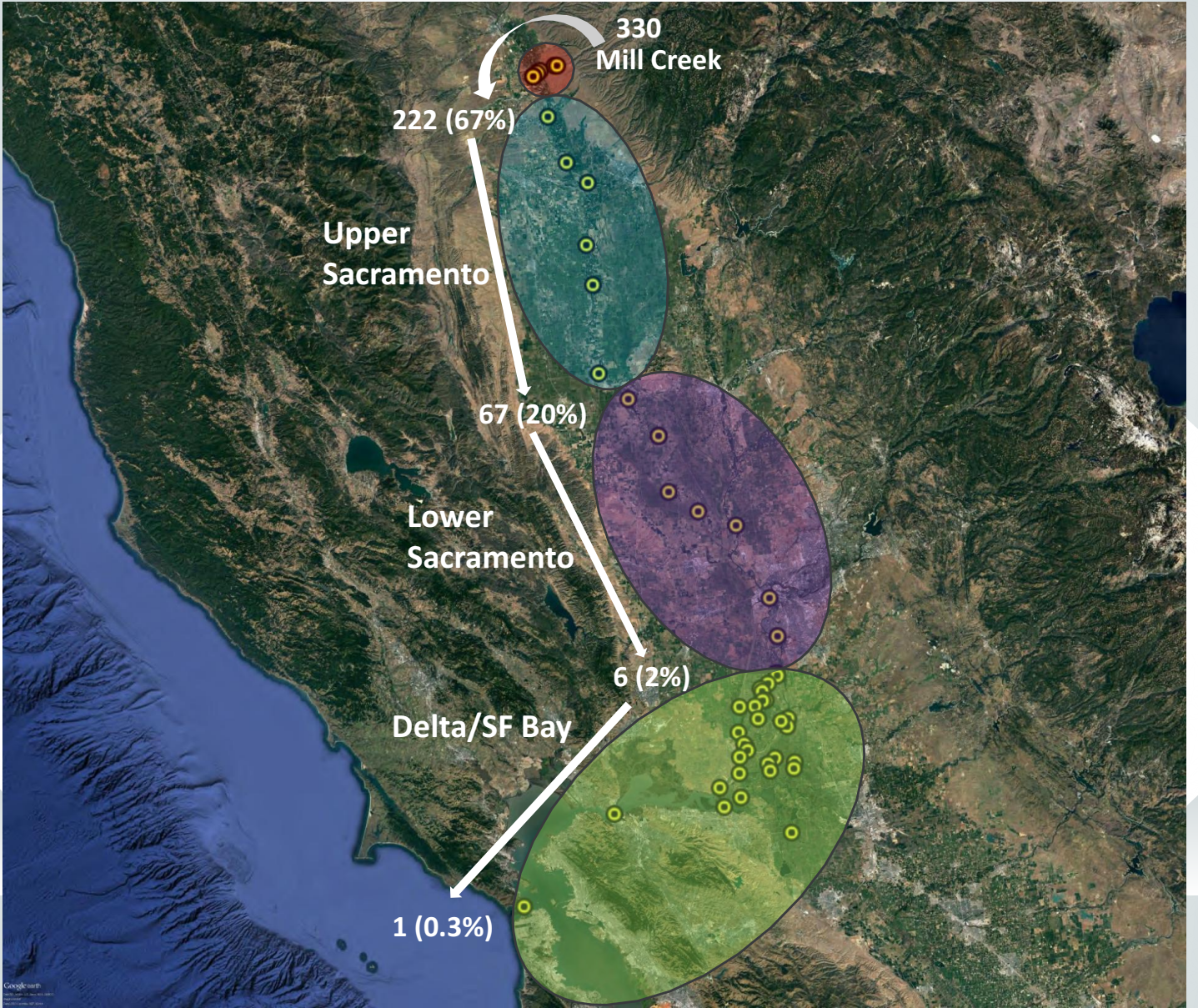


JSATS Receiver Locations

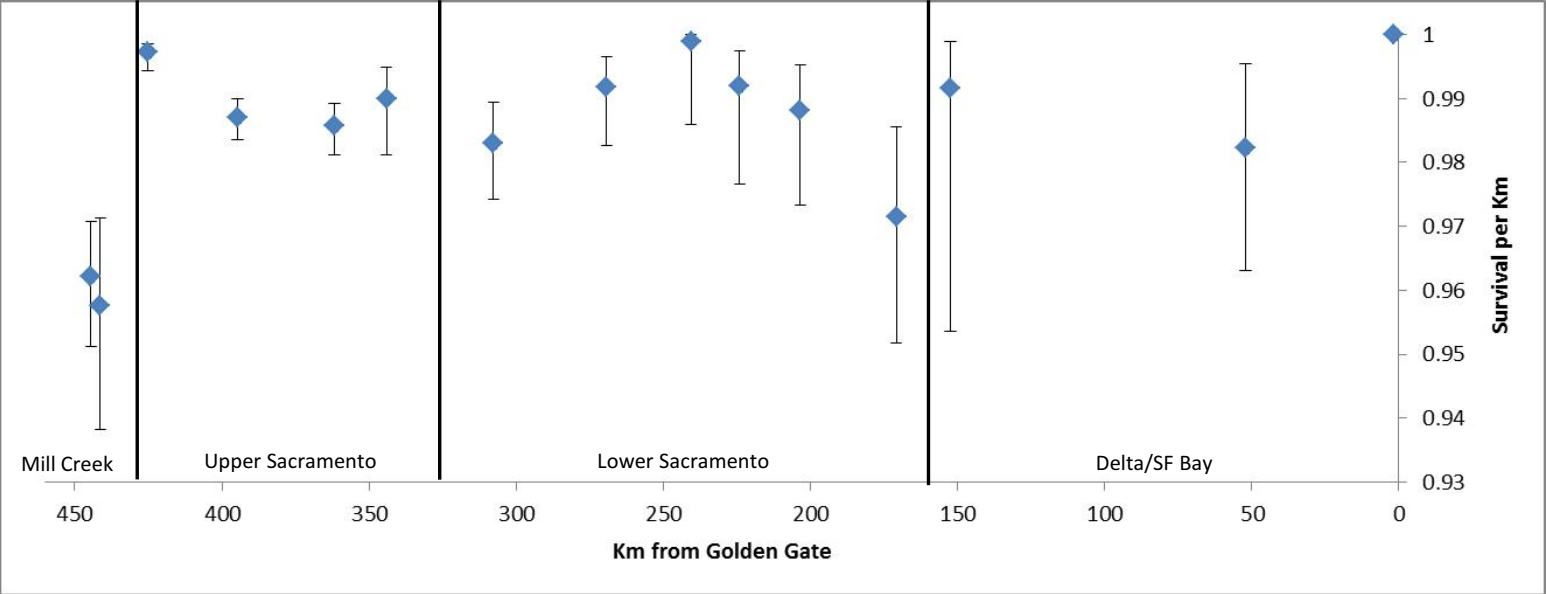


Length of Tagged Mill Creek Smolts

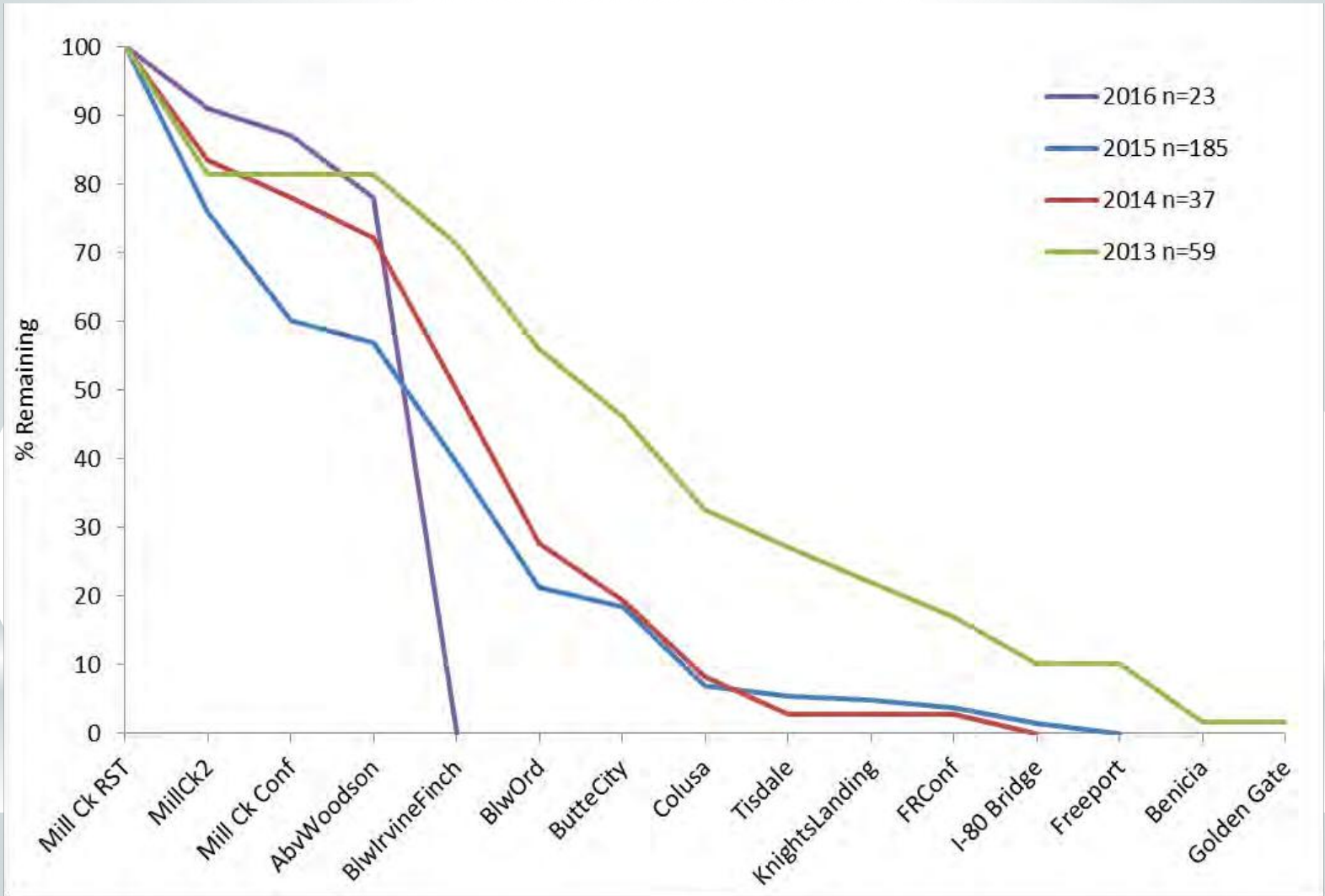




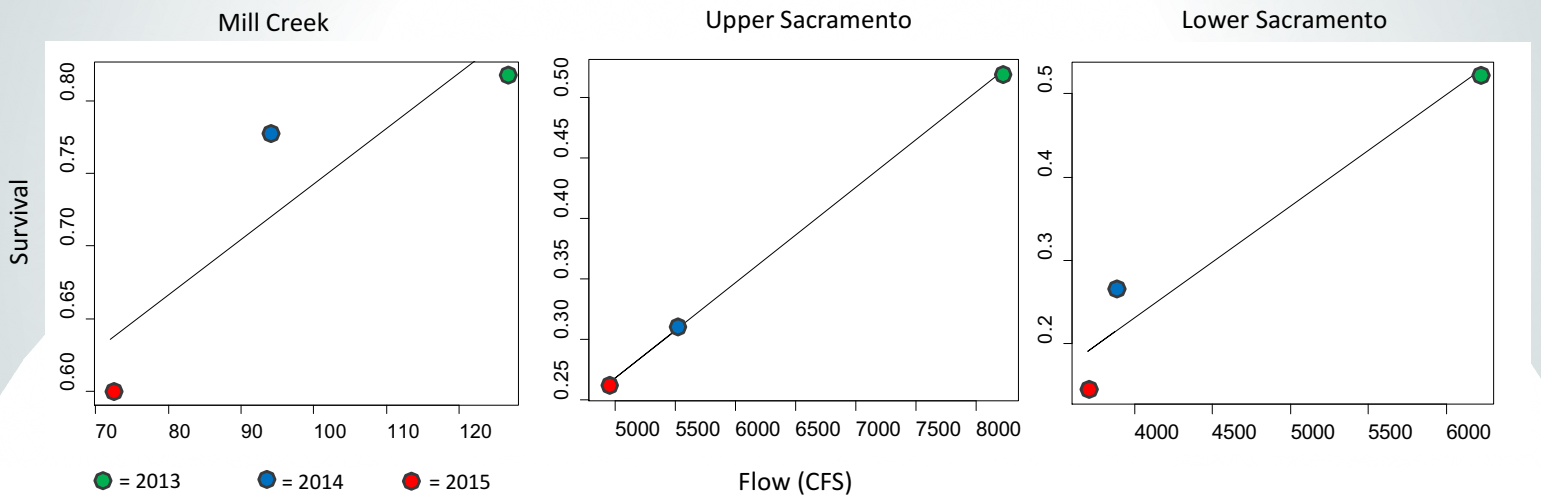
2013-2016 Mill Creek Survival per Km



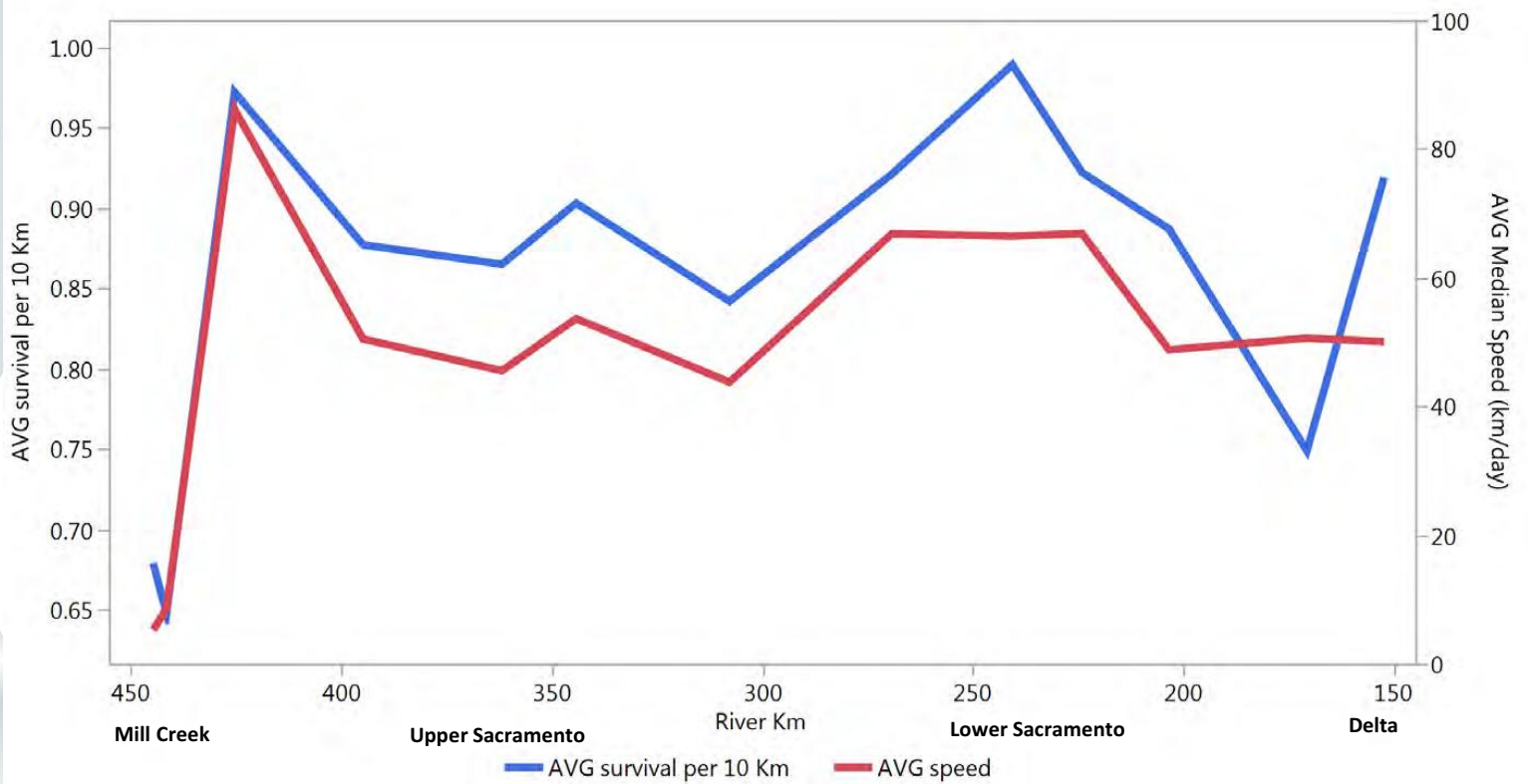
2013-2016 Mill Creek Cumulative Survival



Survival vs Flow



2013 – 2016 Mill Creek Survival vs Movement



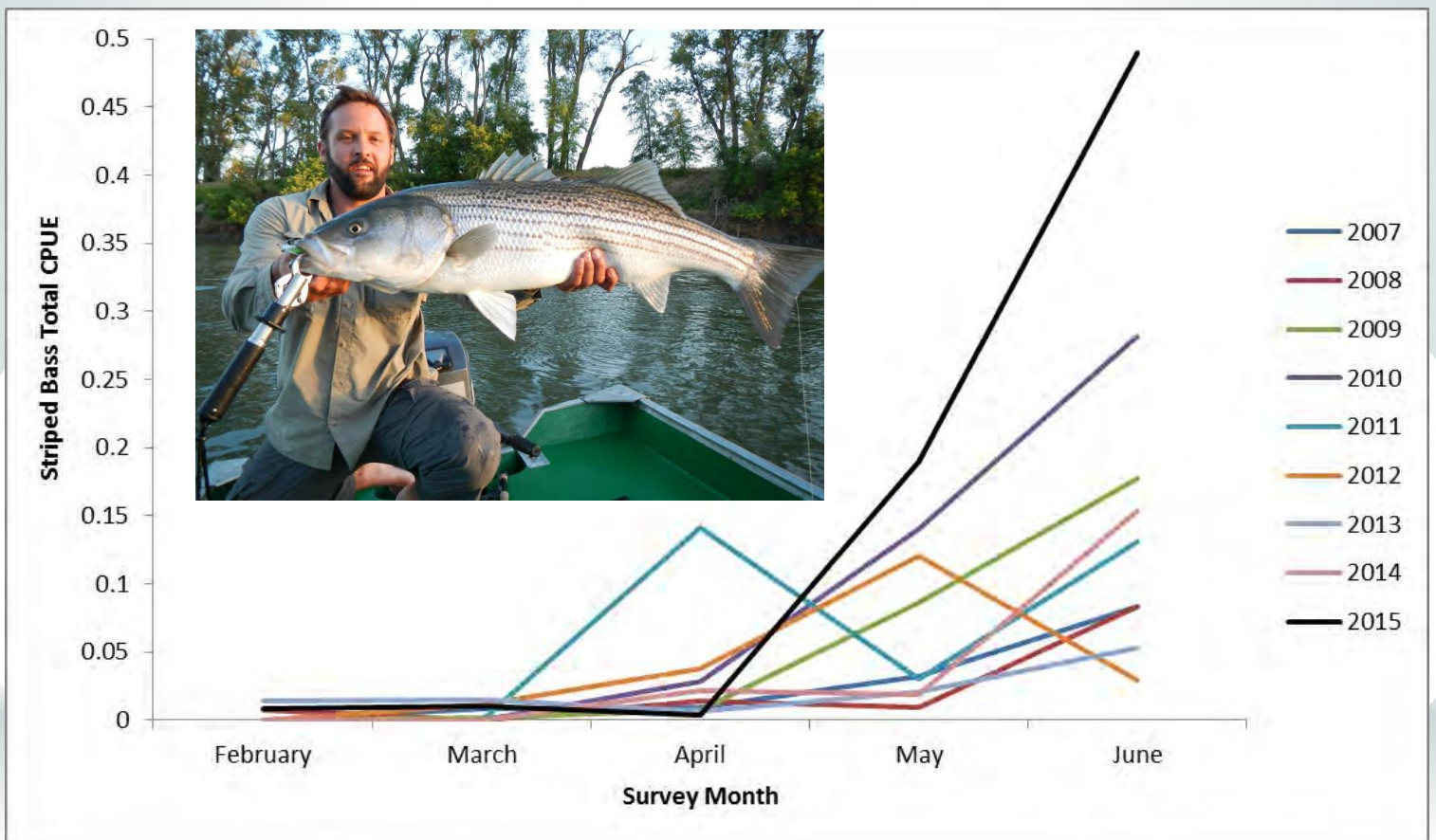
2015



2016



2007 - 2015 Striped Bass CPUE in the Upper Sacramento River



Conclusions

Low survival in Mill Creek and Sacramento River

- Associated with slower movement rates?
- Low flows = increased interaction with predators?

Movement rates highly correlated with survival

- Reaches where smolts move fast = higher survival rates

Late outmigration timing of Mill Creek smolts is unique, and not a successful strategy in recent years

High predator densities in Mill Creek and the Sacramento River coincide with smolt out-migration

Acknowledgements

Funding – AFRP, NOAA Fisheries

Special Thanks to:

- CDFW Red Bluff Fisheries
- The Nature Conservancy
- Los Molinos Mutual Water District



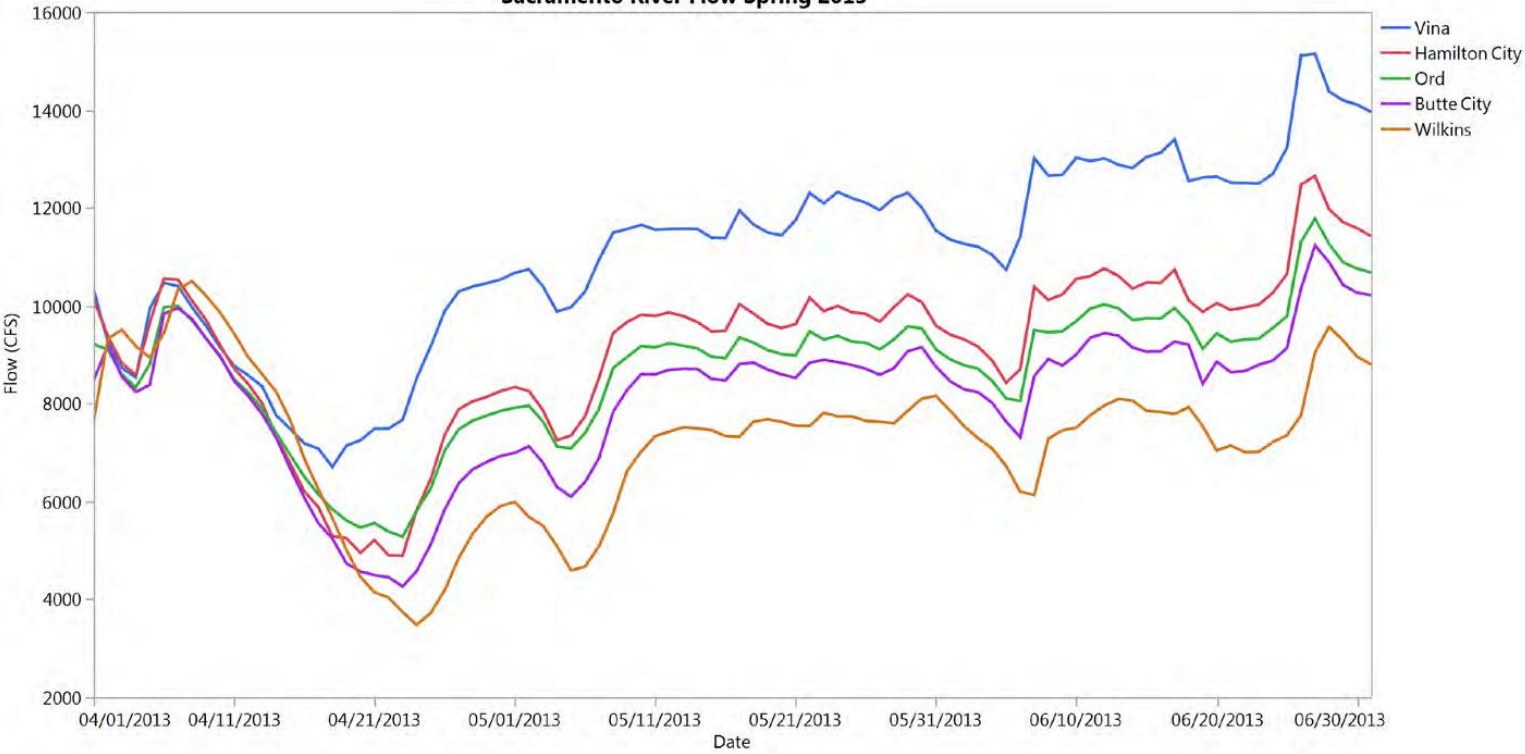


Sutter Bypass

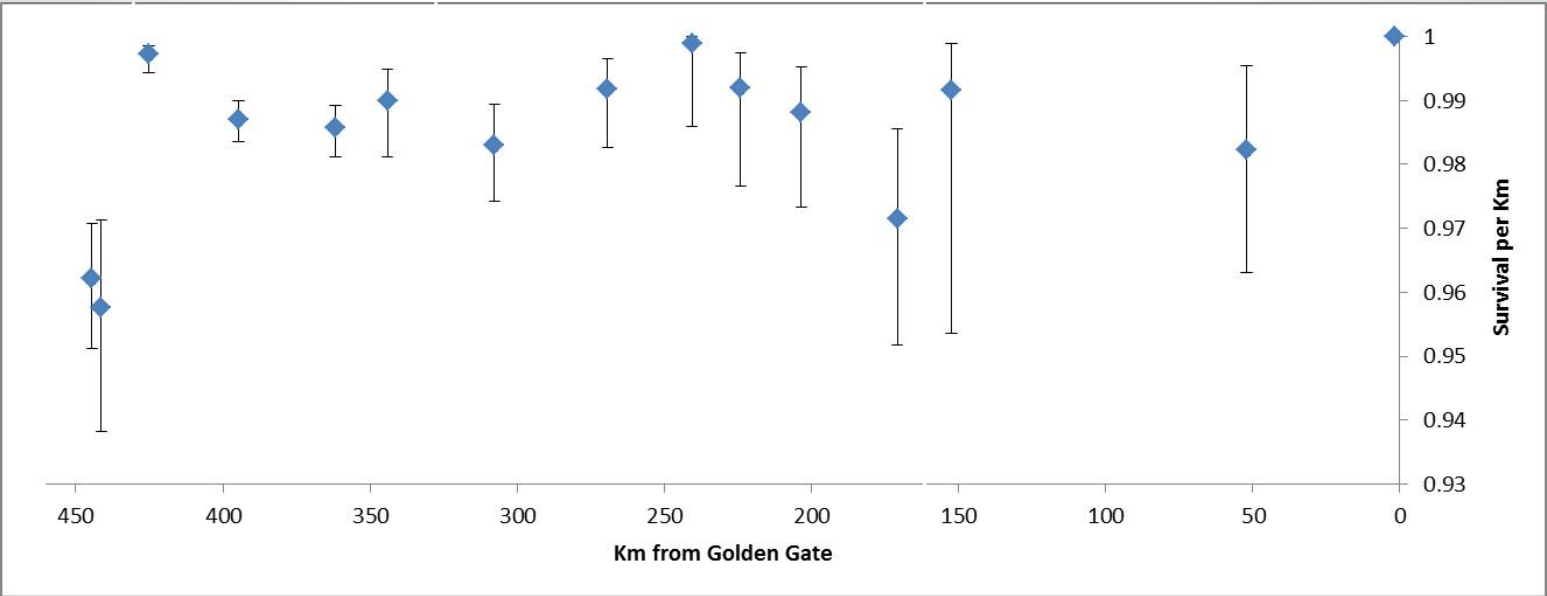


Mill Creek

Sacramento River Flow Spring 2013



2013-2016 Mill Creek Survival per Km





NOAA
FISHERIES
SWFSC

Survival and movement of hatchery winter-run Chinook salmon juveniles

Arnold J. Ammann

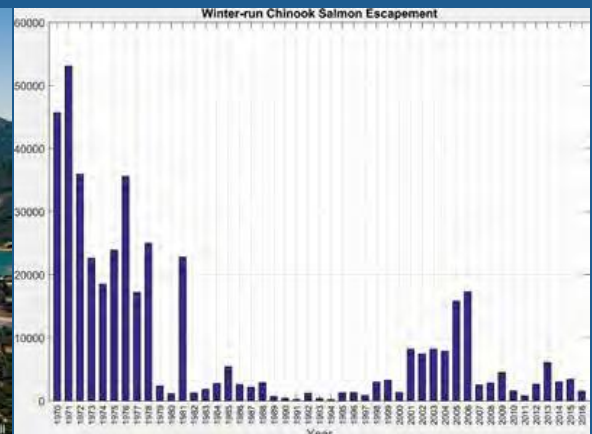
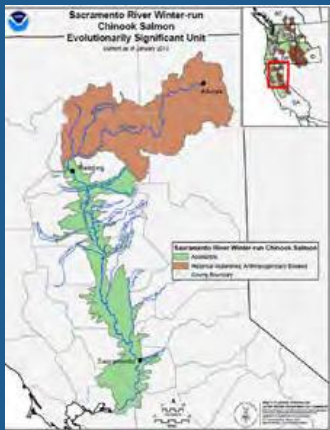
Fisheries Ecology Division, Santa Cruz CA.

12 Sept. 2018

Bay Delta Science Conference

Winter-run Chinook Salmon Status

Lost all historical spawning habitat – Shasta Dam
Only one spawning population – below Keswick Dam,
dependent on humans
ESA listed endangered since 1994



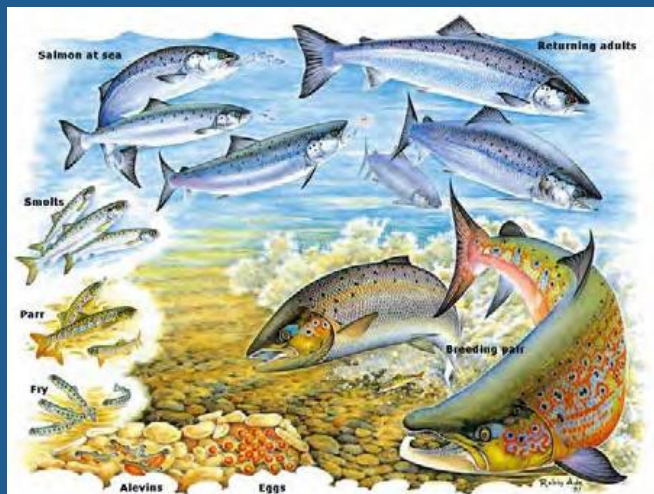
Winter-run Chinook Salmon Life Cycle

3 year life cycle

Adults migrate up rivers in winter / Spawn in summer(!)

Eggs and fry in gravel during summer

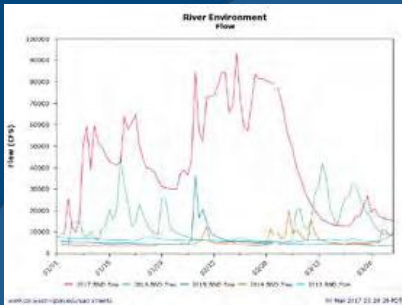
Juveniles migrate down river fall-winter



Life Stage	Survey	Knowledge
Spawner abundance	Carcass Surveys	Good
Egg to fry survival	Red Bluff RST	Good
Juvenile migration	RST/Trawl/Seine	Fair – need survival
Ocean survival	Adult returns	Fair

Challenges to juvenile migration

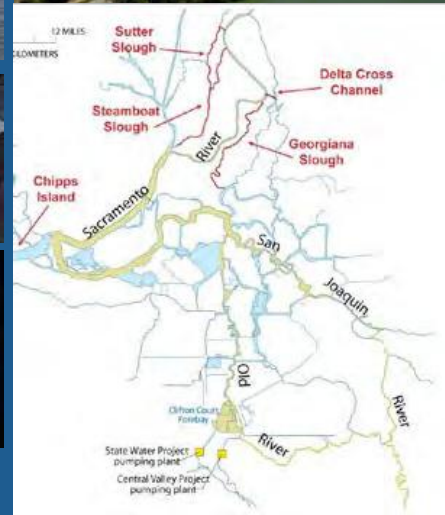
Droughts – less water



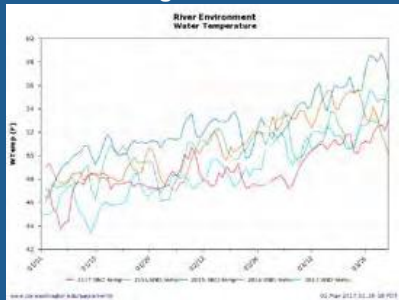
Native predators



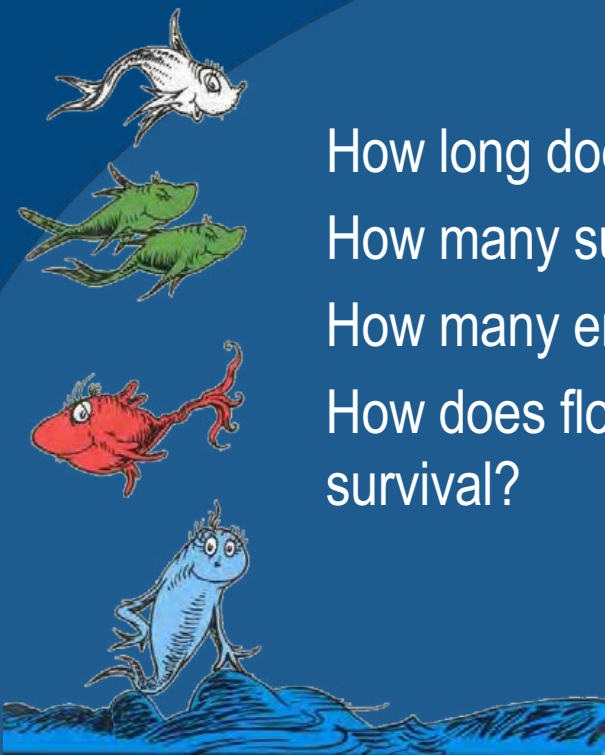
Non-native predators



Climate change – warmer water



Questions about juvenile migration



How long does migration take?

How many survive?

How many enter and leave the Delta?

How does flow affect movement and survival?



Acoustic telemetry technology - Tags

JSATS – Juvenile Salmon Acoustic Telemetry System

Very small size

Fast ping rate – 3 to 15 seconds

Detect many tags – no ‘tag collisions’

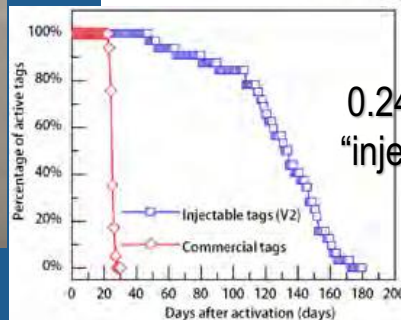
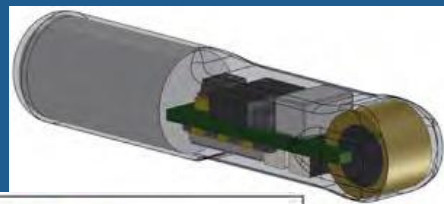
Non-proprietary – competing manufacturers



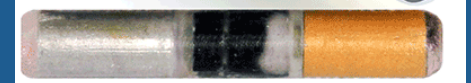
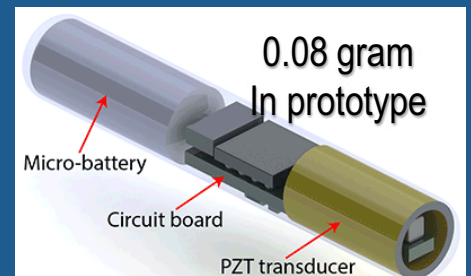
Tag used in this study



0.3 gram



0.24 gram
“injectable”



FUTURE

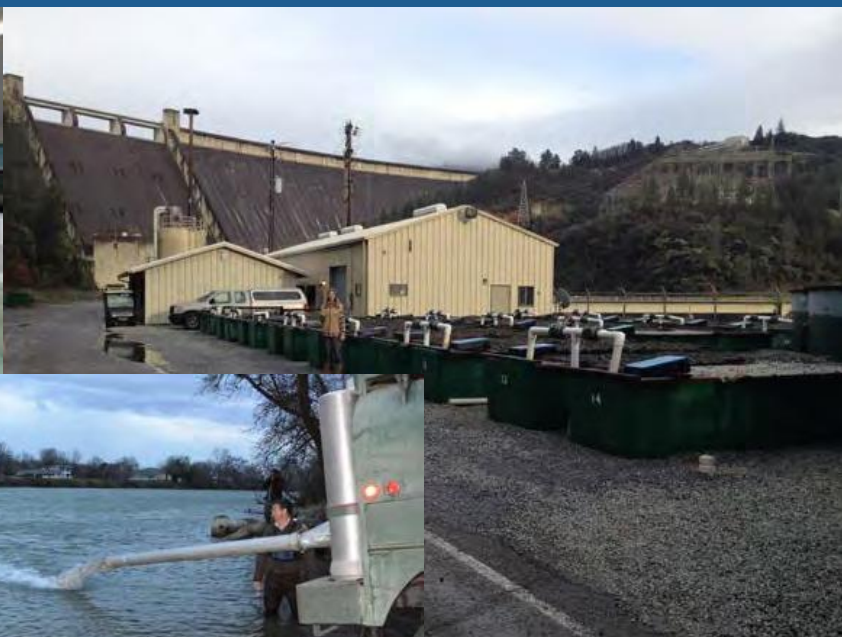
Acoustic telemetry technology - Receivers



Array = 150 individual receivers at over 70 locations

<https://calfishtrack.github.io/real-time/index.html>

Livingston Stone National Fish Hatchery



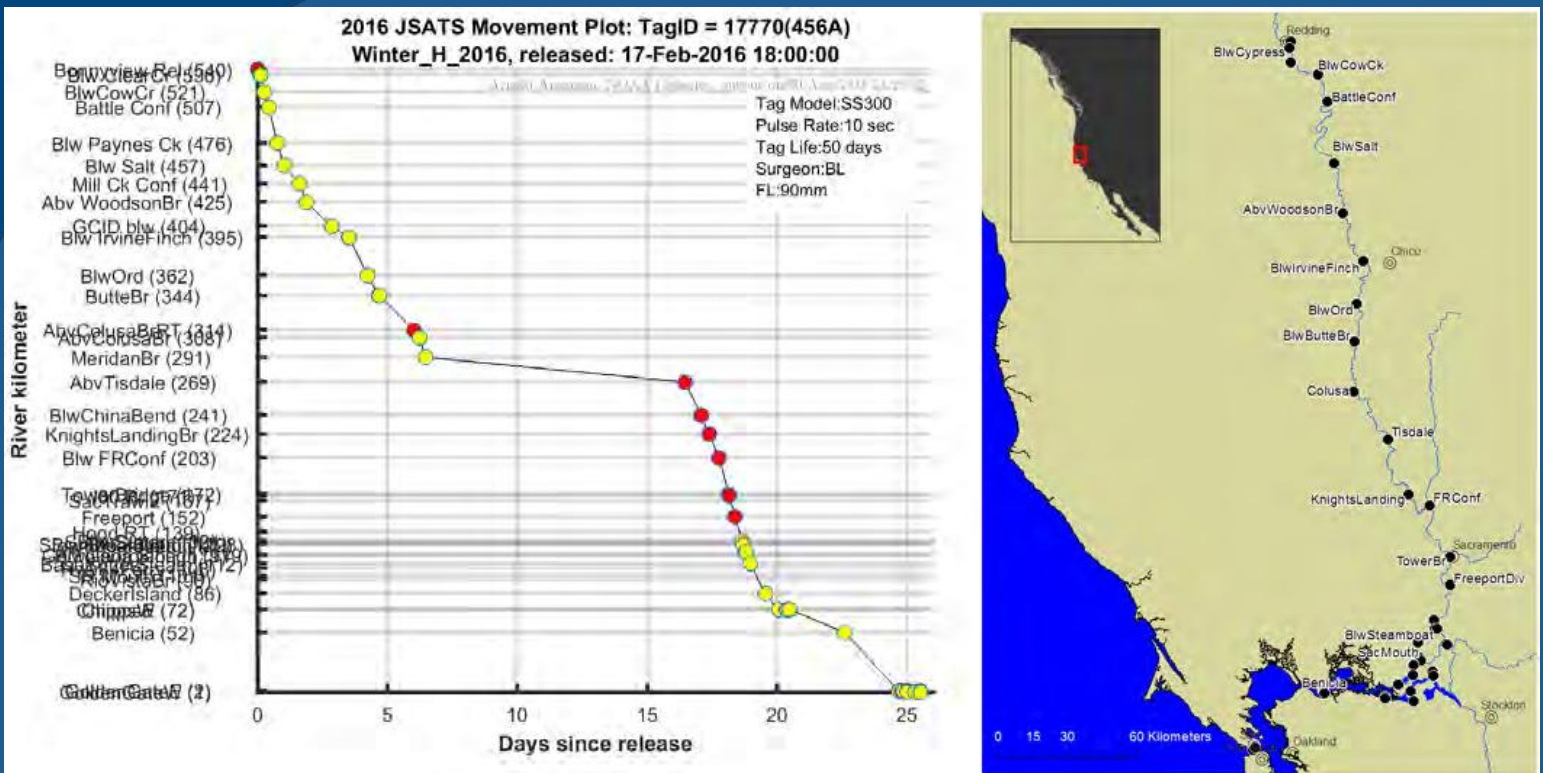
Livingston Stone National Fish Hatchery



Year	N	Date Released	Ave Weight (g)	Ave FL (mm)
2013	148	Feb 7	10.3	98
2014	358	Feb 10	9.4	95
2015	572	Feb 4 and 6	10.6	100
2016	570	Feb 17 and 18	9.4	95
2017	569	Feb 2	9.1	93
2018	598	Mar 1 and 13	14.1	106

Average tag burden: 3.3 to 2.1%

The goal is to track individuals



Migration Regions

River

380 rkm

Redding to Sacramento

Delta

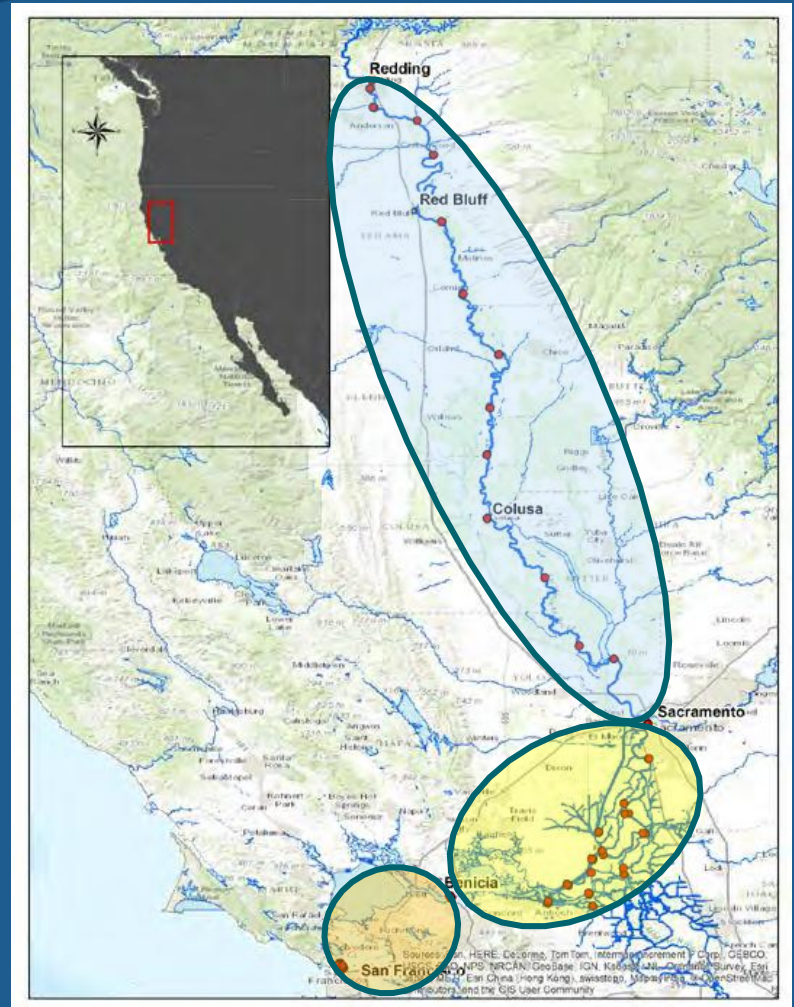
118 rkm

Sacramento to Benicia Bridge

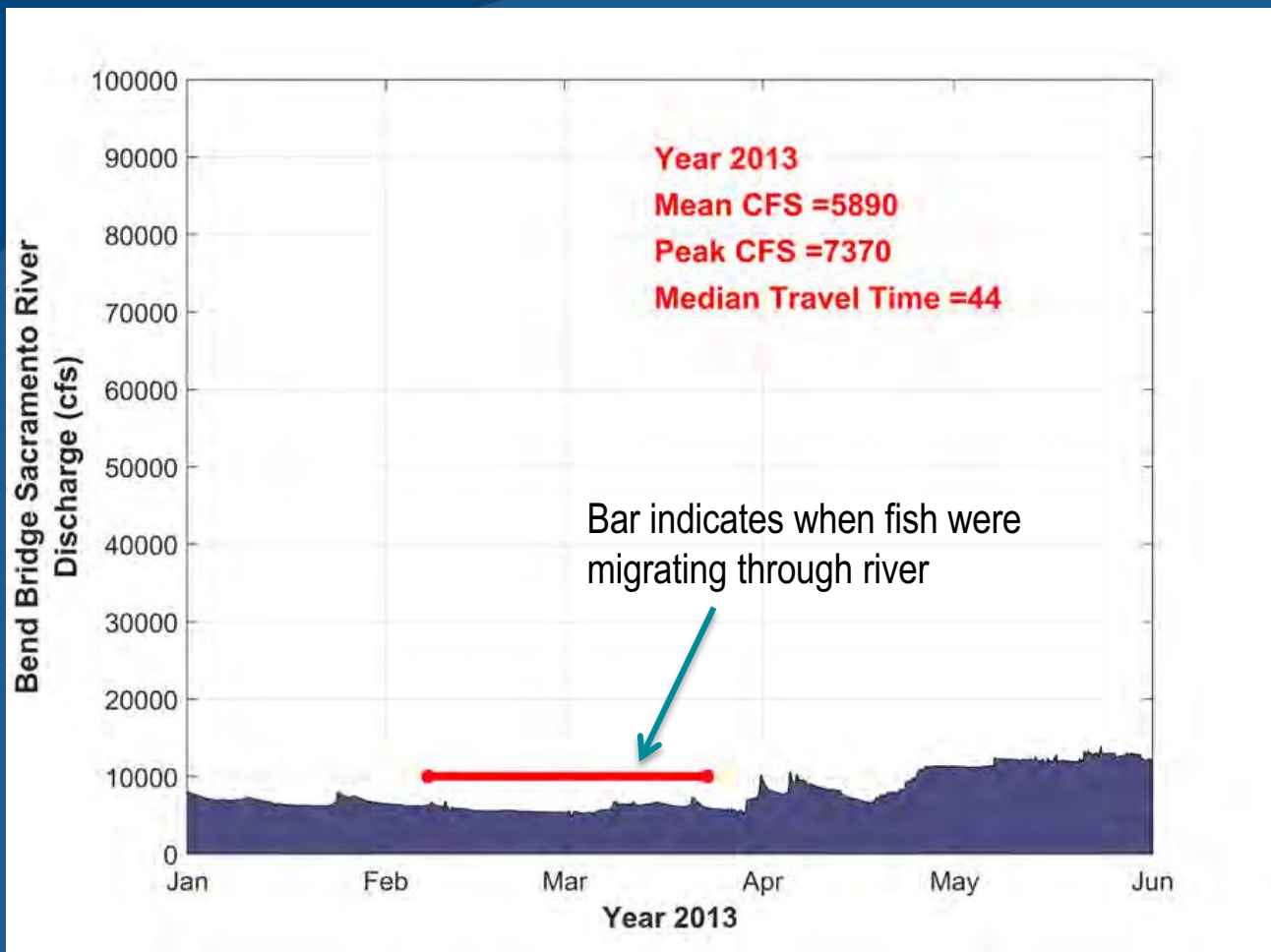
Bay

52 rkm

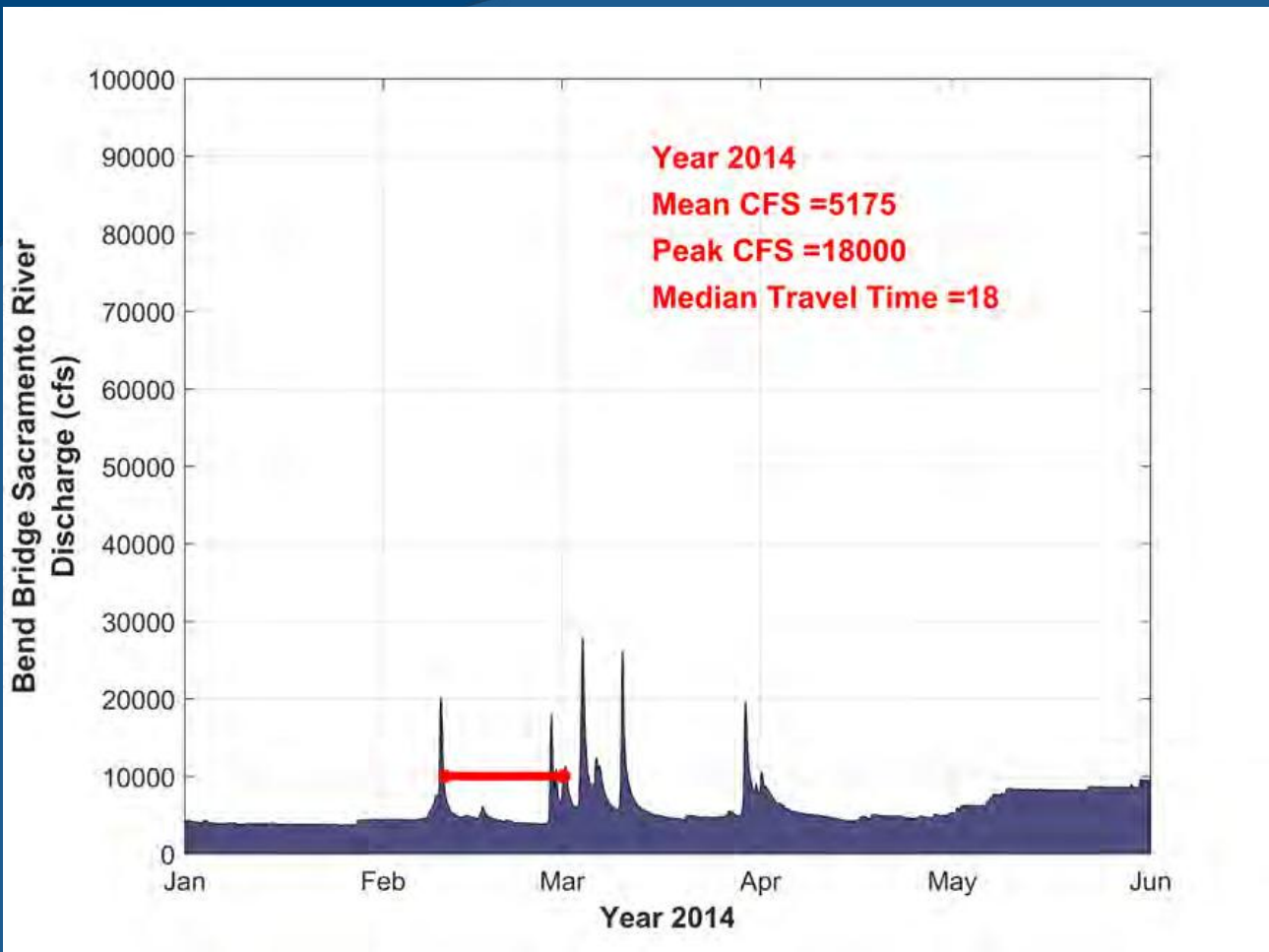
Benicia Bridge to Golden Gate



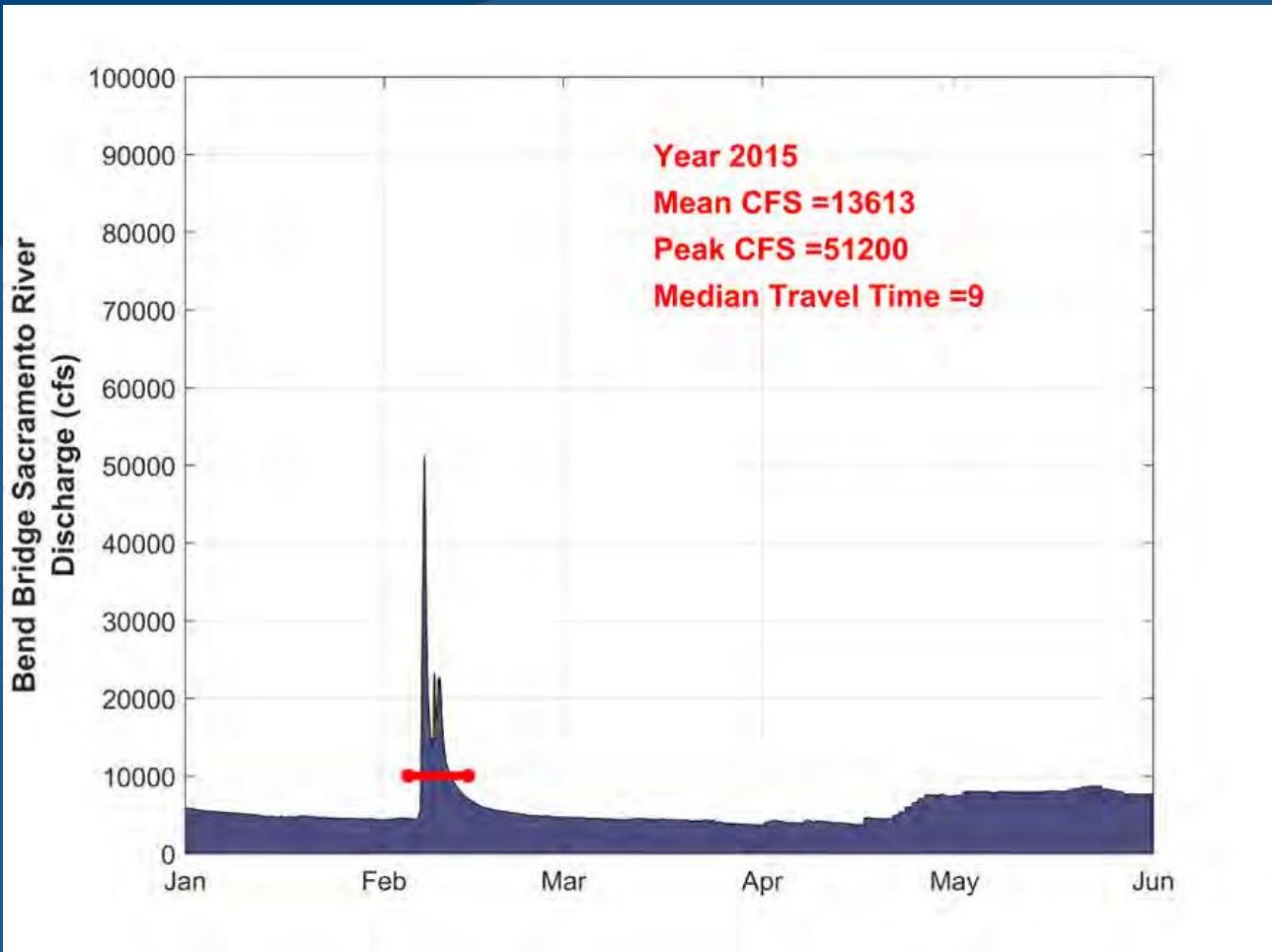
River flow and fish movement



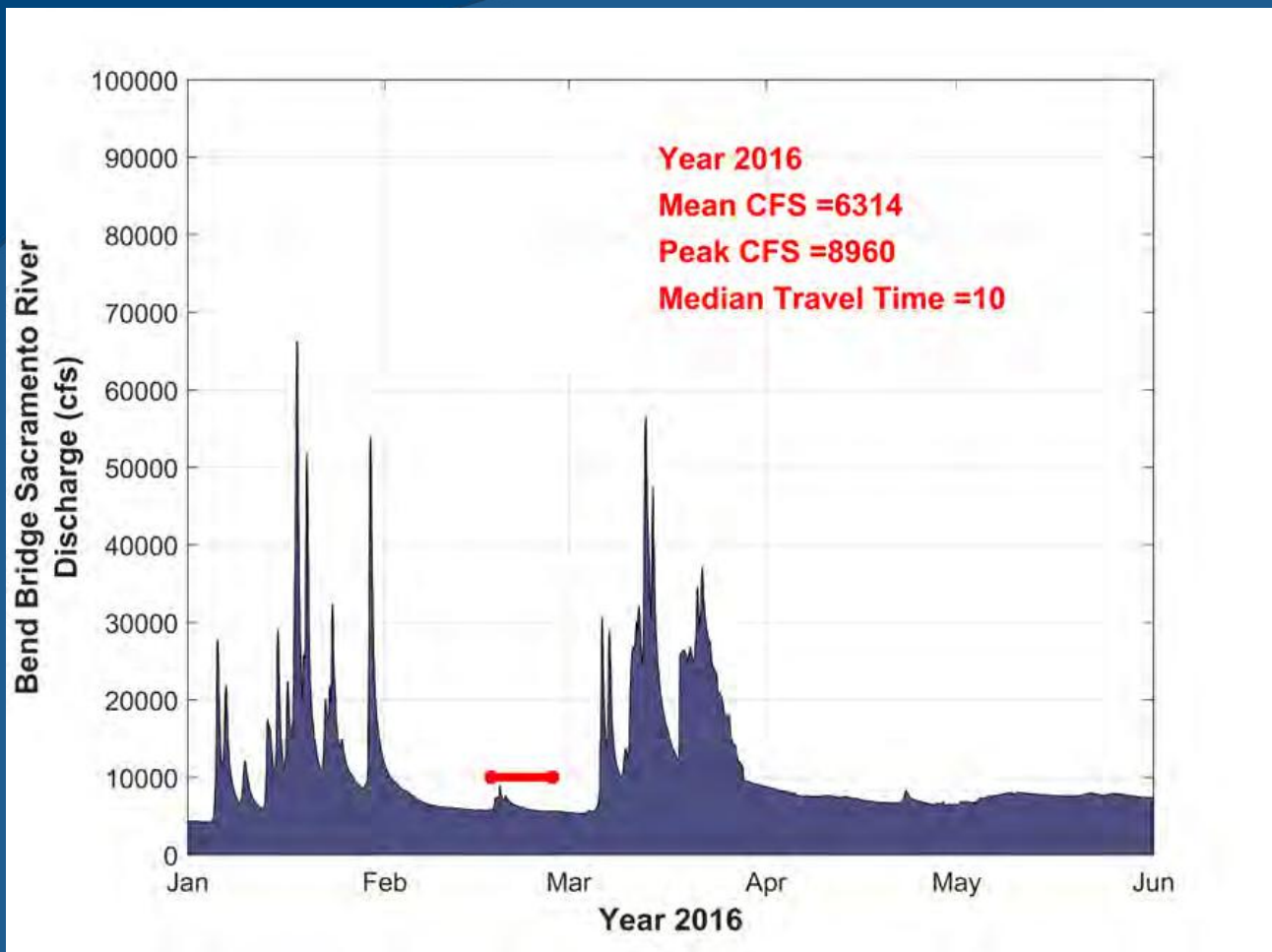
River flow and fish movement



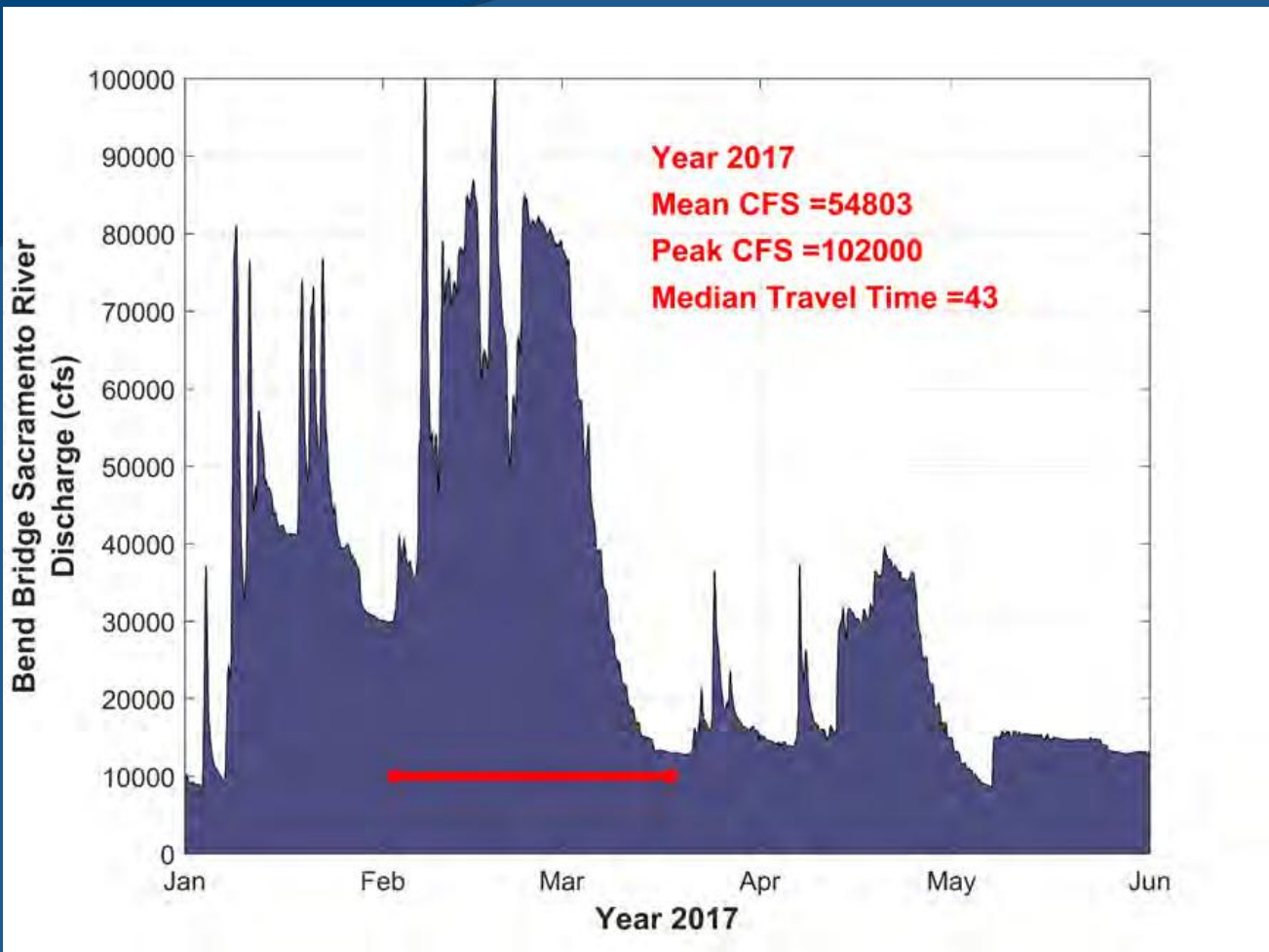
River flow and fish movement



River flow and fish movement



River flow and fish movement

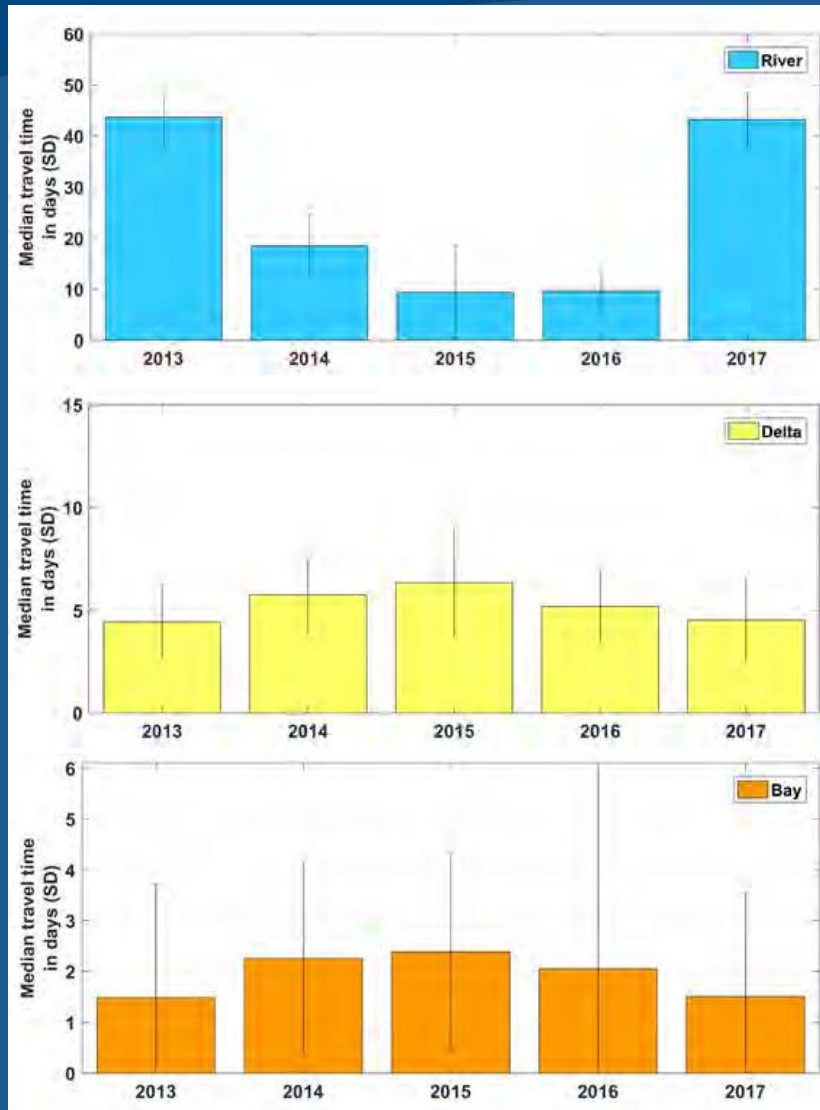


How long does it take to migrate?

River (380rkm) – varies greatly, median 10 to 43 days

Delta (118 rkm)– consistent, median 5 to 7 days

Bay (52 rkm) – consistent, median 1.5 to 2.5 days

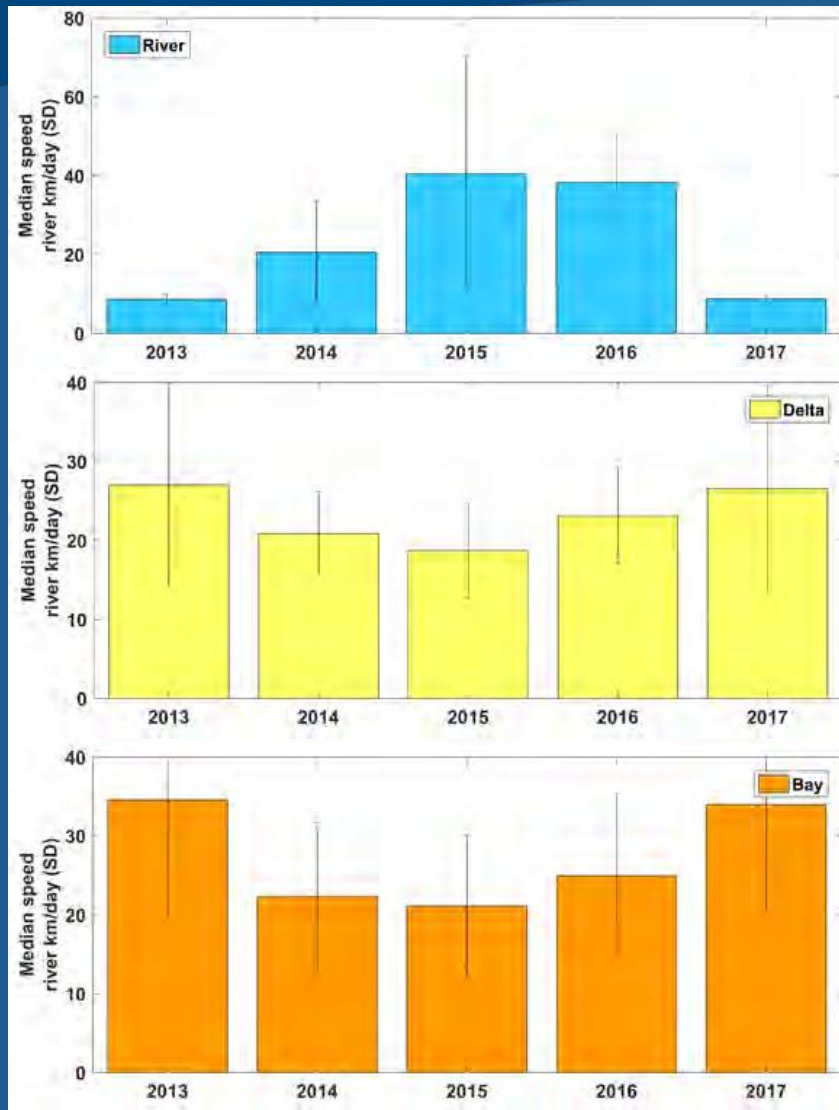


How fast do they go?

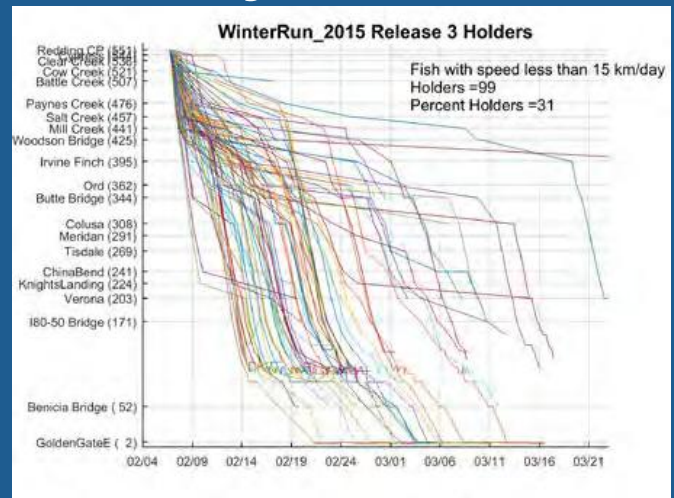
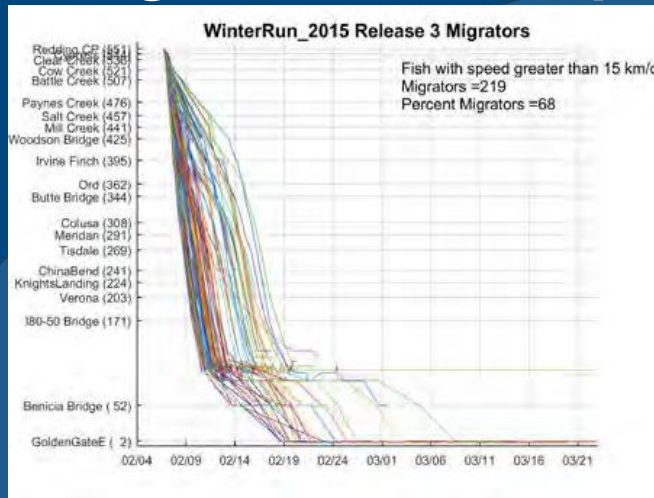
River – variable, median speed of 10-40 km/day

Delta - slower, about 20-28 rkm/day

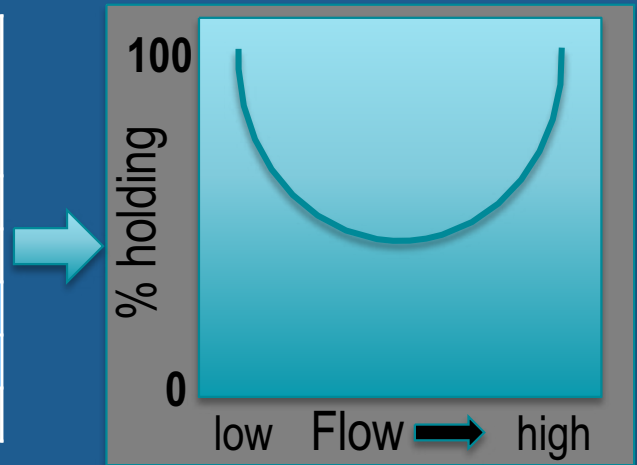
Bay – 20-35 rkm/day



Holding behavior: depends on year



Year	Total Released	Successfully out of river	Number of holders	Percent Successful that are holders
2013	148	18	18	100
2014	358	133	130	98
2015	567	199	81	41
2016	570	282	151	54
2017	569	232	227	98



How many survive?

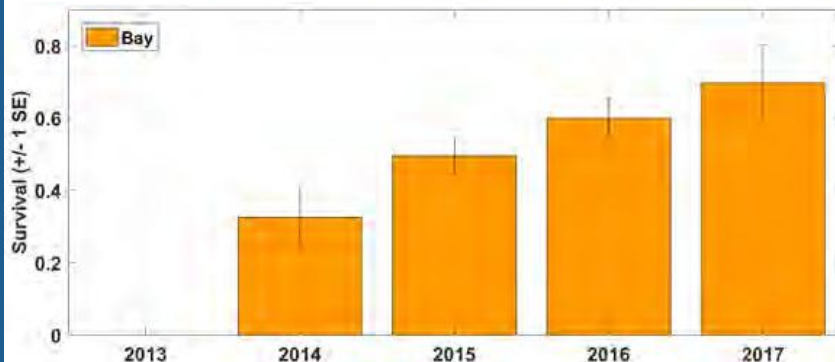
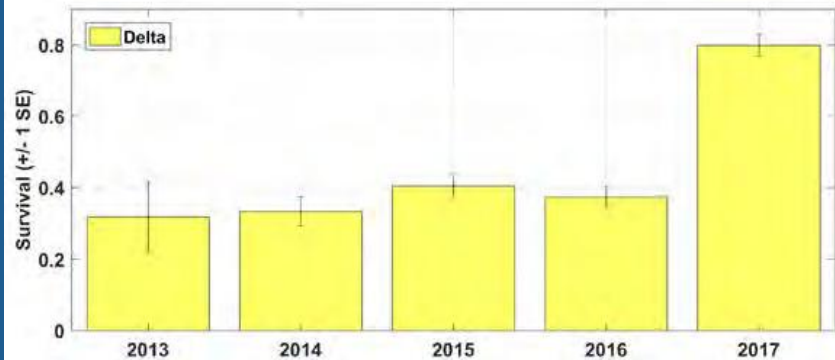
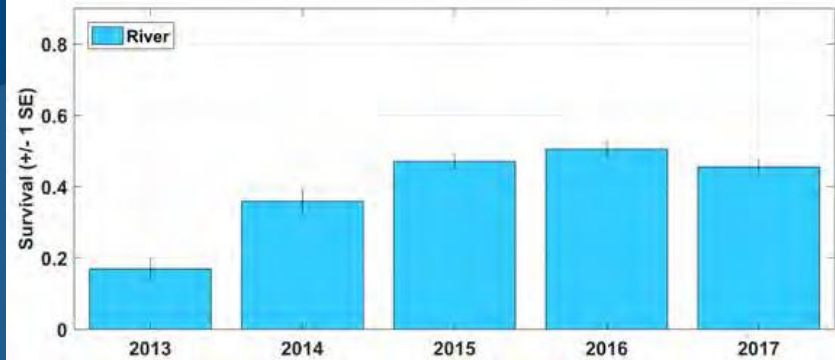
River – variable 18-55%

* 2017 is “to Delta”

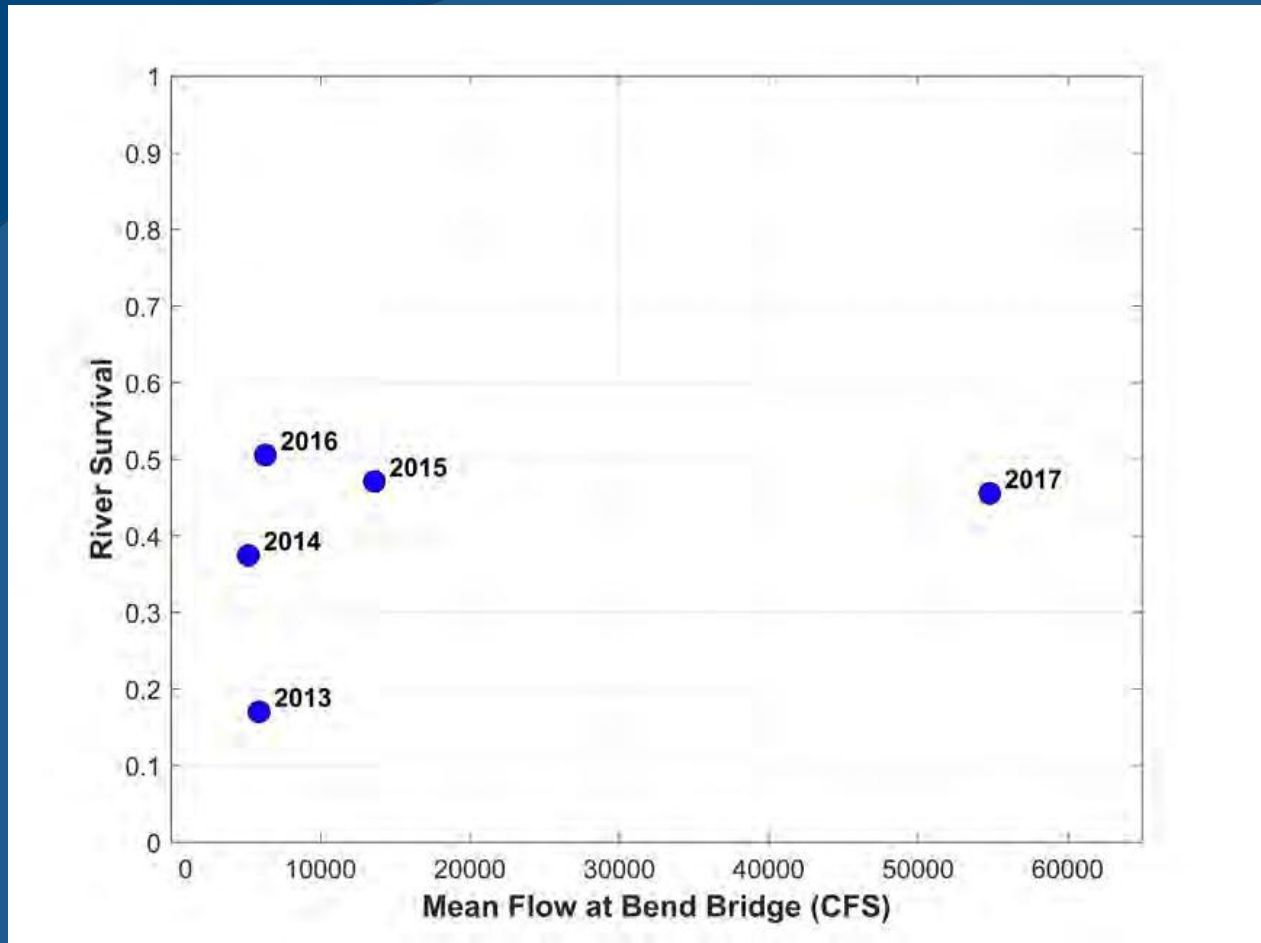
Delta – consistent 35-42%,
until...

2017 – much higher 80%

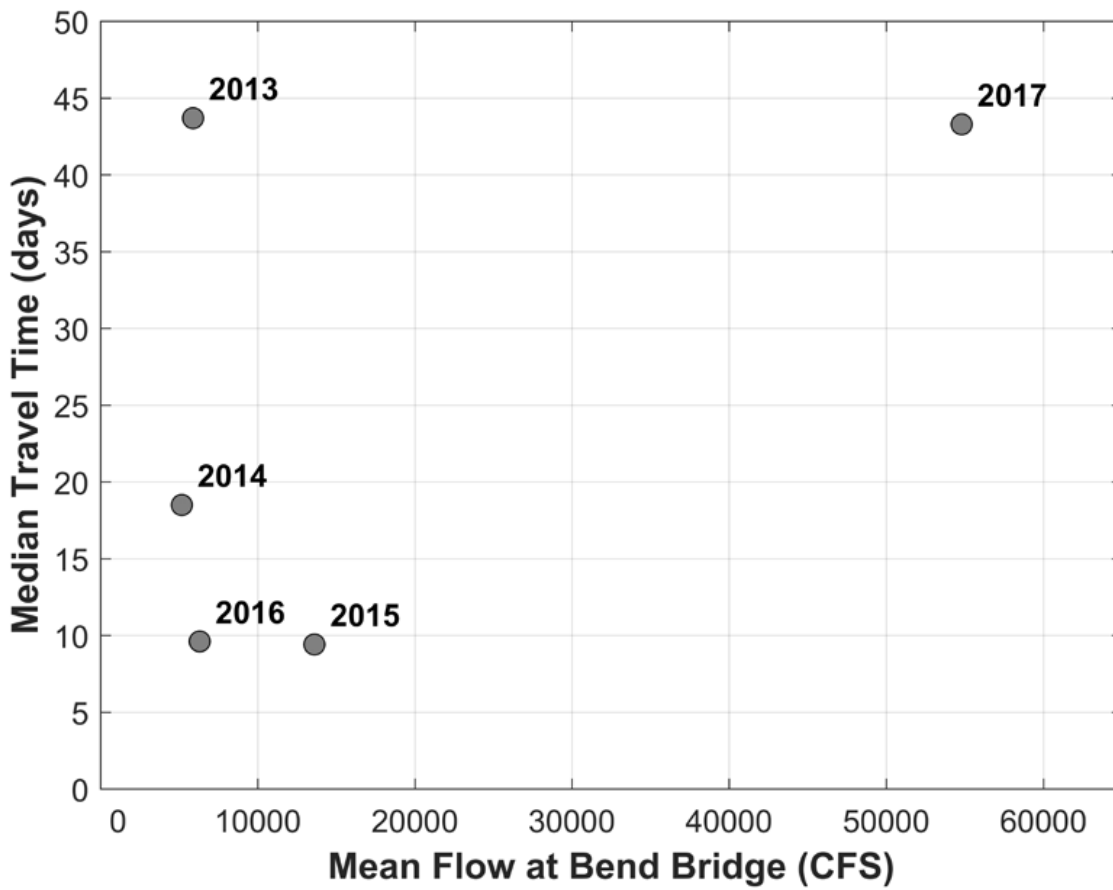
Bay – variable 30-70%



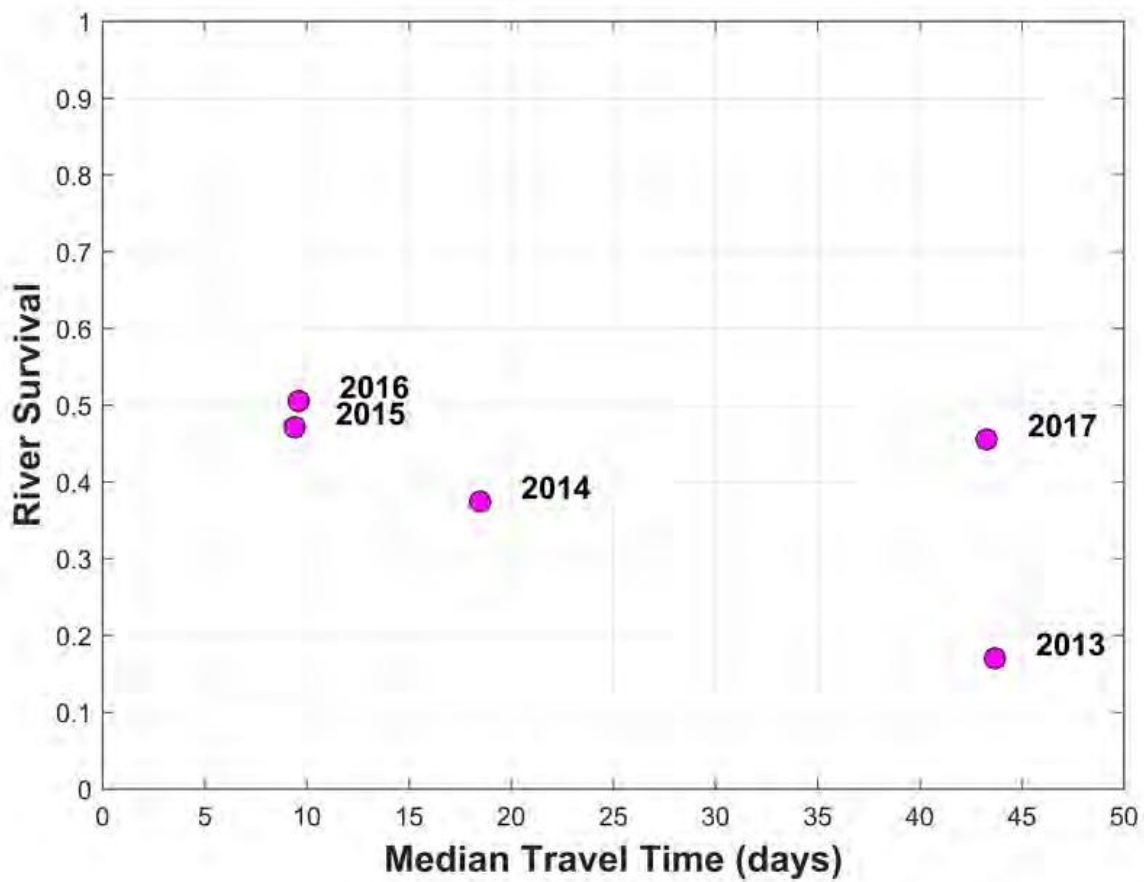
Survival through River versus flow



Travel time through River versus flow



Travel time through River versus survival



Total Outmigration Success Redding to the Golden Gate: 548 rkm

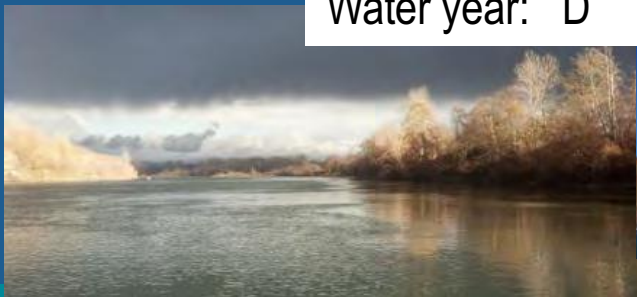
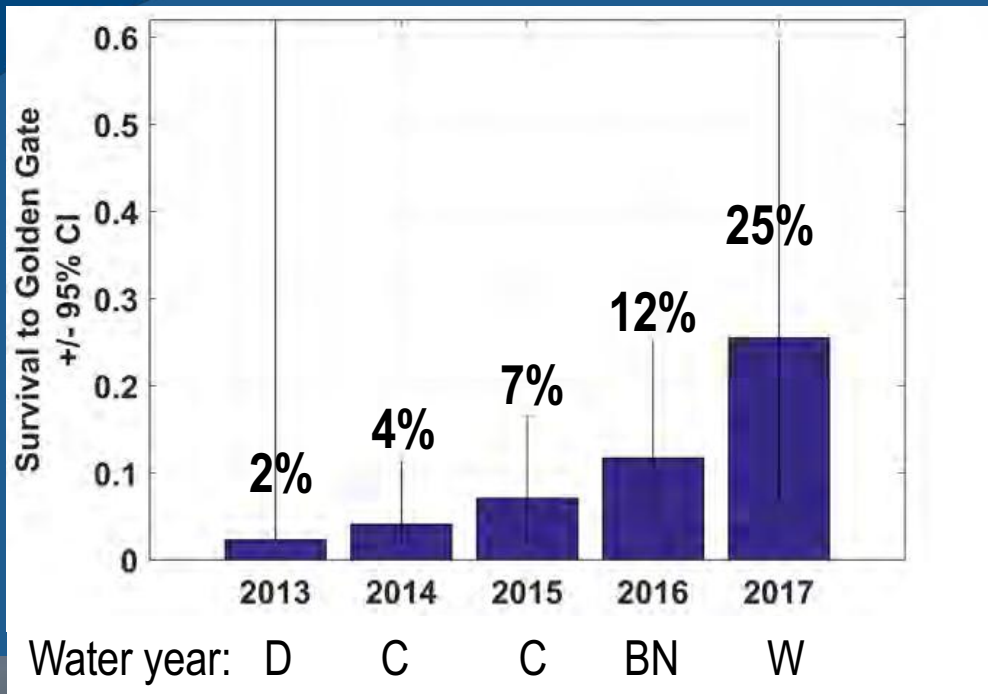


Photo Eric Danner

Take away messages



Acoustic telemetry is a powerful tool

- Movement – travel time, speed, routing
- Behavior – holding
- Survival – broad and fine scale

Winter-run outmigration is complex

- Highly variable
- Holding or rearing behavior
- River movement rate not directly related to flow
- River survival not directly related to flow



Overall outmigration survival is low

- High mortality in less than 2 months
- Bottleneck for recovery?





Thanks:

Jason Hassrick
Jeremy Notch
Alex McHuron
Brendan Lehman
Cyril Michel
Emily Tucker
Nick Demetras
Heidi Fish

Bob Null
Pat Brandes
Russ Perry
Sean Hayes
Beau Hopkins
Kaitlin Gooding
John Rueth
Al Duncan
Chris Vallee
Brennan Helwig

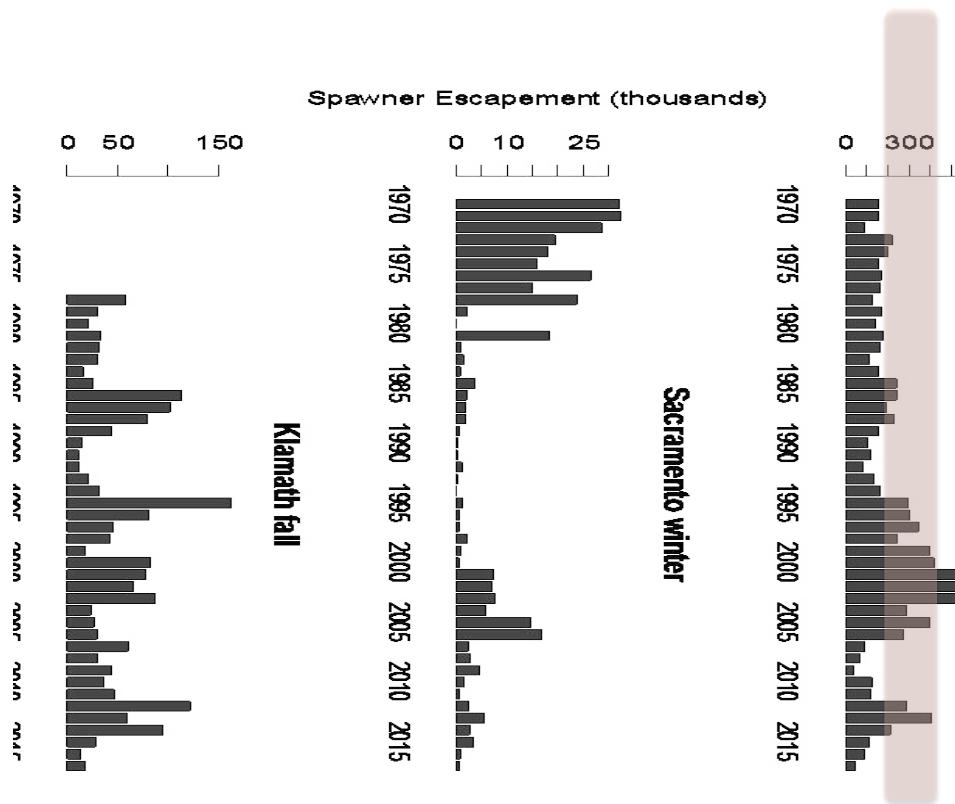
Funding:

US Bureau of Reclamation
California Dept. Fish and Wildlife
Anadromous Fish Restoration Program



California Chinook salmon escapements very poor in 2015, 2016, and 2017

Climate-driven declines in stream and ocean productivity have likely been major contributors



Climate and California salmon 2014-present

Freshwater: California's hot drought from 2012-2016 had extensive negative impacts on salmon

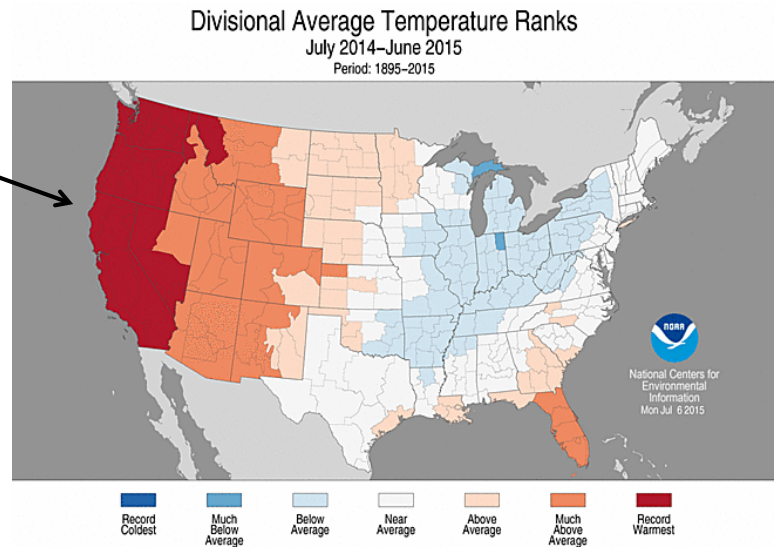
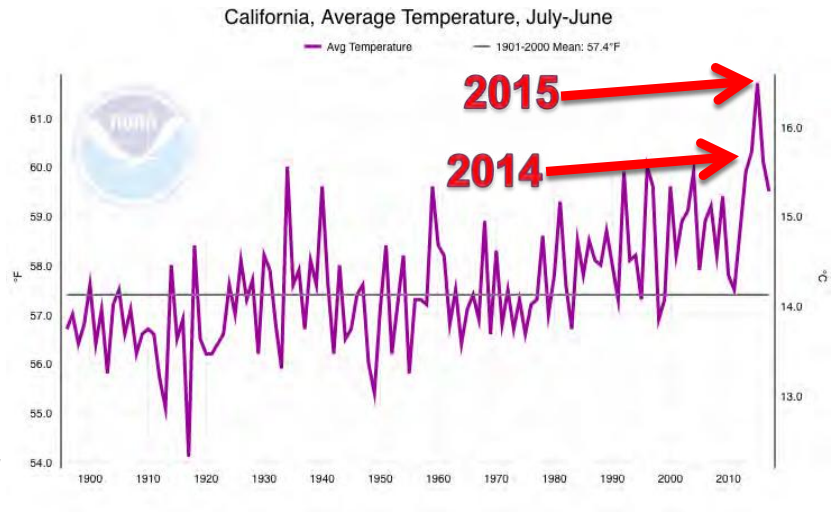
- record-low winter-run egg-to-fry survival rates in 2014-15
- high water temperature and exceptionally high disease and infection rates in Klamath salmon in 2014-15
- JSATS data showed very low outmigration survivals in 2013-14-15-16; much higher outmigration survivals in 2017

Ocean: record-warm ocean temperatures/subtropical conditions in 2014-2015 had extensive negative impacts

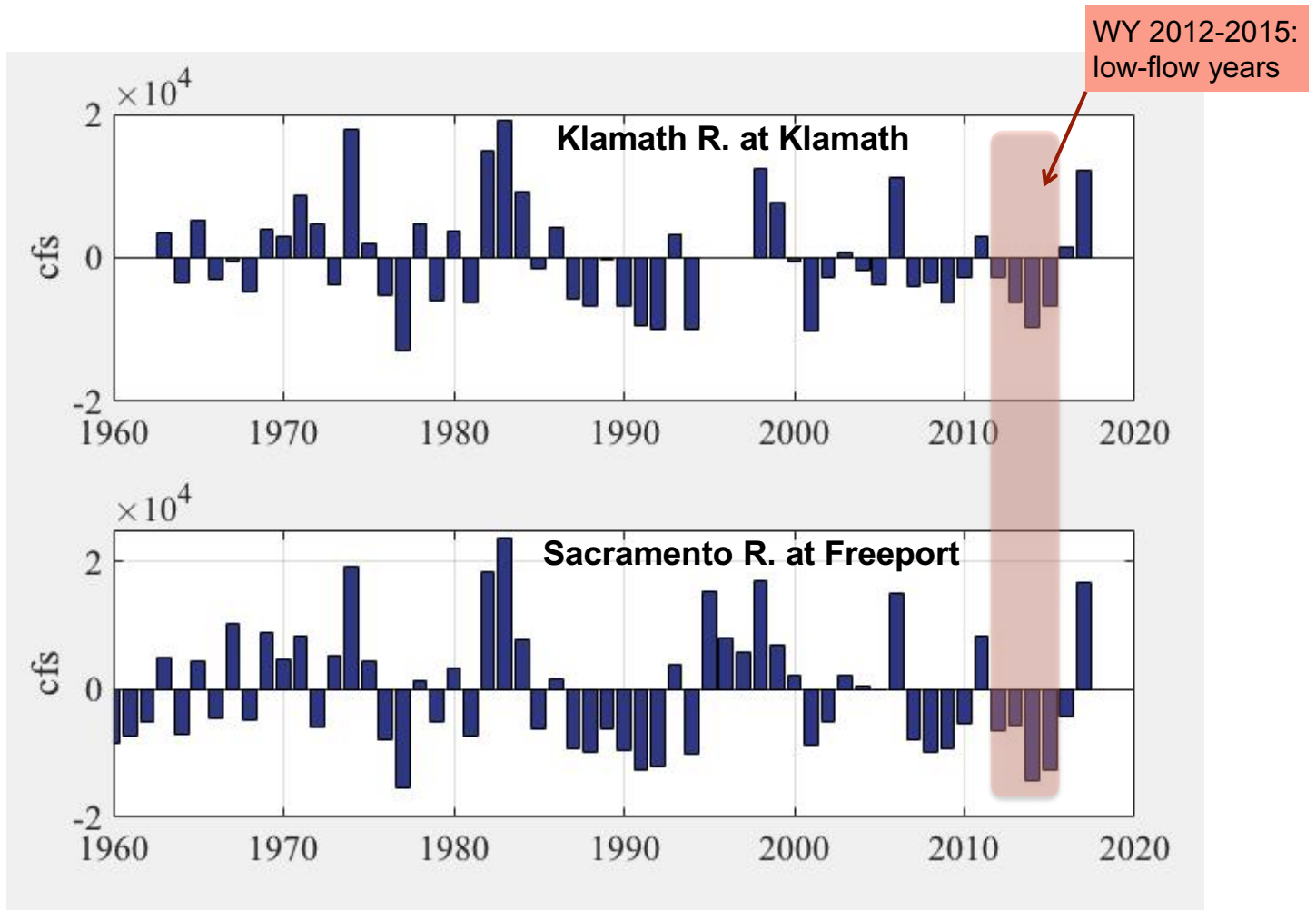
- Ocean indicators point to strong sub-tropical influences on West Coast marine life in 2014-15 coast-wide; recovery to more productive conditions south of Mendocino in 2016-17

2014-17: exceptionally warm years for California

- Surface air temperature record for July 2014-June 2015 was almost off the charts, ~ 1 °C warmer than the previous record
- 2015 Western Snow Drought came with record high temperatures for the entire west coast
- The “hot drought” was amplified ~30% by high temperatures
- 2016 and 2017 a bit cooler than 2014

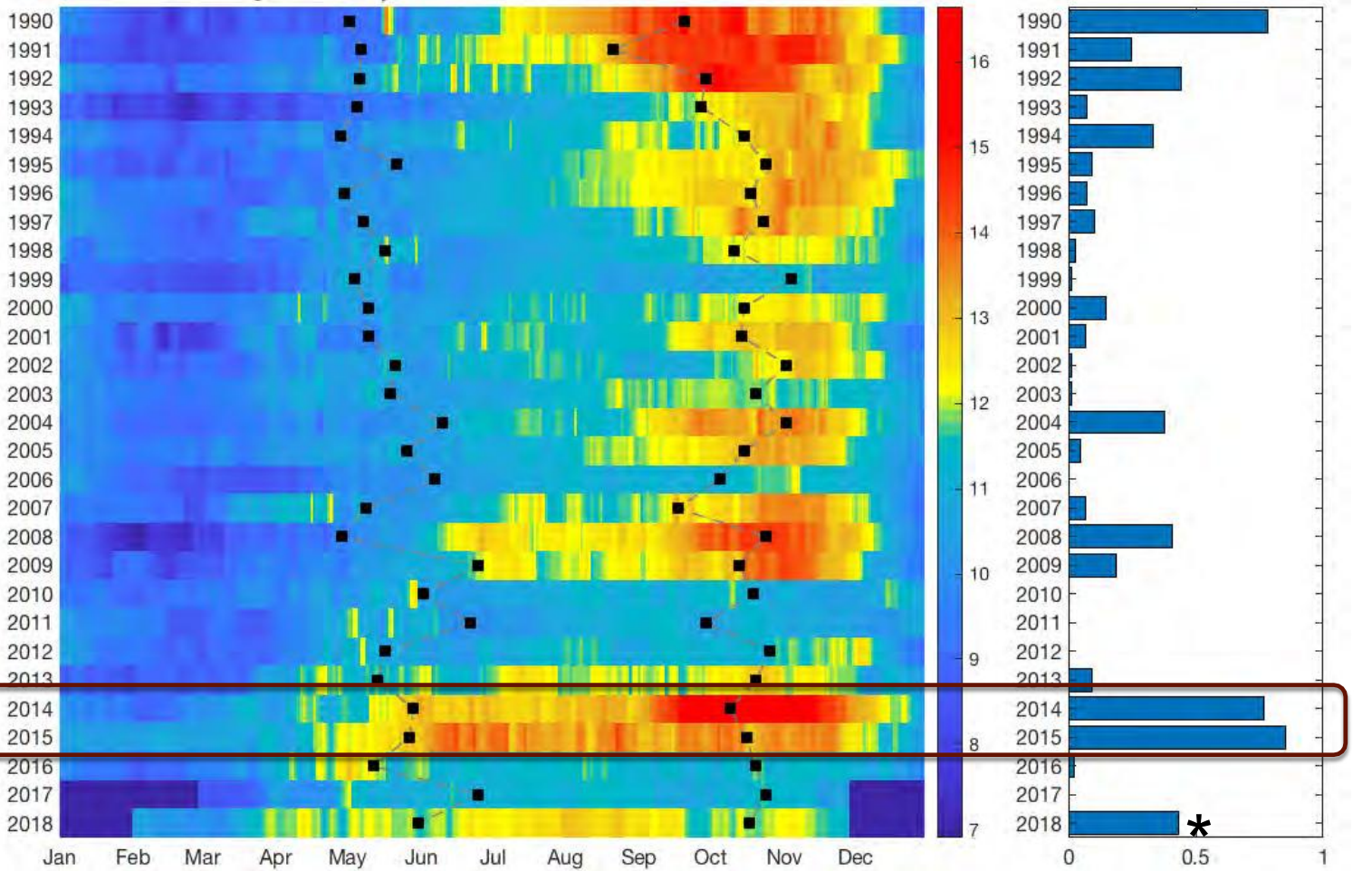


Water year streamflow anomalies in the Klamath and Sacramento Rivers



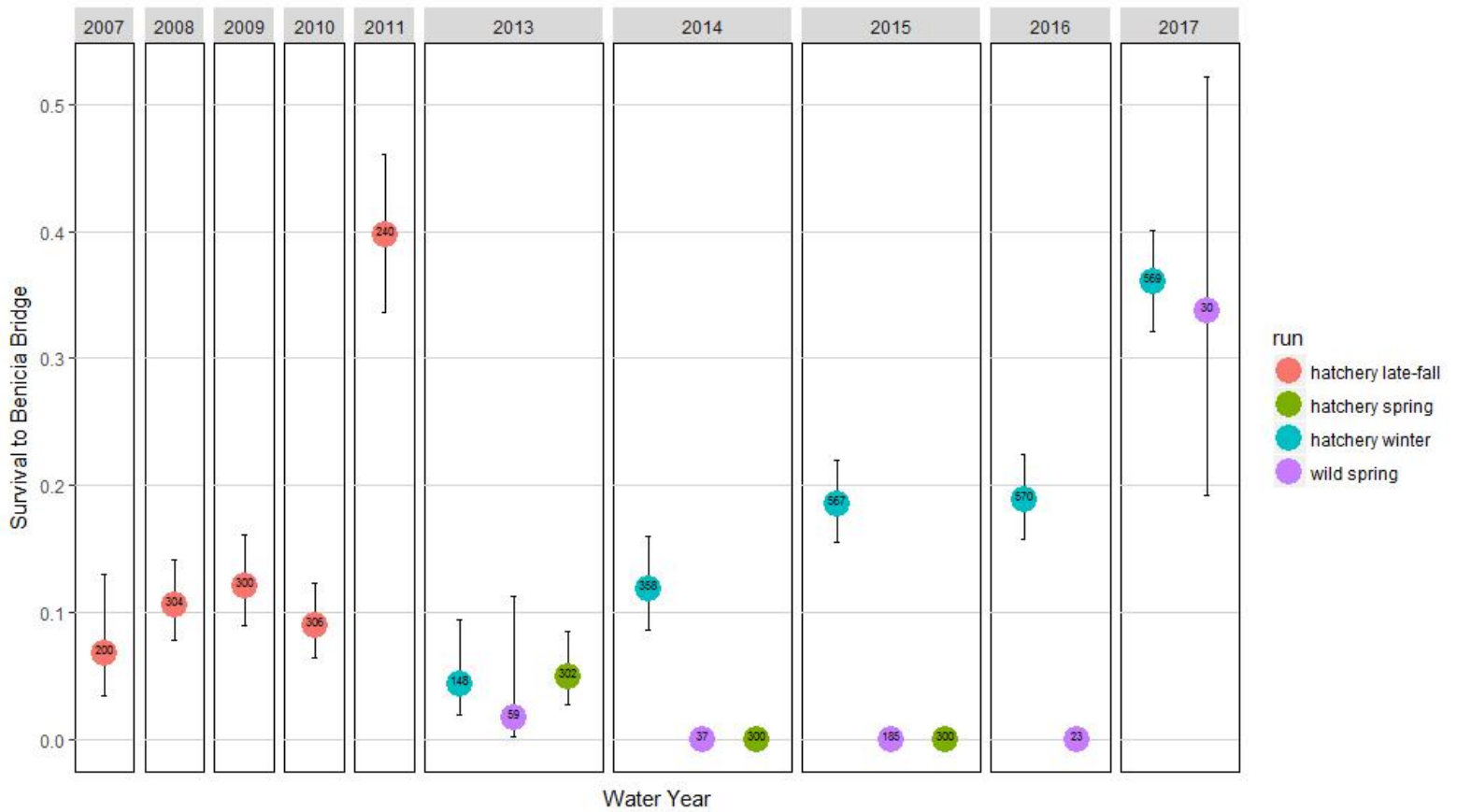
Daily mean water temperatures in winter-run Chinook salmon spawning habitat between Keswick Dam and Clear Creek

* Values for 2018 based on projected reservoir operations provided by the USBR.



Slide provided by Eric Danner, SWFSC/NMFS

Smolt Outmigration Survival Rates to Benicia from JSATs

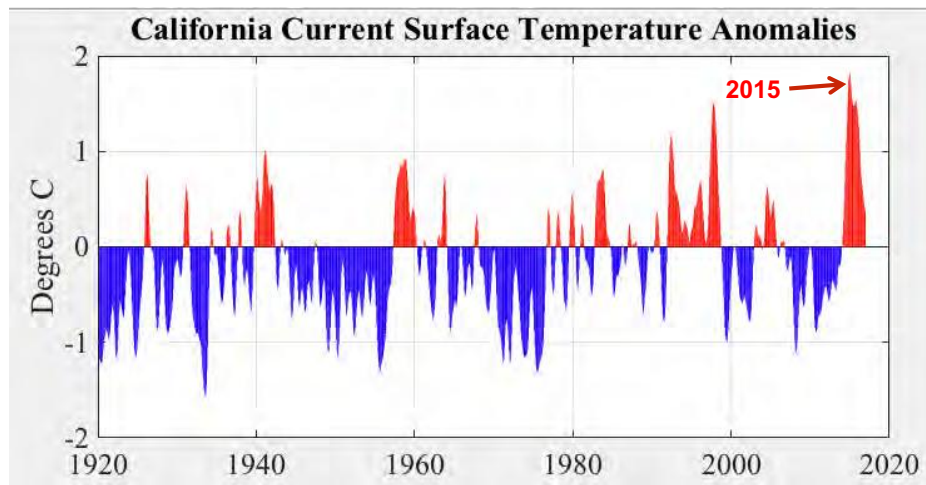
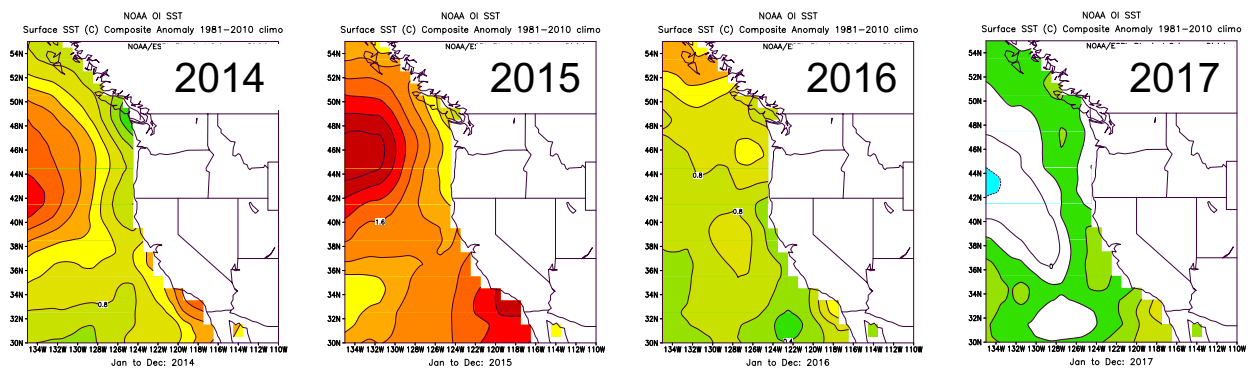


Slide provided by Cyril Michel/UCSC/NMFS

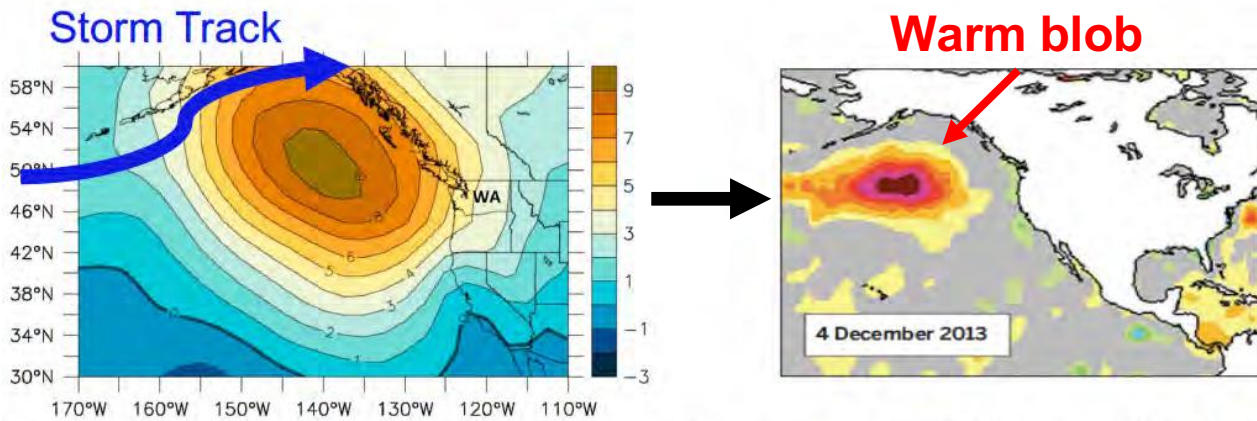
How bad were ocean conditions for CA salmon from 2014-2017?

- Mostly really bad!
- Record high CCS temperatures: 2015 was the warmest year on record, 2014-2016 the warmest 3 year average
- Poor growth/survival conditions for CA salmon and many other top predators (sea lions, sea birds)
- Affected salmon abundance and fisheries 2016-2017, and will likely affect abundance through at least 2018
- High temperatures were caused by “the blob”, weak winds, and the extreme tropical El Niño in 2015-16

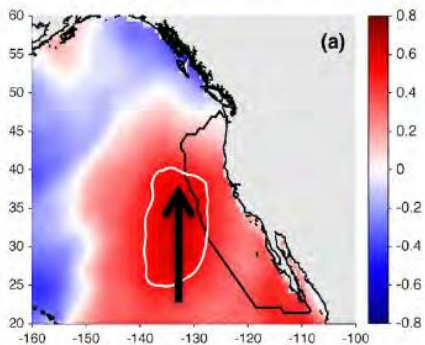
Ocean temperatures from 2014-2017



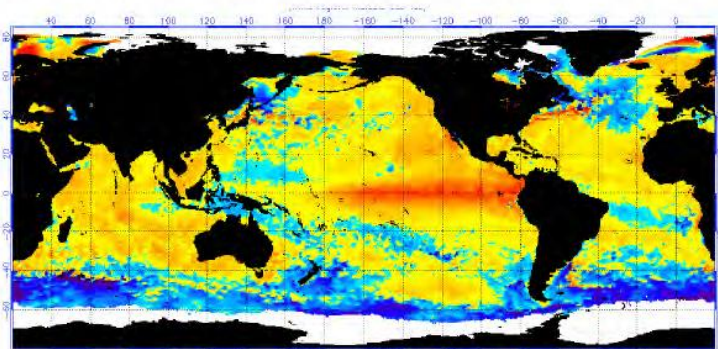
What caused the recent extreme ocean temperatures?



High pressure ridge → Reduced storm-driven mixing → Warm Gulf of Alaska



+ Anomalous winds off US west coast



+ One of the strongest El Niños on record

Biological Impacts

Warming Pacific Makes for Increasingly Weird Ocean Life

A "blob" of warm water that's partly to blame for dead birds and stranded sea lions in the Pacific may share a cause with Boston's snows and California's drought.



Mysterious Sea Lion Die-Off Strikes Again on California Coast

Tiny sea lion pups are washing up on beaches in unusually high numbers—for the third winter in a row.

Experts puzzled as 30 whales stranded in 'unusual mortality event' in Alaska

Scientists 'very concerned' and suspect toxic algae, though NOAA concedes 'bottom line is we don't know what's causing deaths'

Unusual warm ocean conditions off California, West Coast bringing odd species



Huge Toxic Algal Bloom Shuts Down West Coast Fisheries

Pacific Ocean 'blob' draws scrutiny of researchers

A huge swath of unusually warm water that has stretched to the normally cool Pacific has grown to the largest ocean temperature anomaly on record, researchers now say, profoundly affecting climate and marine life from Baja California to Alaska.

Record Algae Bloom Laced With Toxins is Flourishing in "The Blob" — and Spreading in the North Pacific

Unusual species in Alaska waters indicate parts of Pacific warming dramatically

The Gulf of Alaska is unusually warm, and weird fish are showing up



In this Aug. 29 photo, a 7-foot ocean sunfish rarely seen in Washington waters washed ashore on a beach near Skagit, Wash., with Jane Muhler, a biological technician working as an interpretative assistant. (AP Photo/Craig Dussap/Inland Northwest State Park, Eric Wall)

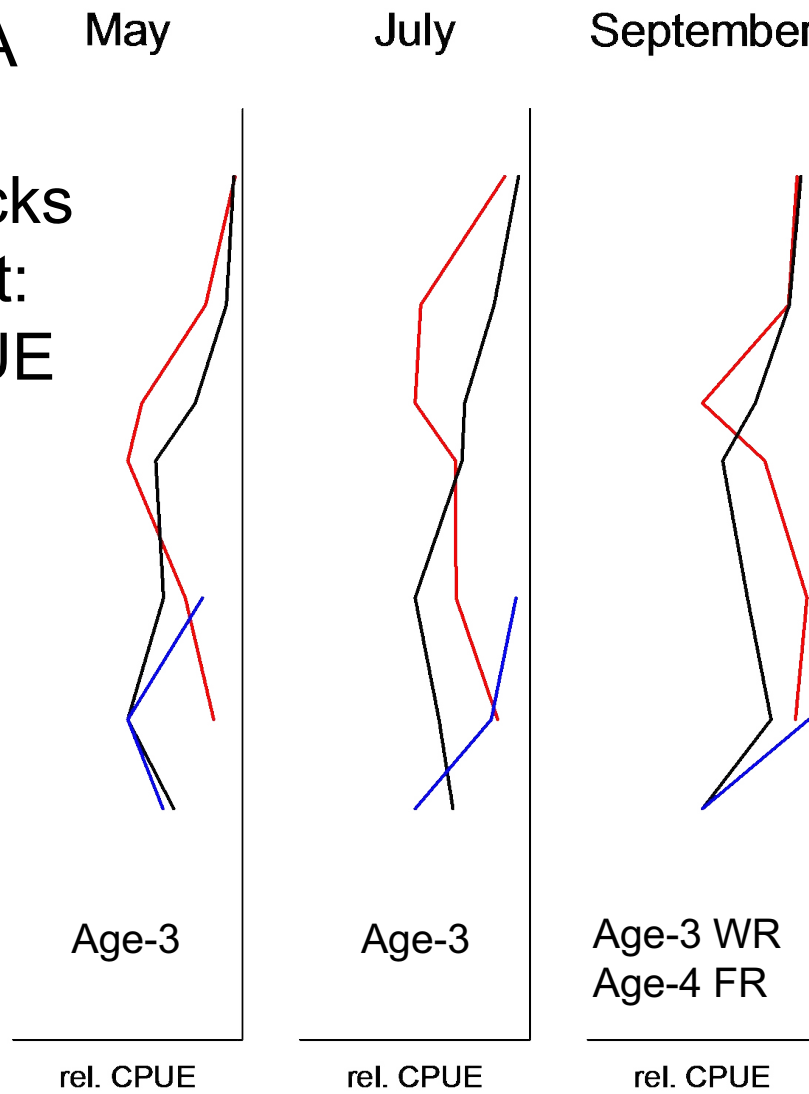


Why are so many whales dying on California's shores?

Where CA Chinook salmon stocks are caught: ocean CPUE

Sacramento R. stocks based on sport fishery recoveries

Klamath stocks based on commercial fisheries

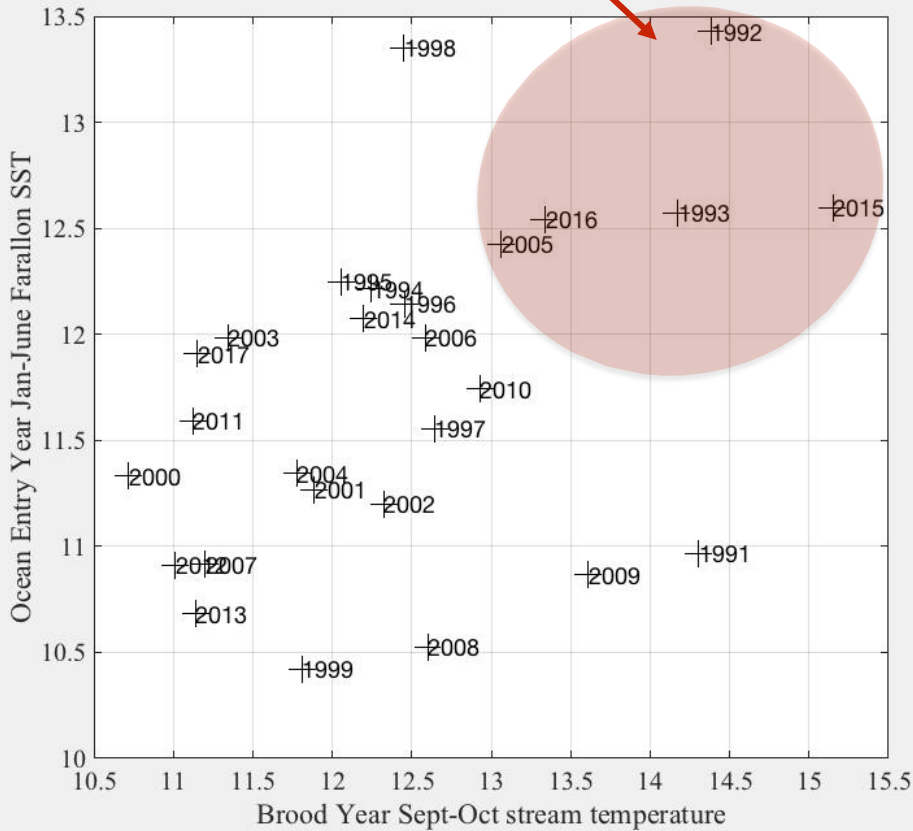


From Will Satterthwaite, SWFSC

Spring 2017 ocean conditions from the State of the CCS report: Northern CCS still unproductive, while Central/Southern CCS were near normal

Indicator	Basin	Northern CCS	Central CCS	Southern CCS
ONI	Average			
PDO	Above average			
NPGO	Near average			
NPH	Below average			
Upwelling		Below average	Average	Above average
Cumulative upwelling		Average	Below average	Average
SST		Above average	Average	Average
Chlorophyll		Below average	Average	Average
Harmful algal blooms		No	No	Yes
Copepods		Southern derived and rich	-	-
Forage		Off-shore and southern derived assemblage	Typical assemblage	Typical assemblage along with increased anchovy abundances.
Salmon survival		Below average juvenile abundance at sea	Ecosystem indicators related to salmon suggest average	-
Seabird productivity (2016)		Reproductive failures	Below/near average	-
Seabird at-sea abundance		Well below average	Below/near average	Well above average
Sea lions (2016)	Signs of recovery after the 2013 Unusual Mortality Event			
Whales	Humpback whales distributed shoreward			

Especially bad combinations of extreme warm stream temperature and ocean temperature for the same brood year



- This plot shows brood year stream temperature between Keswick and Clear Creek for Sept-Oct against January—June ocean entry year SST at the Farallon Islands
- Year labels indicate ocean entry years (Brood Year+1)
- Note the relative lack of extreme Sept-Oct stream temperatures after 1993 (TCD was installed in 1996-97), **until 2014/15**
- **These data suggest that brood years 1991, 1992, and 2014 experienced the 3 worst combined stream/ocean temperature conditions for Central Valley salmon going back to 1990 (when our RAFT-based stream temperature record begins)**

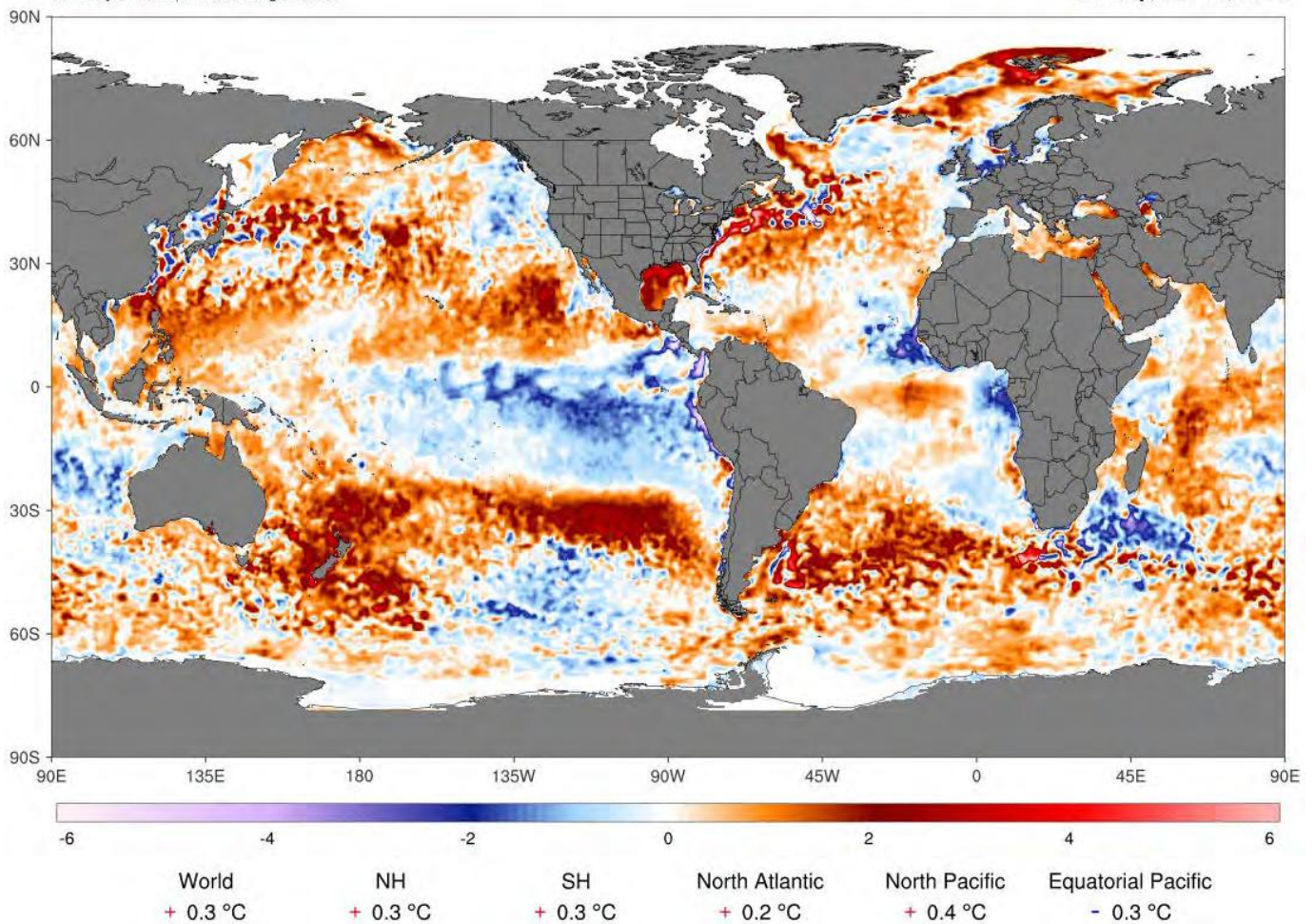
A climate timeline for California's salmon

2013	2014	2015	2016	2017	2018
Yr 2 CA drought, carryover storage	Year 3 CA drought, record heat	West Coast "snow drought" record heat	Near average precip and snowpack but warm w/an early melt	A very wet year with abundant snowpack; refill reservoirs	Extremely warm/dry/low snow; good carryover storage
Cold productive NE Pacific	NEP in transition from good to bad	Record warm SSTs, ecosystem stress	A still warm unproductive NEP, but not as extreme	good productivity south of Mendocino	Near normal SSTs; no info on productivity yet
BY 2013 Chinook	Smolt migration	Ocean year 2	Ocean year 3, most return	Ocean year 4	
	BY 2014 Chinook	Smolt migration	Ocean year 2	Ocean year 3, most return	Ocean year 4
		BY2015 Chinook	Smolt migration	Ocean Year 2	Ocean year 3 Most return

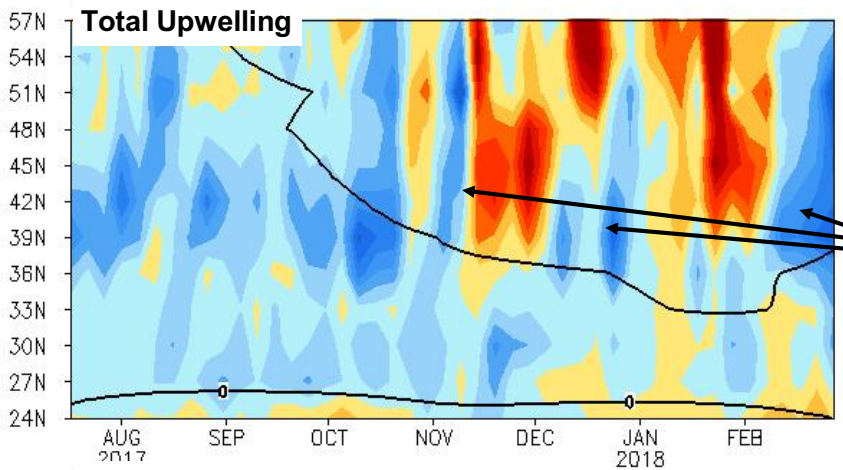
Tropical La Niña has been fading, while persistently strong and cold north winds in late February brought West Coast ocean temperatures back to normal

ClimateReanalyzer.org
University of Maine | Climate Change Institute

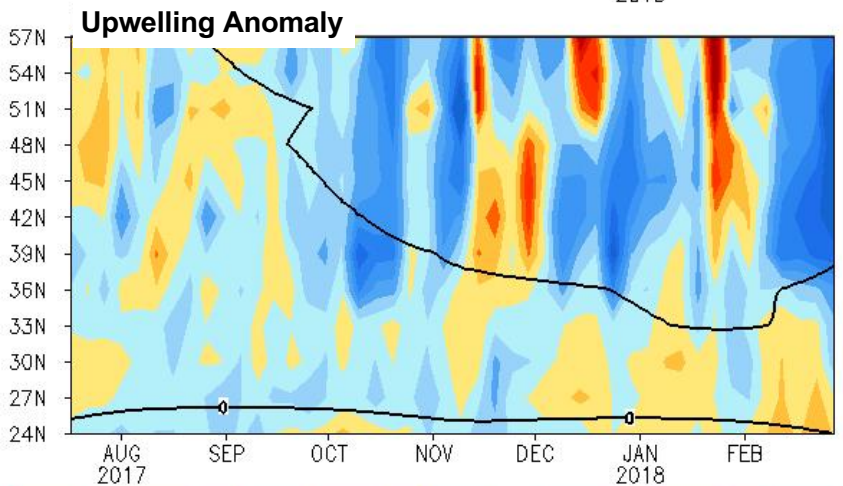
OISST 1-day Avg SST Anomaly (°C) [1971-2000 base]
Monday, Mar 05, 2018



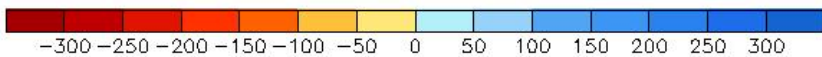
**Pentad Coastal Upwelling for West Coast North America
(m³/s/100m coastline)**



- Fall 2017-Winter 2018 “downwelling” was very weak and intermittent (persistent high pressure ridge blocked storms that come with intense south winds)
- Frequent periods of upwelling along the US West Coast in October, December, and February

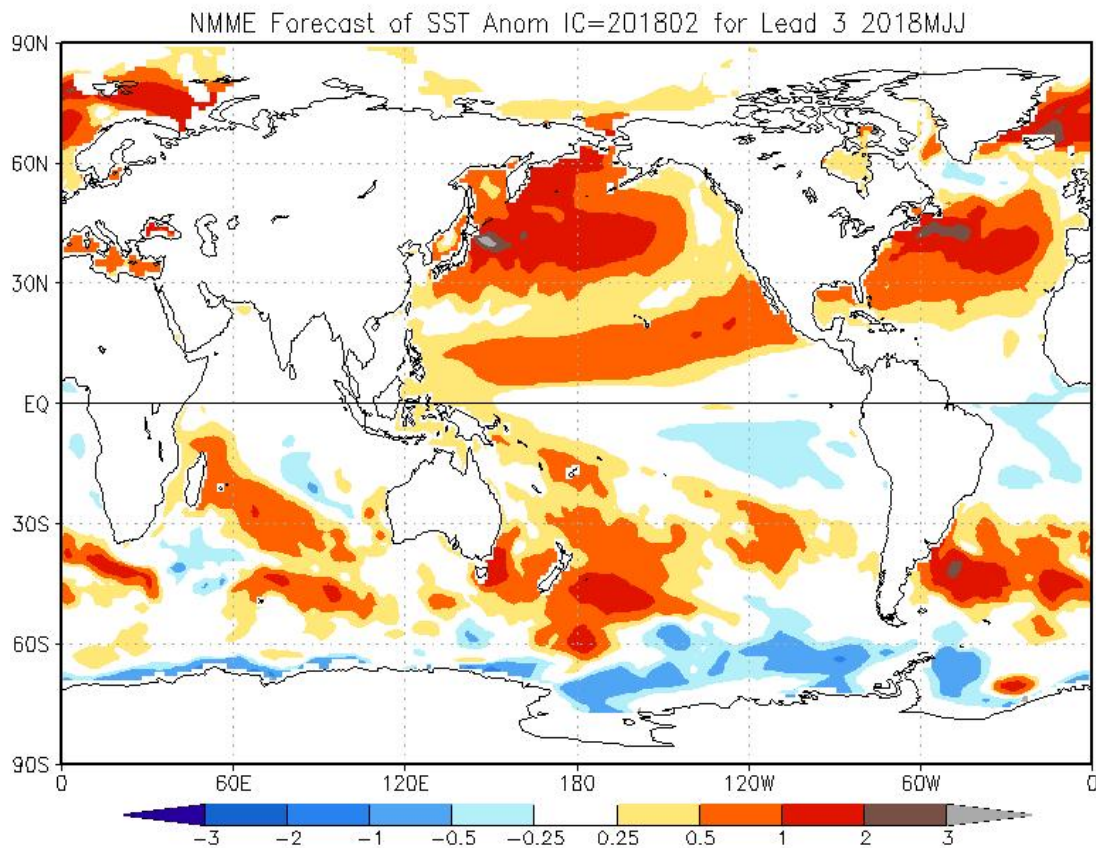


- Note the prevalence of blue shading in the upwelling anomaly plot going back to September 2017 – fall/winter downwelling has been weak, while fall/winter upwelling has been unusually strong and frequent



The latest climate model forecasts for North Pacific ocean temperatures are extraordinary: many models are predicting a rapid warming for much of the North Pacific in spring/summer 2018

North American Multi-model ensemble SST forecast for May-June-July 2018



ARTICLE

Movement and Survival of Wild Chinook Salmon Smolts from Butte Creek During Their Out-Migration to the Ocean: Comparison of a Dry Year versus a Wet Year

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Abstract

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

Balancing human demands for water with the maintenance of a functioning ecosystem capable of supporting healthy Chinook Salmon *Oncorhynchus tshawytscha*

populations has become a central challenge facing natural resource managers in California's Central Valley (CCV). Here, four runs of Chinook Salmon have evolved distinct

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life histories to capitalize on the diversity of habitat available in CCV rivers and streams. The runs are named according to the season in which the adults return to freshwater: fall, late fall, winter, and spring (Healey 1991). Similar to stocks in many large West Coast rivers, Chinook Salmon stocks from the CCV have declined substantially since the mid-1800s, mainly due to the construction of large dams and habitat degradation (Yoshiyama et al. 2001). Spring-run Chinook Salmon were once a major component of CCV Chinook Salmon runs and occupied the headwaters of all major CCV river systems where natural barriers were absent (Williams 2006). Presently, self-sustaining spring-run populations survive only in three tributaries of the Sacramento River: Mill, Deer, and Butte creeks (Lindley et al. 2004). Spring-run fish are reported inconsistently in additional Sacramento River tributaries and are supplemented by stray spring-run adults from the Feather River Hatchery (Yoshiyama et al. 2001). However, these additional stocks are believed to have been hybridizing with fall-run stocks since the 1960s due to dam-created spatial constrictions on previously separate spawning distributions (CDFG 1998). As a consequence of these various stressors, the CCV spring-run Chinook Salmon evolutionarily significant unit (ESU) has been state and federally listed as threatened since 1999 (U.S. Office of the Federal Register 1999).

One of the fundamental objectives for managing spring-run populations for future recovery is ensuring that we are supporting and managing for the full range of life history diversity within the ESU (Beechie et al. 2006). Indeed, spring-run Chinook Salmon populations demonstrate unique juvenile rearing plasticity that is characterized by a wide range of size, timing, and age at which they out-migrate from their natal tributaries to the ocean (e.g., out-migration as subyearling fry, subyearling smolts, or yearlings; CDFG 1998). Such life history diversity has been suggested to convey a stabilizing portfolio effect by providing each population the ability to buffer environmental changes due to anthropogenic forcing or climate, ultimately increasing the resiliency of the entire community (Hilborn et al. 2003; Greene et al. 2010; Schindler et al. 2010). As the largest population of CCV spring-run Chinook Salmon, Butte Creek fish are an important source for promoting diversity in the CCV Chinook Salmon community and have been the focus of considerable investment in the form of population monitoring and restoration efforts. Several restoration actions were implemented in the early 1990s by various state and federal agencies in coordination with water interests and local stakeholders (e.g., CALFED and the U.S. Fish and Wildlife Service's Final Restoration Plan for the Anadromous Fish Restoration Program) in order to restore and maintain CCV spring-run Chinook Salmon populations on a long-term basis. The Lower Butte Creek Project, for

instance, was established in 1997 to improve passage for protected fish species while maintaining the viability of commercial agriculture, private wetlands, government lands, and other habitats (ICF Jones & Stokes 2009). Although increases in returning Butte Creek spring-run Chinook Salmon adults have been observed in recent years, the success of those management efforts in enhancing juvenile survival and maintaining population life history diversity has yet to be determined.

Juvenile mortality during out-migration to the ocean is considered a critical phase to overall population dynamics (Healey 1991; Williams 2006). Tagging and tracking of juvenile Chinook Salmon from their freshwater rearing habitats, through riverine systems, and into the marine environment can help to determine survival rates and identify locations where juvenile mortality is greatest during downstream migration. Acoustic tagging technology has become a well-established tool in estimating movement and survival rates of CCV Chinook Salmon juveniles (Perry et al. 2010; Michel et al. 2013, 2015). These studies have mainly focused on hatchery smolts that are easily captured, tagged, and released in large groups, whereas little is known about the survival and movement of the remaining wild spring-run Chinook Salmon populations. Assessing juvenile mortality of wild spring-run Chinook Salmon is challenging in part due to the small size of these populations and the difficulty in capturing them during their out-migration. However, the utilization of survival data from hatchery stocks as a surrogate for wild salmon survival dynamics is often criticized because the two are different in many ways (Kostow 2004). Wild salmon hatch and rear in a completely different environment and face many challenges in their early life that hatchery smolts are able to avoid due to hatchery management and release practices (e.g., predation, water quality). In this paper, we detail an acoustic tagging study—implemented in lower Butte Creek and extending to the Golden Gate Bridge—that was aimed at assessing the movement and survival rates of the largest population of wild CCV spring-run Chinook Salmon smolts during their out-migration to the ocean. We were particularly interested in evaluating potential dissimilarities between survival through (1) the Sutter Bypass, a floodplain that has been suggested to constitute important rearing habitat for juvenile Chinook Salmon (Garman 2013); and (2) the lower Sacramento–San Joaquin River Delta (hereafter, the Delta), which is considered a strongly degraded habitat (Nichols et al. 1986). Moreover, previous studies have demonstrated that CCV juvenile out-migration survival can vary strongly among years due to various anthropogenic and environmental factors (Baker and Morhardt 2001; Brandes and McLain 2001; Michel et al. 2015). Therefore, we compared fish movement and locations of high mortality during out-migration for a hydrologically dry year (2015)

versus a hydrologically wetter year (2016). We discuss the implications of our results for the long-term dynamics of the Butte Creek population and the implementation of future recovery actions.

METHODS

Study site.—Butte Creek is a tributary of the Sacramento River that originates at Humboldt Mountain on the western slopes of the Cascade Range at an elevation of more than 2,100 m (Figure 1). The Butte Creek watershed encompasses an area of about 2,900 km² and is connected to the Sacramento River at two locations: the Butte Slough Outfall Gates (BSOG); and the downstream end of the Sutter Bypass, a remnant flood basin habitat (Garman 2013). Butte Creek historically entered the Sacramento River at the BSOG but is now diverted away from the Sacramento River for 40 km into the Sutter Bypass (Figure 1). This bypass is composed of two canals as well as the East–West Diversion Weir, which is used to control the flow of water going into the east- and west-side canals of the bypass. Several weirs along both canals divert water for agricultural or managed wetland uses (ICF Jones & Stokes 2009). During high-flow conditions, water from the Sacramento River flows into the bypass through Moulton, Colusa, and Tisdale weirs to prevent flooding of downstream areas.

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

Freshwater life history.—Central Valley spring-run Chinook Salmon demonstrate a unique diversity in life history among the California stocks of Chinook Salmon. Adult spring-run Chinook Salmon ascend un-dammed tributaries to elevations between 300 and 1,500 m when the spring freshet allows access, and they hold in deep pools over the summer before spawning in the fall. The CCV spring-run juveniles emerge from the gravel between November and March depending on water temperatures, and they spend 3–15 months in freshwater before emigrating to the ocean (CDFG 1998). Spring-run Chinook Salmon juveniles exhibit a wide variety of rearing and out-migration strategies. They can (1) migrate out of the spawning habitat soon after emergence as fry during high flows in the winter; (2) rear in their natal habitat and out-migrate as smolts

during the spring; or (3) remain in the stream for an entire year and out-migrate during the following fall, winter, or spring as yearlings (CDFG 1998). Juveniles out-migrating from Butte Creek are assumed to be a mix of fry and smolts, with very few remaining in Butte Creek as yearlings (Clint Garman, California Department of Fish and Wildlife [CDFW], personal communication). Smolt emigration peaks in April and May but can extend from February through June (Ward et al. 2004a, 2004b, 2004c).

Acoustic tagging and receivers.—We used the Juvenile Salmon Acoustic Telemetry System (JSATS; McMichael et al. 2010) to track the movements and estimate the survival of migrating wild spring-run Chinook Salmon smolts from Butte Creek. The transmitters (tags) were manufactured by Advanced Telemetry Systems (ATS); JSATS Model SS300 tags had a weight in air of 300 mg and dimensions of 10.7 × 5.0 × 2.8 mm. The tags emitted a uniquely coded signal at 416.7 kHz with a pulse rate of about 5 s and had an expected life of 32 d at these settings. The tag weight of 300 mg allowed us to tag juvenile Chinook Salmon that weighed at least 6.0 g (approximate FL = 80 mm), resulting in a tag burden no greater than 5%. Laboratory studies comparing growth and survival between acoustically tagged and untagged juvenile salmon have suggested that tag burdens of less than 5% do not significantly affect acoustically tagged fish relative to untagged controls (Brown et al. 2010; Ammann et al. 2013).

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

We collected fish by using a 2.44-m-diameter rotary screw trap (RST) installed at Weir 2 in the Sutter Bypass (Table 2). We chose Weir 2 as the trapping site to ensure that fish collected and tagged were actively migrating downstream, as this weir is relatively low in the Butte Creek system. Additionally, this downstream site ensured that the 30-d acoustic tag battery life was utilized efficiently, allowing fish movement through the Sutter Bypass, the Sacramento River, the Delta, and San Francisco Bay to be recorded. The RST was operated continuously (24 h/d) and was emptied of fish each morning. All salmonids were measured (FL; mm), and an acoustic tag was implanted into each fish larger than 80 mm.

On the riverbank adjacent to the RST, we set up a shaded work station to surgically implant the tags before

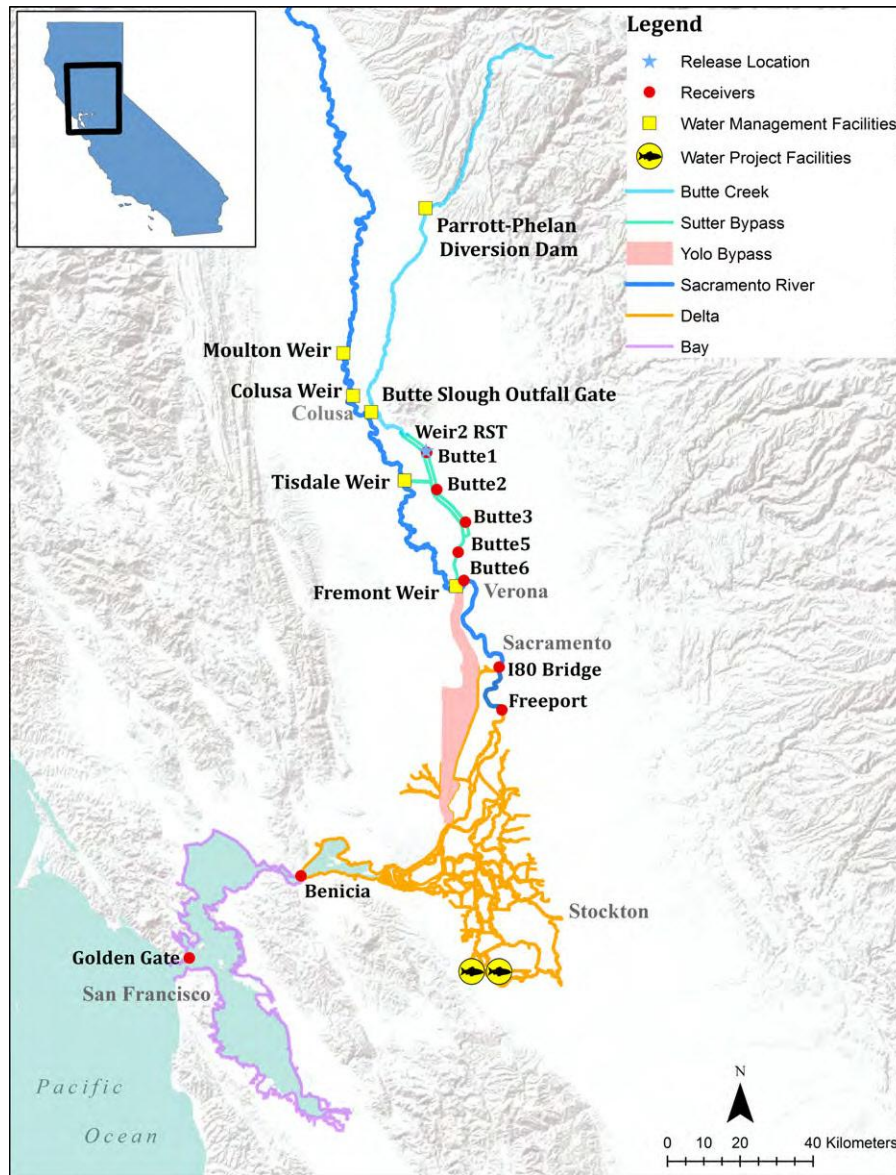


FIGURE 1. Map of California's Central Valley, showing the different regions considered in the study, the release location, and the receiver locations. [Color figure can be viewed at afsjournals.org.]

the sun was overhead and before temperatures became too warm. The same surgeon implanted tags into the coelom of all fish for both years of the study. Fish were anesthetized (tricaine methanesulfonate at a concentration of 90 mg/L), weighed, measured, photographed, and then placed ventral side up in a padded V-channel. During surgery, the fish's gills were irrigated with water containing a maintenance dose of anesthetic (30 mg/L). An incision was made on the ventral side of the fish between the pelvic girdle and pectoral fins with a SharpPoint 3-mm, 15° stabbing blade scalpel. The incision was 6–8 mm long and 3 mm off the ventral midline. The tag was inserted into the coelom and oriented such that the tag transducer was

posterior. The incision was closed with a single suture of 6-0 polydioxanone absorbable monofilament, and the suture was tied with a double-wrapped square knot (i.e., surgeon's knot). We placed each tagged fish into a recovery bucket and monitored the fish until it resumed its normal swimming behavior. After surgery, we held the tagged individuals in holding pens just below Weir 2 for 12 h before releasing them at 2200 hours (Pacific Standard Time), primarily to ensure that the fish were fully recovered but also because juvenile salmon tend to migrate at night (Chapman et al. 2013).

We collected tissue samples from all tagged fish to identify their origin by using genetic stock identification

TABLE 1. Study reach locations where out-migrating Chinook Salmon from Butte Creek (California) were tracked, the distance of each reach from the Golden Gate Bridge (river kilometers [rkm]), the individual reach lengths, and the total region length (km). Weir2_RST represents the rotary screw trap installed at Weir 2 in the Sutter Bypass; Butte1–Butte6 and additional receiver locations are depicted in Figure 1.

Region	Reach	Distance from ocean (rkm)	Reach length (km)	Region length (km)
Sutter Bypass	Weir2_RST to Butte1	249.54–249.05	0.49	
	Butte1 to Butte2	249.05–238.46	10.59	
	Butte2 to Butte3	238.46–226.46	12.00	
	Butte3 to Butte5	226.46–216.98	9.48	
	Butte5 to Butte6	216.98–206.48	10.50	43.06
Sacramento River	Butte6 to I-80 Bridge	206.48–170.74	35.74	
	I-80 Bridge to Freeport	170.74–152.43	18.31	54.05
Sacramento–San Joaquin River Delta	Freeport to Benicia	152.43–52.04	100.39	100.39
San Francisco Bay	Benicia to Golden Gate Bridge	52.04–0.80	51.24	51.24

TABLE 2. Weight (g) and FL (mm; mean, minimum [min], and maximum [max]; SDs in parentheses) of juvenile Chinook Salmon that were captured, tagged, and released at the rotary screw trap in the Sutter Bypass during 2015 and 2016 (CCV = California Central Valley; n = sample size). Group assignment is shown only for fish with genetic stock assignment posterior probabilities exceeding 75%.

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

(Clemento et al. 2014). For each fish, we calculated the posterior probability that it originated from a given stock, and we assigned the fish to the stock with the highest posterior probability. Based on Satterthwaite et al. (2014) and communication with John C. Garza (National Marine Fisheries Service [NMFS], Southwest Fisheries Science Center [SWFSC], Santa Cruz), we considered assignments of fish with a maximum posterior probability exceeding 75% as robust stock assignments for purposes of this study. We did not assign a stock to fish with posterior probabilities less than 75%. The genetic analysis was performed at the NMFS-SWFSC.

Data analysis.—Tagged fish either completed their migration out of the study reaches or completed a partial migration and died before exiting the detection arrays. We used a spatial form of the Cormack–Jolly–Seber model (Cormack 1964; Jolly 1965; Seber 1986) to estimate the reach-specific survival rate (ϕ_i) and detection probability (p_i). We considered the initial tag location as a “mark” and subsequent detections at downstream

receivers as “recaptures.” We used the method of maximum likelihood to estimate survival and detection probabilities along with their 95% confidence intervals (Lebreton et al. 1992).

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

To evaluate year and location effects on out-migrating smolt survival and detection probabilities, we compared

the constant model (i.e., constant survival and detection rates through space and time) to models that included parameters allowing year and/or reach to vary (e.g., $\varphi[\sim\text{reach} \times \text{year}]$; see Appendix Table A.1 for a list of models). Because it is impossible to measure or estimate all potential factors that influence salmon survival, we hypothesized that the fully parameterized model (full model) that included year and reach as factors would have the best fit to the data and would provide the best estimates of reach survival by year. We therefore used this model to generate reach-specific, regional, and overall survival estimates. However, to gain a better understanding of the underlying mortality mechanisms, we also looked at models that included fish characteristics (i.e., FL and Fulton's condition factor K) and environmental variables (i.e., Sutter Bypass flow and water temperature at release). We used flow data from Butte Slough near Meridian (California Data Exchange Center [CDEC] station BSL, http://cdec.water.ca.gov/cgi-progs/stationInfo?station_id=BSL), located downstream of the BSOG (the closest flow gauge to the Sutter Bypass release site), and we used temperature data from the Buttel acoustic receivers (postcalibrated at the NMFS-SWFSC). All continuous covariates were standardized by subtracting the mean and dividing by the SD.

To facilitate our ability to partition the influence of each covariate of interest on survival variability through time, we used the base model, $\varphi(\sim\text{reach})$, and included covariates in an additive framework (see Table 3 for a list of models). We deliberately excluded the year variable from all covariate models because the inclusion of this variable would have accounted for the majority of interannual variability in survival, thereby masking any influence of the individual/environmental covariates and providing no information on mechanisms. However, we compared the $\varphi(\sim\text{reach} + \text{year})$ model to the models including covariates in order to assess how much interannual variability explained by the year variable could be explained by these covariates instead. Once the relative importance of covariates had been determined from the model selection exercise, we extracted the standardized β parameter coefficients for these covariates to identify the relationship direction between the covariates and fish survival. These β parameter coefficients allowed for comparison of the influence of covariates between models; they can be interpreted as the predicted change in survival for a 1SD increase in the covariate. Model selection was conducted by using Akaike's information criterion corrected for small sample sizes (AIC_c ; Akaike 1973; Burnham and Anderson 2002). We performed this analysis in the RMark package (Laake 2013) within R version 3.1.1 (R Development Core Team 2013).

Finally, to obtain additional information on the movements of the tagged fish during their out-migration and

TABLE 3. Comparison of the $\sim\text{reach} + \text{year}$ survival (φ) model versus models that included reach and individual or environmental covariates (fish length, Fulton's condition factor K , Sutter Bypass flow at release, and water temperature at release). The detection probability (p) was set as a constant for each model (N_{par} = number of model parameters; AIC_c = Akaike's information criterion corrected for small sample size; ΔAIC_c = difference in AIC_c score between the given model and the most parsimonious model). Models are ordered from lowest to highest AIC_c . Lower AIC_c scores indicate greater relative model parsimony. The β parameter estimates (defined in Methods) are shown for the two covariate models with substantial support over the reach-only model.

Model	N_{par}	AIC_c	ΔAIC_c	β
$\varphi(\sim\text{reach} + \text{year})$, $p(\sim 1)$	11	1,394.074	0.00	
$\varphi(\sim\text{reach} + \text{release}$ flow), $p(\sim 1)$	11	1,396.929	2.85	0.24
$\varphi(\sim\text{reach} + \text{fish}$ length), $p(\sim 1)$	11	1,402.226	8.15	0.17
$\varphi(\sim\text{reach} + \text{release}$ temp), $p(\sim 1)$	11	1,404.477	10.40	
$\varphi(\sim\text{reach})$, $p(\sim 1)$	10	1,405.719	11.64	
$\varphi(\sim\text{reach} + K)$, $p(\sim 1)$	11	1,406.765	12.69	

relate that to their survival, we estimated the average migration rates for the different regions along the migration pathway. We did this by considering the movement rate of each fish between its last detection in one reach to its first detection at the next reach.

RESULTS

In 2015, we deployed the RST on April 1 and tagged Chinook Salmon for 11 d between April 6 and April 16. During that period, we tagged and released a total of 141 smolts. In 2016, we started tagging on April 14, and we were able to tag and release our target of 200 juvenile Chinook Salmon by April 18. In 2015, the mean FL of tagged fish was 104.75 mm and the mean weight was 13.47 g, whereas the averages in 2016 were 110.02 mm and 16.68 g, respectively (Table 2).

Genetic Assignment

The genetic analysis suggested that the smolts tagged in the Sutter Bypass were a mix of CCV fall-run and spring-run origin. In 2015, 6 smolts were confidently identified as CCV fall-run fish, and 124 smolts were identified as CCV spring-run fish; in 2016, a higher proportion of tagged individuals were genetically classified as CCV fall-run fish (121 fall-run versus 65 spring-run fish; Table 2). Although fall-run smolts were slightly larger in both years, fall-run and spring-run smolts appeared to exhibit similar size ranges (Table 2; Appendix Figure A.1). We performed an F -test ("var.test" function in R) to compare fall-run versus

spring-run smolt length variances for each year and found no statistical difference between their length distributions (2015: $P = 0.1489$; 2016: $P = 0.9086$). This implied that no length cutoff could be robustly applied to these two runs and that visual distinction based on length is problematic. Therefore, although not all of the tagged fish were spring-run Chinook Salmon, we assumed that due to their overlapping size range and migration timing, fall-run juveniles served as a good proxy for the purpose of this study.

The RST was located below the spawning habitat of the Butte Creek fall run; it is therefore likely that many of the captured fall-run smolts were wild Butte Creek fall-run Chinook Salmon. In addition, because Sacramento River water spilled into the lower Butte Creek watershed via Moulton, Colusa, and Tisdale weirs several times before the tagging experiment took place, it is also possible that some of the tagged fall-run fish originated from the mainstem Sacramento River or another tributary and used the Sutter Bypass as a migratory corridor.

Hydrological Conditions

During the 2015 water year, California experienced an extreme drought that was classified as “critical,” whereas the 2016 water year was considered “below normal” by the California Department of Water Resources (CDWR; CDEC data). Although 2016 was not considered a wet year, a series of rain events leading to the flooding of the Sutter Bypass occurred during the CCV spring-run smolts’ out-migration period. Therefore, the hydrological conditions experienced by the migrating smolts changed considerably between the 2 years of the study. In spring 2015, likely because of very dry winter conditions, the flow recorded in the lower Butte Creek system had already dropped substantially and stayed very low during the entire study period, averaging 4.03 m³/s at the BSL station (Figure 2A). In 2016, we tagged and released fish after a flood event, and although the flow decreased throughout the study period, it remained substantially above the maximum flow value recorded during the same period in 2015. The 2016 BSL flow averaged 12.91 m³/s. The same pattern was observed in the Sacramento River reach, with an average flow of 160.29 m³/s in 2015 and an average of 381.53 m³/s in 2016 (CDEC station at Verona, http://cdec.water.ca.gov/cgi-progs/stationInfo?station_id=VON; Figure 2A).

In 2015, water temperatures in the Sutter Bypass and the Sacramento River increased throughout the tagging experiment (Figure 2B). Water temperature at the Butte1 receiver peaked at 18.5°C during the tagging period, then kept increasing and reached 21°C by the end of April. Similarly, water temperature in the Sacramento River increased from 14°C to 22°C during April 2015 (CDEC station at Verona, <http://cdec.water.ca.gov/cgi-progs/sta>

tionInfo?station_id=VON). In 2016, water temperature in the Sutter Bypass during the tagging period varied between 18°C and 19.5°C. The peak water temperature at the Butte1 receiver was 21°C on April 21, 2016. The Sacramento River water temperature in 2016 slowly increased throughout the month of April but never exceeded 18°C.

Fish Movement

In 2015, 27 (19.1%) of the 141 tagged fish were detected as entering the Sacramento River, 14 fish (9.9%) were detected as entering the Delta, and only 1 fish (0.7%) was detected at the Golden Gate Bridge. In 2016, 71 (35.5%) of the 200 tagged fish were detected as entering the Sacramento River, 49 fish (24.5%) were detected in the Delta, and 4 fish (2%) were detected at the Golden Gate Bridge. Although some variability in movement rates among fish was observed each year, especially in the Sacramento River, most of the tagged smolts moved quickly throughout the migration corridor (Figure 3). On average, fish took 6 d in 2015 versus 2 d in 2016 to transit the Sutter Bypass, and they took 2 d in 2015 versus 1 d in 2016 to transit the Sacramento River (Table 4). The single fish that survived to the Golden Gate Bridge in 2015 migrated through the Delta in less than 5 d and migrated from the release site to the Pacific Ocean in 27 d. In 2016, it took an average of 5 d for fish to migrate through the Delta and 18 d for them to migrate from the release site to the ocean (Table 4).

Tagged fish migration rates were higher in the Sacramento River compared to the Sutter Bypass and the Delta during both years (Figure 3; Table 4). Based on a Tukey’s honestly significant difference test (“TukeyHSD” function in R), the migration rate in 2016 was significantly higher than that in 2015 within the Sacramento River ($P < 0.001$) and the Sutter Bypass ($P < 0.001$); migration rates were significantly higher in the Sacramento River compared to the Sutter Bypass during both years (2015: $P = 0.0$; 2016: $P = 0.0$). We calculated mean migration rates of 10.24 km/d in the Sutter Bypass and 33.21 km/d in the Sacramento River during 2015 versus estimates of 22.13 and 56.83 km/d, respectively, during 2016 (Table 4). Since only one fish was successfully detected at Benicia (the Delta exit location) and the Golden Gate Bridge in 2015, it was not possible to estimate Delta and San Francisco Bay travel rate statistics for that year. However, more fish were detected in 2016, and the average movement rate through the Delta was estimated at 22.48 km/d.

Survival Estimates

The full model, which was strongly supported as the single best model ($AIC_c = 1,383.726$; the difference in AIC_c value [ΔAIC_c] between the best model and the second-best model was greater than 8; Table A.1), included

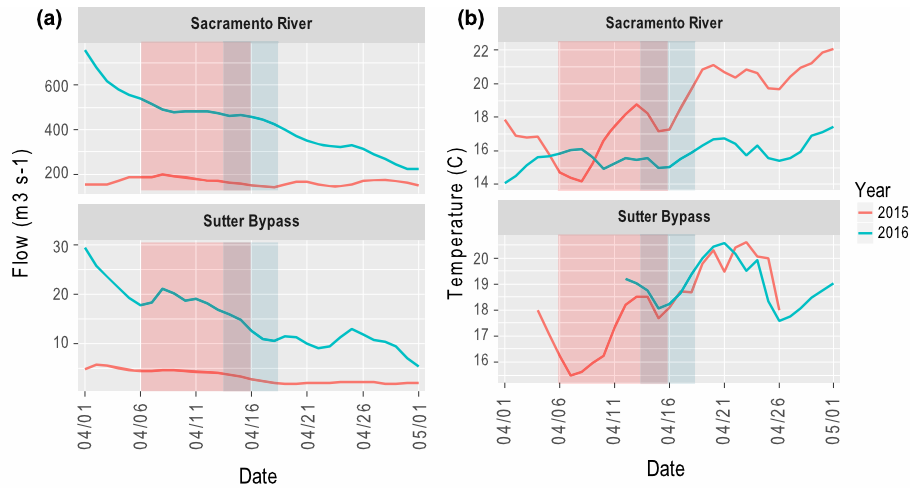


FIGURE 2. (A) Mean daily flow (m³/s) in April 2015 and 2016 for the Sacramento River (California Data Exchange Center [CDEC] Verona station: http://cdec.water.ca.gov/cgi-progs/stationInfo?station_id=VON) and Sutter Bypass (CDEC station BSL [Butte Slough near Meridian]: http://cdec.water.ca.gov/cgi-progs/staMeta?station_id=BSL); and (B) mean daily water temperature (°C) during April 2015 and 2016 for the Sacramento River (CDEC Verona station) and Sutter Bypass (Buttel site; Advanced Telemetry Systems receiver thermistor). The shaded rectangles indicate the tagging and release time periods in Sutter Bypass for 2015 (in red) and 2016 (in blue). [Color figure can be viewed at afsjournals.org.]

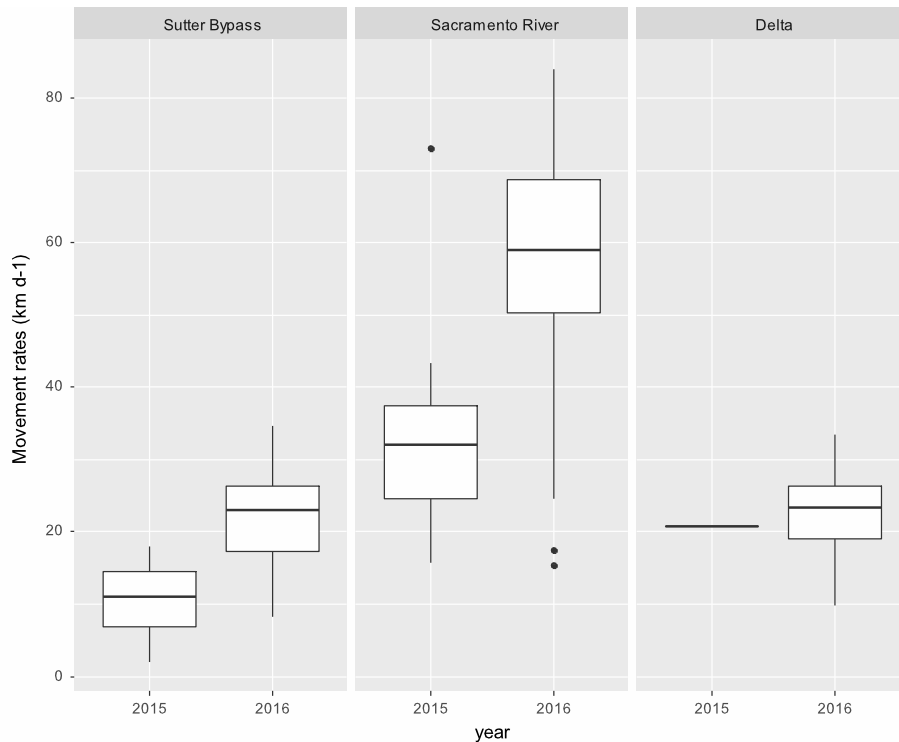


FIGURE 3. Box plot of region-specific movement rates (km/d) for out-migrating Chinook Salmon in 2015 and 2016 (Delta = Sacramento–San Joaquin River Delta). The horizontal bold line represents the median value; vertical whiskers represent the 95th percentiles; and dots denote extreme values.

survival as a function of reach × year and a constant detection probability. This suggested that out-migrant smolt survival varied by location and year. Additionally,

although the best model supported a constant detection probability, the spatially explicit models (i.e., $p[-reach]$) suggested that detection rates throughout the migratory

TABLE 4. Overall and region-specific percent survival, mean migration rate (km/d), and mean migration time (d), along with SE or SD (in parentheses), for juvenile Chinook Salmon tagged during each year (NA = not applicable).

Year	Region	Percent survival (SE)	Mean (SD) migration rate (km/d)	Mean (SD) migration time (d)
2015	All	0.7 (0.7)	NA	NA
	Sutter Bypass	19.1 (3.3)	10.24 (4.61)	5.75 (4.28)
	Sacramento River	51.8 (9.6)	33.21 (14.31)	1.88 (0.73)
	Sacramento–San Joaquin River Delta	7.1 (6.9)	NA	NA
	All	3.0 (1.2)	33.69 (15.32)	18.44 (3.93)
2016	Sutter Bypass	35.5 (3.4)	22.13 (6.21)	2.15 (0.81)
	Sacramento River	69.0 (5.5)	56.83 (16.26)	1.09 (0.57)
	Sacramento–San Joaquin River Delta	12.2 (4.7)	22.48 (8.03)	5.18 (2.59)

corridor were consistently high, ranging from 0.851 to 1.000. For all model exercises presented in this paper, detection probability was therefore set to be constant through space and time and was estimated at 0.993.

After including individual and environmental variables in the analysis, the $\phi(\sim\text{reach} + \text{year})$ model was selected as the best model, emphasizing the strong year effect on smolt survival (Table 3). The model that incorporated Sutter Bypass flow at release as a covariate was substantially better supported ($\Delta\text{AIC}_c > 3$) over the base model $\phi(\sim\text{reach})$. Furthermore, it shared similar support ($\Delta\text{AIC}_c < 3$) relative to the $\phi(\sim\text{reach} + \text{year})$ model (which benefited from a free parameter), suggesting that the flow model explained much of the variation in interannual survival. The model including fish length also had substantial support over the base model ($\Delta\text{AIC}_c < 6$) and suggested a positive influence of fish length on survival. However, the models including water temperature at release and Fulton's K were not better supported than the base model, indicating that these covariates had no detectable influence on survival.

We used the full model (i.e., $\phi[\sim\text{reach} \times \text{year}]$) to estimate survival per 10 km, per region, and cumulatively. Overall, survival through the entire migratory corridor (from the release site to the Golden Gate Bridge) was better in 2016 (3.0%) than in 2015 (0.7%; Table 4). At the regional level comparing 2015 to 2016, survival increased in the Sutter Bypass from 19.1% to 35.5%, in the Sacramento River from 51.8% to 69.0%, and in the Delta from 7.1% to 12.2% (Figure 4; Table 4). For both years, the highest regional survival was observed in the lower Sacramento River, while the lowest estimate was for the Delta region. However, the length of each region varied considerably (the Delta region was about twice as long as the Sutter Bypass and Sacramento River regions; Table 1),

and survival often decreases proportionally with increasing region length.

Rates of survival per 10 km varied dramatically between reaches within the Sutter Bypass, the Sacramento River, and the Delta, and some similar survival patterns were observed between years (Figure 5). In the Sutter Bypass, relatively low survival was observed between the release site (the RST at Weir 2 ["Weir2_RST" in Table 1]) and the first receiver (Butte1; 27.1% in 2015) and between the Butte3 and Butte5 receivers (39.3% in 2015; 65.1% in 2016). Survival was higher in the other reaches of the Sutter Bypass, ranging from 72.5% to 94.0% in 2015 and from 79.8% to 84.7% in 2016. In the Sacramento River for 2015, survival decreased from the first reach (Butte6 to the I-80 Bridge; 91.9%) to the second reach (I-80 Bridge to Freeport; 82.5%), whereas it increased in 2016 (92.6% and 95.1%, respectively). Survival in the Delta was lower than in the Sacramento River for both years (76.8% in 2015; 81.1% in 2016). Finally, due to the low number of tagged fish surviving to the Golden Gate Bridge ($n = 1$ in 2015; $n = 4$ in 2016), the 2015 survival rate in the San Francisco Bay could not be estimated, and the 2016 San Francisco Bay survival rate should be used for discussion purposes only.

DISCUSSION

This is the first study to investigate the survival and migration rates of wild Butte Creek spring-run Chinook Salmon smolts during their out-migration to the Pacific Ocean. The acoustic telemetry system used in this study had high detection probabilities (>85%) at all receiver locations. The mark-recapture models provided estimates of survival at fine spatial scales during a dry water year and a wet water year. We showed that Chinook Salmon smolts migrated faster throughout their migratory corridor

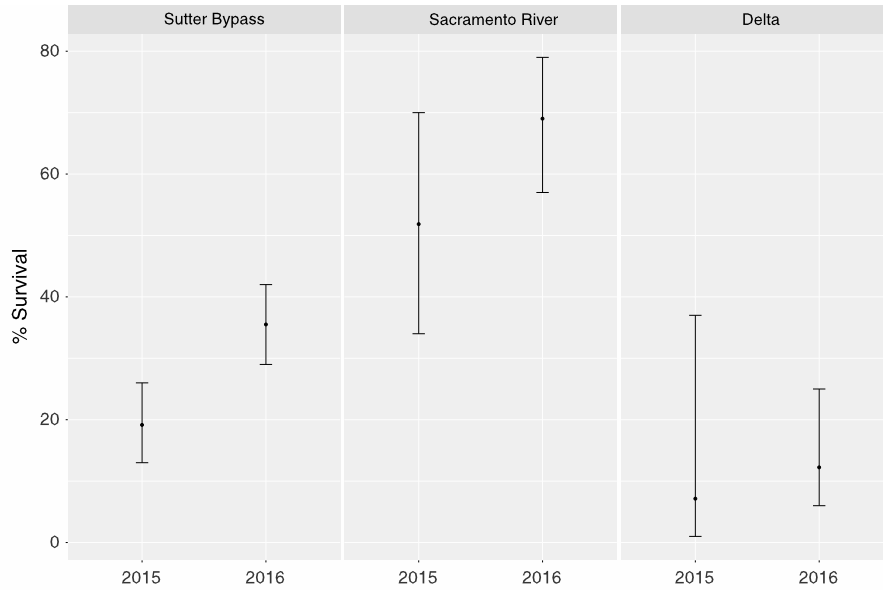


FIGURE 4. Region-specific survival rates (%; mean \pm 95% confidence interval) for out-migrating Chinook Salmon in 2015 and 2016 (Delta = Sacramento–San Joaquin River Delta).

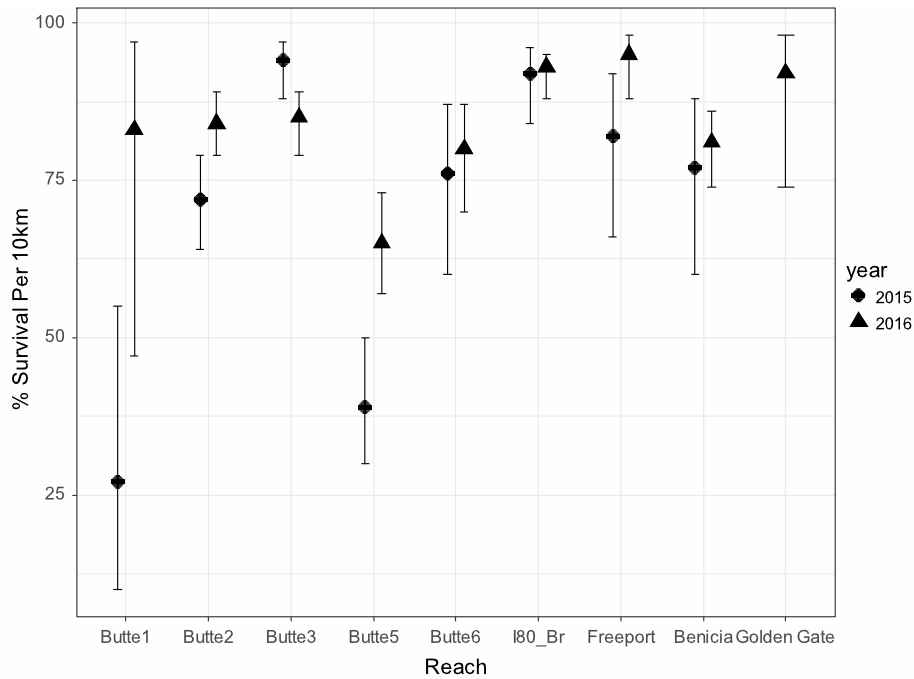


FIGURE 5. Reach-specific rates of survival per 10 km (%; mean \pm 95% confidence interval) for out-migrating Chinook Salmon in 2015 and 2016.

in 2016 (a wetter year) than in 2015 (a dry year). This difference is likely due to higher flow velocities, both in the Sutter Bypass and in the Sacramento River, during 2016 compared to 2015. The mean migration rate to the ocean (Golden Gate Bridge) was 33.7 km/d for 2016, which is faster than the total mean migration rate reported for

Sacramento River late-fall Chinook Salmon (14.3–23.5 km/d in 2007–2009) by Michel et al. (2013).

Survival to the ocean was also higher in 2016 (3.0%) than in 2015 (0.7%; Table 4). However, these survival rates are lower than most of the survival estimates obtained by Michel et al. (2015) for acoustic-tagged late-

fall-run Chinook Salmon yearlings (survival per year ranged from 2.8% to 15.7%). The survival rates we report are also low in comparison with the 2015 and 2016 survival rates estimated by Faulkner et al. (2016, 2017) for populations of wild spring/summer Chinook Salmon from the Snake River (a tributary of the Columbia River) migrating through a much longer watershed than in our study (mean survival rates through the entire 910-km watershed = 38.3% in 2015 and 33.0% in 2016). However, the fish tracked by Michel et al. (2015) and Faulkner et al. (2016, 2017) were larger in size than the fish we tagged in the Sutter Bypass, and we have shown that fish length influences out-migrant survival. Similar to our study, Notch (2017) found very poor survival (0.3%) to the ocean for acoustic-tagged, wild-caught smolts from Mill Creek, an upper Sacramento River tributary. This suggests that out-migration survival of spring-migrating wild Chinook Salmon smolts can be very low and may represent a bottleneck to the recovery of these populations.

In the Sutter Bypass, there were two reaches with substantially lower survival than the other reaches: (1) from the release site to Butte1 during 2015; and (2) between the receivers Butte3 and Butte5 in both years. These two reaches had the lowest survival per 10 km among all reaches in 2015, and the Butte3–Butte5 reach had the lowest survival per 10 km among all reaches in 2016. Common to both these reaches are in-river diversion weir structures (i.e., at the start of Weir2_RST–Butte1 reach and in the middle of Butte3–Butte5 reach). Studies have shown that Striped Bass *Morone saxatilis* and Sacramento Pikeminnow *Ptychocheilus grandis*—both of which are considered major predators of juvenile salmon in the CCV—tend to congregate below in-river diversion weirs and are effective at preying upon disoriented salmon smolts that pass over these structures (Brown and Moyle 1981; Tucker et al. 2003; Sabal et al. 2016). Various nonnative (e.g., Largemouth Bass *Micropterus salmoides*, Striped Bass, and Channel Catfish *Ictalurus punctatus*) and native (e.g., Sacramento Pikeminnow) predators of salmon have been reported in the lower Butte Creek watershed (ICF Jones & Stokes 2009). These predators were also caught in the RST during the present study in both years. If predators are generally concentrated below these diversion weirs, and furthermore if predator concentrations were enhanced during the low-flow conditions in 2015, this may explain the lower survival of juvenile Chinook Salmon in these two reaches.

Similarly, predation could play an important role in the Sacramento River and Delta reaches, as spring-run smolt out-migration timing overlaps with the Striped Bass spawning season. Adult Striped Bass migrate into the San Joaquin and Sacramento rivers in large numbers during the spring to spawn, and they are likely to prey on juvenile out-migrants during that time (Turner 1976; Tucker

et al. 2003). The increase in survival observed for 2016 in the Sutter Bypass and the Sacramento River corroborates the assumption that an increase in flow induces an increase of fish transport as well as a potential increase in turbidity, which could both reduce spatiotemporal exposure to predation (Gregory and Levings 1998; Michel et al. 2013 and references therein). The higher flow observed in the Sacramento River in comparison to the Sutter Bypass could explain the higher survival and faster migration rate observed in this region.

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

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

Our results have strong implications for the management of threatened CCV spring-run Chinook Salmon populations. Butte Creek currently supports the most abundant population of spring-run Chinook Salmon in the CCV and provides a key component for the diversity and viability of the spring-run stock. The Sutter Bypass has been designated by National Oceanic and Atmospheric Administration (NOAA) Fisheries as a critical

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

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Appendix

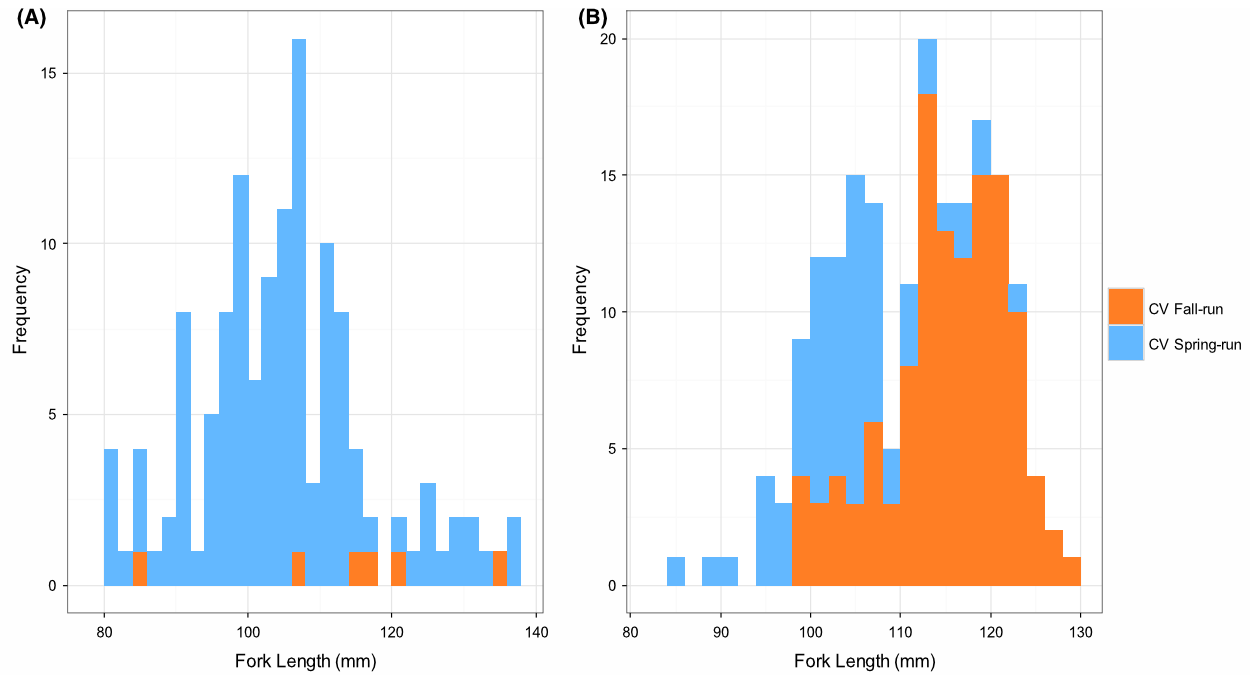


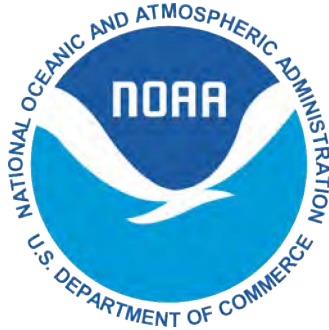
FIGURE A.1. Length frequency histograms of out-migrating Chinook Salmon with genetic distinction that were tagged in the Sutter Bypass during (A) 2015 and (B) 2016. CV = Central Valley. [Color figure can be viewed at afs.journals.org.]

TABLE A.1. Comparison of constant versus year- and/or reach-varying survival (φ) and detection (p) models for out-migrating Chinook Salmon (N_{par} = number of model parameters; AIC_c = Akaike's information criterion corrected for small sample size; ΔAIC_c = difference in AIC_c score between the given model and the most parsimonious model). Models are ordered from lowest to highest AIC_c . Lower AIC_c scores indicate greater relative model parsimony.

Model	N_{par}	AIC_c	ΔAIC_c
$\varphi(\sim\text{reach} \times \text{year}), p(\sim 1)$	19	1,383.726	0.00
$\varphi(\sim\text{reach} \times \text{year}), p(\sim\text{reach})$	27	1,392.249	8.52
$\varphi(\sim\text{reach} + \text{year}), p(\sim 1)$	11	1,394.074	10.35
$\varphi(\sim\text{reach} \times \text{year}), p(\sim\text{reach} + \text{year})$	28	1,394.997	11.27
$\varphi(\sim\text{reach} + \text{year}), p(\sim\text{reach})$	19	1,402.255	18.53
$\varphi(\sim\text{reach} + \text{year}), p(\sim\text{reach} + \text{year})$	20	1,403.608	19.88
$\varphi(\sim\text{reach}), p(\sim 1)$	10	1,405.719	21.99
$\varphi(\sim\text{reach} \times \text{year}), p(\sim\text{reach} \times \text{year})$	36	1,409.928	26.20
$\varphi(\sim\text{reach}), p(\sim\text{reach} + \text{year})$	19	1,416.271	32.55
$\varphi(\sim\text{reach}), p(\sim\text{reach})$	18	1,416.436	32.71
$\varphi(\sim\text{reach} + \text{year}), p(\sim\text{reach} \times \text{year})$	28	1,420.496	36.77
$\varphi(\sim\text{reach}), p(\sim\text{reach} \times \text{year})$	27	1,429.291	45.56
$\varphi(\sim\text{year}), p(\sim\text{reach})$	11	1,568.503	184.78
$\varphi(\sim\text{year}), p(\sim\text{reach} + \text{year})$	12	1,570.401	186.67
$\varphi(\sim 1), p(\sim\text{reach})$	10	1,577.198	193.47
$\varphi(\sim\text{year}), p(\sim\text{reach} \times \text{year})$	20	1,586.445	202.72
$\varphi(\sim 1), p(\sim\text{reach} \times \text{year})$	19	1,594.144	210.42
$\varphi(\sim 1), p(\sim\text{reach} + \text{year})$	11	1,658.943	275.22
$\varphi(\sim\text{year}), p(\sim 1)$	3	1,678.890	295.16
$\varphi(\sim 1), p(\sim 1)$	2	1,682.151	298.43

Chinook salmon smolt mortality zones and the influence of environmental factors on out-migration success in the Sacramento River Basin

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(Corrected)



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Errata (March 26th, 2018)

The cumulative survival estimates on page 14 have been corrected. They were incorrect in the original distributed version of this report.

Abstract

A small percentage of imperiled Chinook salmon in the Central Valley survive the passage from natal habitat to the ocean, yet managers charged with ameliorating this loss struggle to identify specific causes amongst the myriad potential contributing factors. We incorporated a breadth of individual fish attributes, environmental covariates and reach specific habitat types into mark-recapture survival models in order to gain a holistic perspective on which factors are most influential in determining outmigration success for hatchery origin late-fall run yearling smolts. Reach-specific survival estimates within the Sacramento mainstem revealed high levels of spatial heterogeneity in the landscape of mortality, with a general trend of increased survival through the lower reaches. River flow, hatchery release strategy (whether or not fish were released in a large group), fish condition and swim speed were strongly correlated with survival dynamics, suggesting potential causative mechanisms. Habitat features, specifically diversion density, off-channel habitat availability and sinuosity were also correlated to survival, but to a lesser extent than flow and individual covariates. Of the numerous mortality factors we included, spanning multiple spatial scales, flow correlated the strongest with out-migration success, providing further evidence of the importance of flow and water management practices to the out-migration mortality of hatchery origin Chinook salmon in the Central Valley.

Introduction

Historically, steep montane tributaries conveyed water, unencumbered, through the mainstem Sacramento River. Juvenile salmon utilized vast expanses of seasonal habitat to rear and grow before emigrating to sea. Loss of habitat, combined with overfishing and water diversion have contributed to precipitous declines in Chinook salmon populations (Yoshiyama et al. 1998, Yoshiyama et al. 2000), potentially portending extinction of salmon in California (Katz et al. 2013). Factors impeding recovery include continual habitat loss, sustained extraction of water for consumptive and agricultural use, and out-migration mortality of smolts (CDFW 2015).

Out-migration is oft considered the most perilous stage in the Chinook salmon life-cycle (Healey 1991). Overall survival of smolts from the Sacramento River through the Sacramento-San Joaquin Delta and on to the San Francisco Estuary and the Pacific is low compared to other salmon watersheds (Michel et al. 2015). Whereas survival through the Sacramento-San Joaquin delta is consistently low (Kjelson and Brandes 1989, Baker and Morhardt 2001, Newman and Brandes 2010, Buchanan et al. 2013, Singer et al. 2013), survival through the Sacramento River mainstem fluctuates more than other regions and increased survival in this region can increase overall survival to the ocean (Michel et al. 2013). Further, while Chinook salmon smolt survival in the delta has been extensively studied and manipulated in order to identify effective management actions within locations of considerable mortality, there is a paucity of comparable information for the Sacramento River mainstem. Thus, our research focuses on identifying potential drivers of out-migrating smolt mortality in the Sacramento River and identifying large-scale areas within the river where mortality rates are consistently high. Small improvements in the survival of early life stages can enhance adult returns (Baker and Morhardt 2001) and as such, the identification of factors that affect smolt mortality could provide managers with direction on how to improve survival (Perry et al. 2013, Singer et al. 2013).

In order to evaluate which factors may contribute to out-migration mortality, it is imperative to consider out-migrant behavior. Chinook smolts in the Sacramento River and delta have been shown to emigrate nocturnally and hold during the day (Zajanc et al. 2012, Chapman et al. 2013). Chapman et al. (2013) found that while nocturnal migration dominated overall, the proportion of nocturnal movement varied by river region (with almost exclusive nocturnal migration in upper reaches). Zajanc et al. (2012) offered evidence that the probability and duration of holding by juvenile Chinook salmon is influenced by specific nearshore habitat types such as large woody debris, cover and substrate type; although temporal and spatial factors had a greater overall effect. Thus, smolt holding behavior can be facilitated by environmental interactions driven at the basin wide and habitat level scales. Weins (2002) highlight the need to explore stream fish habitat associations across a broad riverscape in order to be meaningful for management. We incorporate scale in our analysis by examining smolt survival with respect to environmental factors influenced by broad, basin-wide level dynamics such as flow and temperature, as well as reach-specific habitat features such as shaded riverine aquatic cover, diversion structures and bank habitat, all of which can influence survival.

Numerous environmental factors are implicated in the survival of out-migrating Chinook salmon (Michel et al. (2013). Studies evaluating survival have revealed flow (Kjelson and Brandes 1989, Michel et al. 2015), temperature ((Kjelson and Brandes 1989, Newman and Rice 2002, Newman and Brandes 2010), water management practices (Kjelson and Brandes 1989, Brandes and McLain 2001, Perry et al. 2010, Cavallo et al. 2013) and predation (Cavallo et al. 2013) to be important mortality factors effecting the survival of tagged juvenile Chinook salmon transiting the Sacramento River and Sacramento- San Joaquin delta. Singer et al. (2013) and Michel et al. (2015) found evidence for differences in reach specific survival among years, with Michel et al. (2015) elucidating the role of hydrographic conditions in this result. Michel et al. (2013) recorded an effect of width to depth ratio and flow on movement rates of out-migrating smolts. While environmental variables affect the movement and survival of juvenile salmon in the Sacramento River and Sacramento-San Joaquin delta regions, there has yet to be a comprehensive study which incorporates the holistic interaction of reach-specific habitat features, basin scale environmental characteristics, as well as individual fish attributes, to explicitly detail survival in the Sacramento mainstem.

Directed management efforts to improve the survival of salmon smolts during outmigration are mired by the challenge of determining which elements, and at which scale, environmental factors exert the greatest influence on survival. Our study examines the spatial heterogeneity of mortality across an out-migration landscape, in order to resolve the existence and stability of mortality zones. We also systematically compare the impact of environmental covariates (flow, temperature, depth and velocity), habitat features (riverine cover, off channel habitat, diversion structures, bank type and adjacent land use) and individual fish covariates (fish condition, length and hatchery release strategy), in order to determine which factors, driven by processes occurring at disparate scales, have the greatest impact on survival. Finally, based on established relationships between juvenile Chinook salmon mortality rates and specific environmental factors, we posit potential mechanistic hypothesis for these observed relationships and propose potential management directions to improve out-migration success in the Central Valley.

Methods

Study Area

Although the historical northern extent of late-fall run in the Sacramento Basin likely stretched beyond present day Keswick and Shasta dams (Fisher 1994, Yoshiyama et al. 2001),

our northernmost extent was the standard release location for late-fall run smolts at the Coleman National Fish Hatchery (see figure 1). Tracing the outmigration of tagged smolts, our study area included three major river segments: the upper, middle and lower Sacramento River as defined in Chapman et al. (2013). Upper reaches are composed of shallow riffles, gravel bars and deep pools, the middle is defined by areas of deeper water with sand banks and large woody debris, and the lower reaches are channelized, with extensive levees, rip-rap and water diversion. Although previous work on late-fall run outmigration in the Central Valley utilized the entire outmigration extent, including the delta and estuary (see Michel et al. 2015 and Singer et al 2013), we focus here on the Sacramento mainstem portion of the outmigration corridor, as the riverine portion has received less attention, but is crucial for understanding population level changes in downstream migration success.

Acoustic tagging

Late-fall run Chinook salmon, obtained from the United States Fish and Wildlife Service - Coleman National Fish Hatchery, were implanted with acoustic tags and released annually for five years (2007-2011). For details regarding the surgical procedures undertaken and initial acoustic tag study design, please see (Michel et al. 2013, Michel et al. 2015). During the first year of this study (Dec-Jan 2007), smolts were tagged and released directly into Battle Creek. For subsequent years, each winter (Dec-Jan), tagged smolts were released concurrently from three locations along the mainstem Sacramento River: Jelly’s Ferry, Irvine Finch and Butte City, and in 2011 all fish were released at Jelly’s Ferry (see figure 1). In addition to the acoustic tag data utilized in Michel et al. (2013) and Michel et al. (2015), we utilized acoustic tag data collected by the USFWS. The USFWS fish were tagged in accordance with the same procedures as above, but released directly into Battle Creek in 2010 and 2011, and concurrent to the release of the remaining hatchery production (batch released), while the NMFS fish were released separately (table 1). Upon release, smolts passed through a series of acoustic receivers (again see Michel et al. (2013) and Michel et al. (2015) for more details), which extended from the release locations in the upper and middle Sacramento River, to the interface with the Pacific Ocean. We divided the Sacramento mainstem study region into 19 reaches demarcated by the location of 20 acoustic receivers, which had consistent locations between each of our study years.

Table 1: Release locations for all tagged late-fall run Chinook salmon yearling smolts. Fish were tagged by either NOAA-NMFS (National Marine Fisheries Service), Southwest Fisheries Science Center, or by the USFWS (United States Fish and Wildlife Service). All fish regardless of year were tagged at the Coleman National Fish Hatchery, located along Battle Creek- a tributary to the Sacramento River.

Study year	Release locations
2007	All NMFS tagged fish released into Battle Creek
2008	All NMFS tagged fish released from Jelly’s Ferry, Irvine Finch and Butte City
2009	All NMFS tagged fish released from Jelly’s Ferry, Irvine Finch and Butte City
2010	All NMFS tagged fish released from Jelly’s Ferry, Irvine Finch, and Butte City USFWS tagged fish released into Battle Creek with main hatchery production
2011	All NMFS tagged fish released exclusively from Jelly’s Ferry USFWS tagged fish released into Battle Creek with main hatchery production

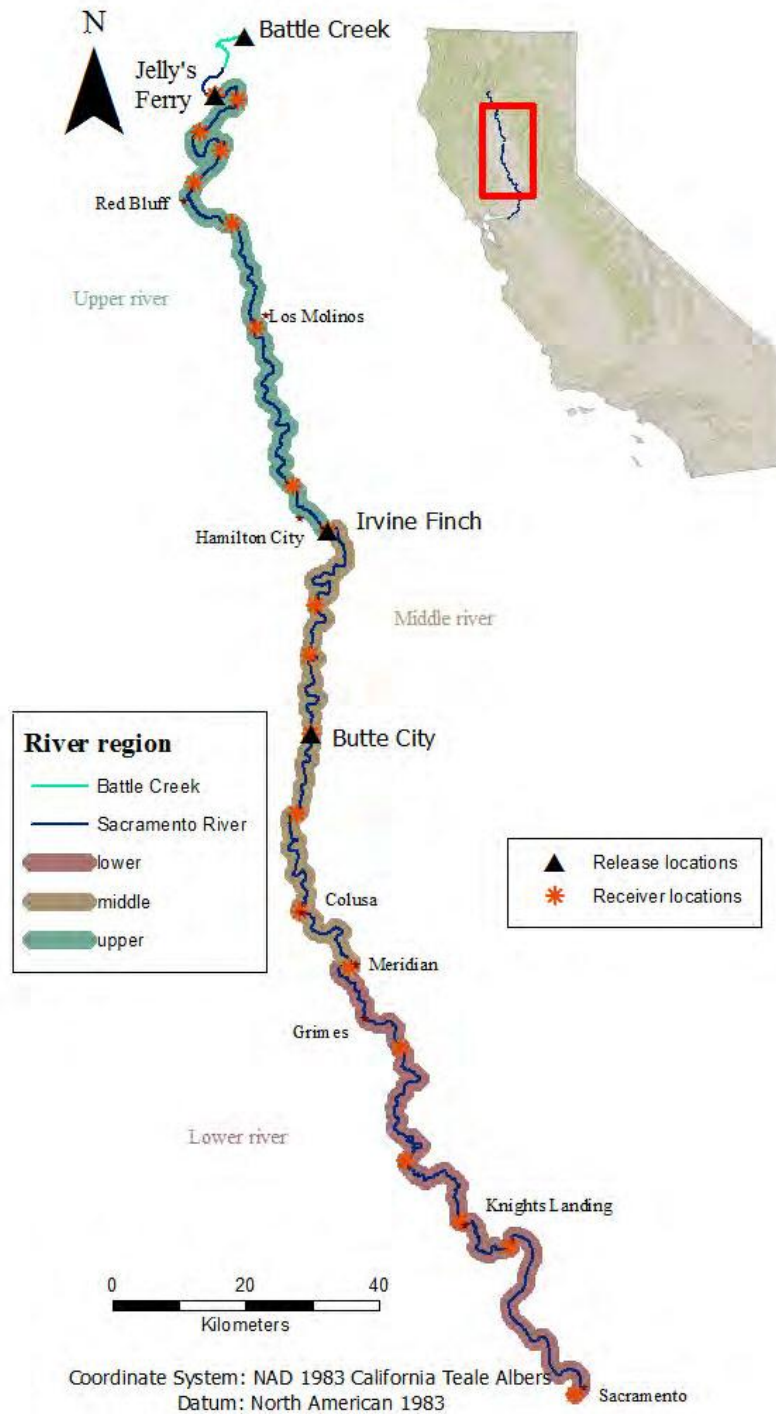


Fig 1: Map of the mainstem Sacramento River study area. Late-fall run Chinook yearling smolts were released at Battle Creek, Jelly’s Ferry, Irvine Finch or Butte City during our study period (water years 2007- 2011). While the Southern extent of our study area ended at the I-80 bridge near Sacramento, smolts must continue their outmigration through the delta and eventually the San Francisco Bay before entering the Pacific Ocean.

Habitat and environmental factors

In order to incorporate physical habitat features and environmental factors in survivorship models, we first had to establish basic hydrography for the Sacramento River. We utilized the most recent National Hydrography Database (NHD), high-resolution data to create our river hydrography layer. The Sacramento River has meandered considerably through time in response to varying flow conditions and bank erosion (Larsen 2007). This dynamism meant that many GIS layers depicting the course of the Sacramento River were incongruous to one another when data came from disparate years and sources. Our NHD Flowline was thus necessarily edited to match our other environmental data layers by manually editing the NHD flowline layer to match 2009 imagery from the National Agriculture Imagery Program aerial.

The California Department of Water Resources (DWR) provided a bankwidth layer (Adam Henderson, personal communication), which was created as part of the Central Valley Riparian Mapping Project in support of the Central Valley Flood Protection Program. This layer traces all visible surface water along the mainstem Sacramento River and was used as our baselayer for calculating habitat features within and adjacent to the Sacramento River.

The GIS- derived data we use to define habitat features in this study were static; the same values were used for each of the 5 years of our study. As such, we accept that our static descriptions of habitat do not necessarily reflect the conditions experienced by smolts during out-migration. However, as we were interested in describing physical habitat conditions for the entirety of the mainstem Sacramento River, and since many of these features do not change appreciably between years, we determined that this was the best available approximation of physical habitat. Dynamic environmental factors, the values of which were driven by basin-wide forcings, were modeled using existing River Assessment for Forecasting Temperature (RAFT) model output. RAFT is a 1-dimensional physical model that estimates temperature, flow, depth, and velocity every 15-minutes at a 2 km spatial resolution (Pike et al. 2013).

Habitat features: GIS

Data from each of the environmental factors, the source and limitations of which are outlined in table 2, were plotted in a Geographic Information System (using ArcGIS 10.3) and summarized by the 19 reaches we used to define our study reaches. River area, adjacent land use and off-channel habitat were calculated as area per reach. Shaded Riverine Aquatic Cover (SRA) and revetment (riprap) were summarized by reach as a measure of the length of bank with SRA and length of bank with revetment per reach. Densities of the number of diversions and number of tributaries were calculated per reach, and sinuosity was calculated for each river segment separately. In addition to mapping the landscape of habitat features in GIS, we explored the numerical relationships between environmental and habitat factors and river region (upper, middle and lower). All analysis and interpretation were conducted in the open software package R (R Core Team 2016). We first standardized each habitat factor by reach length (as defined by the length of bank per reach) for all habitat features except sinuosity which was already a measure per reach, and then plotted each of the environmental variables across river regions in order to ascertain whether there exist any clear differences among regions. For detailed information regarding the biological relevance of each of our environmental variables on juvenile salmon, please see the supplemental information section.

Table 2: A description of the source, extent and modifications to spatial habitat features along the Sacramento mainstem river. All spatial features had limitations in their applicability to out-migrating Chinook salmon, but are the best spatial representation of habitat we could produce at this time.

Habitat Feature and Metric	Data source and modifications
<p>River area</p> <p>Defined the bankwidth of the Sacramento mainstem</p>	<p><u>Source:</u> These data come from the “Mapping standard land use categories for the Central Valley Riparian Mapping Project,” developed for the Central Valley Flood Protection Program System wide Planning Area. Prepared for: DWR by Geographical information center, Cal State Chico, and shared with permission. This layer was heads-up digitized based on National Agriculture Imagery Program (NAIP) 2009 imagery.</p> <p><u>Extent:</u> This layer represents the mainstem Sacramento River from Keswick to the I-80 bridge. Only riverine habitats directly connected to the mainstem were included in this layer.</p> <p><u>Modifications:</u> This layer was modified to match the bankwidth outlines from the DWR revetment layer for the Sacramento River-which may reflect slight changes to the banklines as a result of recent revetment actions. The parent datasets were DWR layers [Vegetation-Central Valley Riparian Vegetation and Land Use, 2011 (medium scale)] ds292 and ds723 (metadata)</p>
<p>Sinuosity</p> <p>Index of 0 to 1 calculated per reach</p>	<p><u>Source</u> NHD high-resolution river line layer (edited to match NAIP 2009 imagery).</p> <p><u>Modifications:</u> Sinuosity values were derived from the python Sinuosity toolbox in ArcGIS, using the NHD high resolution flowline depiction of our study reaches. Sinuosity is calculated as the distance the river travels between reaches compared to the Euclidean distance of that same reach.</p>
<p>Diversion density</p> <p># of diversions per reach</p>	<p><u>Source:</u> Field data were collected through a joint effort by the authors at the National Marine Fisheries Service (NMFS), Southwest Fisheries Science Center (Santa Cruz) and the State of California Department of Fish and Wildlife, Fish Screen Fish Passage Program (FSFPP). Field surveys involved verifying the position and condition of diversions from the Passage Assessment Database (ds069). PAD</p> <p><u>Extent</u> Sacramento River from ACID diversion in Redding to the I-80 Bridge in Sacramento. NMFS covered the portion from ACID to the Meridian Bridge, Colusa and the state FSFPP collected data from the I-80 Bridge in Sacramento to Hamilton City (although in this study we only utilized state collected data below our Southern survey extent at the Meridian bridge)</p> <p><u>Data collection</u> field data were collected by jet boat in the Spring of 2016 – the location of each diversion was recorded with a GPS device and the condition of diversion intakes examined. New diversions were added when encountered. Additionally, intake diameter measurements were measured either directly (FSFPP) or estimated visually (NMFS).</p> <p><u>Limitations:</u> Diversion records inaccessible to boat (at least in the Northern, NMFS surveyed section) were omitted from analysis, as well as diversions that may still have been operational and accessible but were off the main channel. Abandoned records were removed. Also, there was no reliable method for obtaining information regarding the quantity or timing of water pumping.</p>
<p>Adjacent land use</p> <p>Mean area of adjacent land use type (within 120m of river) [m²] per reach</p>	<p><u>Data source:</u> Multi-Resolution Land Characteristics Consortium (MRLC), National Land Cover Database (NLCD) Metadata</p> <p>This is a raster layer with each 30x30 meter cell representing one of 16 land use classes.</p> <p><u>Extent</u> We clipped this nation wide dataset to our study area (Jelly’s Ferry to the I-80 bridge)</p> <p><u>Modifications:</u> We reclassified land use from 16 classes to 3 (“natural”, developed and agricultural) and clipped data to within a 120m buffer around our bankwidth river layer. We calculated land use area per reach by taking the mean land use data from 2006 and 2011.</p> <p><u>Limitations:</u> The 30m grid size meant that there were some gaps and overlap between the river bankwidth layer and adjacent land use data.</p>
<p>Revetment</p> <p>Length of rip-rapped river bank</p>	<p><u>Data source:</u> This data layer was provided upon request from the Department of Water Resources and is part of the joint revetment-bank-SRA layer. <i>This data was developed as part of the DWR Floodsafe CA initiative-specifically the development of the Conservation Strategy in support of the Central Valley Flood Protection Plan 2017 update.</i> Metadata</p> <p><u>Extent</u> Red Bluff to I-80 bridge (this section of data was an update to data previously collected by DWR Northern Region). Colusa to Verona (updated data previously collected by US Army Corps (USACE)- Sacramento Bank Protection Project, 2007). Data collected</p>

per reach [m]	<p>in the fall of 2013 and spring of 2014 by DWR and synched to NAIP 2013 and overlaid on 2009 channel features.</p> <p><u>Modifications/Limitations:</u> In order to extend the coverage from Red Bluff to Jelly’s Ferry, this portion of the dataset was estimated by the authors via 2015 Google Earth imagery. Thus, the northern section is an approximation of riprap and does not necessarily reflect current conditions</p>
<p>Tributaries</p> <p># of large tributaries per reach</p>	<p><u>Data source:</u> The data used for this analysis come from NHDPlus Version 2 (http://www.horizon-systems.com/nhdplus/NHDPlusV2_data.php), which was released in 2012- but houses data from disparate times. In some cases this data did not match current hydrography conditions.</p> <p><u>Extent</u> although there are many tributaries leading into the Sacramento River, we were only interested in large perennial tributaries, and assume that those smaller inputs are captured in the bankwidth layer which traced water body outlines using NAIP 2009</p> <p><u>Modifications:</u> We created a geometric network, joined the flowlines to the VAA attribute table and selected only those tributaries to the Sacramento River with stream order >3 (only the major tributaries). Canals and Sloughs were removed-although there are some sections of the tributaries, which may be canal features during part or most of their course.</p> <p><u>Limitations :</u> This data set only includes large tributaries, and omits potentially valuable seasonal and small tributaries to the Sacramento River.</p>
<p>Shaded Riverine Aquatic Cover (SRA)</p> <p>Meters SRA per reach [m]</p>	<p><u>Data source:</u> This layer contains information from the DWR revetment data as well as the DWR vegetation layers (ds723 and ds292) [Vegetation-Central Valley Riparian Vegetation and Land Use, 2011 (medium scale)]. We followed the DWR convention of defining SRA as: non-riprapped bank with adjacent natural woody vegetation, as adapted from (USFWS 1992)</p> <p><u>Extent</u> This layer covers our study region from Jelly’s Ferry to the I-80 bridge in Sacramento.</p> <p><u>Modifications:</u> While the vegetation layer covered the full extent of our study region, the revetment layer, as mentioned previously, missed the Northernmost portion of the river from Red Bluff to Keswick, which was estimated by hand via Google Earth Imagery (with 2015 imagery). We then selected those areas of SRA using select by attributes in ArcMap, and divided per reach.</p> <p><u>Limitations:</u> This is an estimation of overhanging cover and in-stream cover, but is an inferred proxy, not confirmed in the field. Thus, this is only an approximation of cover.</p>
<p>Off-channel habitat</p> <p>Area off-channel habitat [m²] per reach</p>	<p><u>Data source:</u> This data came from the DWR [Vegetation-Central Valley Riparian Vegetation and Land Use, 2011 (medium scale)] layer, which was digitized from NAIP 2009 aerial imagery. This data layer digitally traced all water bodies along the mainstem at the time of analysis (a snapshot of the area in 2009).</p> <p><u>Extent</u> This layer covers our study region from Jelly’s Ferry to the I-80 bridge</p> <p><u>Modifications:</u> We selected all water bodies within 50 m of the mainstem while removing tributaries and canals.</p> <p><u>Limitations:</u> This layer may contain off-channel water bodies that are inaccessible to out-migrating smolts (such as holding bays beyond diversions or pools not always connected to the mainstem) and would naturally vary depending on prevailing water conditions.</p>

Acoustic telemetry data processing

The acoustic receivers automatically process all detection data and drop false detections or incomplete codes from the detection file. To ensure that no false detections due to pulse train collisions occurred in the dataset, we performed a number of quality control procedures. We first removed all detections that occurred prior to the release date and time of each tag. We then removed all detections from fish that had only a single detection throughout the study. Finally, we examined the detection history of each individual fish and removed any detection history that appeared out of the ordinary. For example, any upstream movements had to be validated by three or more detections at the same receiver. Furthermore, we examined travel time between receivers and removed any detections resulting from a fish traveling time greater than 10 km per hour that were not subsequently validated by more than three detections.

Mark-recapture analysis

To estimate survival of out-migrating late-fall run Chinook salmon we fit a Cormack-Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) model using the marked (Laake et al. 2013) and RMark package (Laake and Rexstad 2008, Collier and Laake 2013) within the R programming language (version 3.3.1, R Core Team 2016). The CJS model was originally conceived to calculate survival of tagged animals over time by recapturing individuals and estimating survival and recapture probabilities using maximum likelihood. For species that express an obligate migratory behavior, a spatial form of the CJS model can be used, in which recaptures (i.e., tagged fish detected acoustically downstream from release) occur along a migratory corridor (Burnham 1987). Using this space for time substitution, we were able to estimate overall survival of an individual fish through a given reach, as the model uses individual fish capture histories to estimate the likelihood that a fish would survive and be detected at each receiver (Lebreton et al. 1992).

Although our analysis shares similarities with Michel et al. (2015), we did make some modifications in processing the data. We did not restrict our analysis to only those detections at the receivers separating the 19 reaches of interest. Instead, detections that occurred at any receivers within the reach of interest were included as detections for that reach. The 20 receiver locations that we used to delineate our reaches were consistently positioned in the same location throughout the five years of the study; however, there were additional receivers throughout the river that were either added, removed, or moved inter-annually. Further, we focused our modeling efforts on the Sacramento mainstem, and only utilized encounter history data collected within the delta and estuary (below our study site) to estimate apparent survival through these reaches, and did not include any spatial or spatial-temporal covariates. In the standard formulation of the CJS model, detection probabilities are estimated for a single resampling occasion (i) in time or space. For example, Michel et al. (2015) estimate the probability of detection at a given receiver location. We used detections at the receiver delineating the upstream boundary of the reach as well as detections at any receiver between the upstream boundary and the downstream boundary. Thus, the estimated detection parameter is a measure of the probability of detection from receiver (i) to receiver ($i+1$). We also made the assumption that any tag that was consistently detected at a receiver for more than 4 weeks was a mortality. These fish were censored and did not have any impact on the estimated survival or detection probabilities downstream from where the presumed mortality occurred.

We included a number of individual and spatial covariates in our analysis to identify the factors contributing to the mortality of out-migrating smolts. Fish size influences juvenile salmon survival (Zabel and Achord 2004), thus we included length and condition factor (Fulton's k) as individual covariates. We also included a binary individual covariate to distinguish fish released together with thousands of other hatchery fish and those released in small batches. Our a priori hypothesis was that large batches of fish could improve survival by saturating predators. The spatial covariates included in the model for each reach were: revetment area, shaded riverine aquatic area, tributary density, diversion density, off-channel habitat, and the proportion of the adjacent land use that was developed, natural, or agriculture.

Due to the importance of the environmental factors to salmon movement and survival (Michel et al 2010), we included individual spatial-temporal covariates. These covariates were flow, velocity, depth, water temperature, and individual swim speed. Including individual spatial-temporal covariates requires an estimate for every fish in each reach regardless of whether or not the fish was detected. To input data for locations where fish were not detected, we developed a mixed effects model to estimate individual swim speeds as a function of release year, release week, reach, and fish condition (Fulton's $K = \frac{W}{L^3} * 100$). We also included a random intercept for each individual fish to account for individual behavioral variability. The uncertainty in location based on the mixed effects model is inherently carried through the model by the way the

mark-recapture likelihood is built. The likelihood in all reaches, after the last time a fish was detected, account for the possibility that the fish died and the possibility that the fish survived and was not detected. The fate of fish that survive through a reach, in which case we knew when a fish was within that reach (and its actual, not predicted swim speed), are more influential in estimating the model likelihood than those whose fate (and in turn conditions) were unknown. However, we plan to test the impact of the swim speed predictions on survival estimates with an uncertainty analysis in a future iteration of this study. To verify that the mixed effects model did not violate any assumptions, we examined model diagnostics (QQplot and residuals) using the DHARMA package (Hartig 2016). We used the results from the mixed effects model to estimate swim speeds for all fish in all reaches. This also provided an estimate of the dates and times undetected fish were within each reach.

We then used environmental covariate data derived from the RAFT model (Pike et al 2013) to approximate the physical conditions experienced by each fish in each reach. We extracted all estimated values for the physical variables (temperature, flow, velocity and depth) for each fish in each reach and then calculated the mean for that variable, which we used as the environmental covariate in the CJS model.

We fit a series of different CJS models to determine which covariates had the greatest impact on out-migrating smolt survival. Prior to fitting the CJS models, all continuous covariates, including the individual and spatial covariates, were normalized by subtracting the mean and dividing by the standard deviation. We also conducted pairwise comparisons of all continuous individual, spatial, and spatial-temporal covariates to determine if any covariates were collinear (Table 3). We did not include covariates that had correlation coefficients greater than 0.7 in the same model. Likewise, we did not include models that had both fish length and fish condition since they are both measures of individual fish health. We then fit three different groups of models: 1) a model that included year and reach as factors, which we refer to as our “full model” 2), models that excluded year but included reach as a factor, as well as the various individual and spatial-temporal covariates, referred to as our “temporal-covariates” models and 3) models that excluded year and reach as covariates, but included the various individual, spatial-temporal and spatial covariates, referred to as our “spatio-temporal-covariates” models. The reason for fitting the different groups of models was to better understand how the covariates that we included in our model affected salmon survival, while accounting for the inherent differences between different covariate types. Because it is impossible to measure, or estimate, all potential factors that influence salmon survival, we hypothesized that the model that included year and reach as factors would have the best fit to the data and provide us with the best available estimates of reach survival by year. Conceptually, year and reach can be considered all-encompassing factors that account for a large portion of the spatial and temporal variability in survival, when in actuality it is likely the variability in the individual and environmental covariates that are driving these changes. Therefore, by fitting models that exclude both year and reach we can partition that variation between the covariates we have included in the model and thus, gain a better understanding of the mortality mechanisms. However, we emphasize that the factors included in our best models are based on correlations, so any potential mechanism must be inferred.

For each model set, we fit models with all possible combinations of covariates and selected the most appropriate model using Akaike’s information criterion (AIC). Due to the large number of potential models, and the long execution times required for models with spatial temporal covariates, we first fit the models using the Automatic Differentiation Model Builder (ADMB) option available through the marked package (Laake et al. 2013). In contrast to RMark, the marked package fits models based on the hierarchical likelihood construction described by Pledger et al. (2003). Although we were able to successfully fit models and estimate AICc criterion using the marked package, we were unable to estimate standard errors for all model parameters due to indefinite Hessian matrices. However, the models converged when we ran them without estimating the hessian matrix, and we used those models in the model selection

process. Thus, we used the marked package to conduct model selection and then refit the top models using RMark to calculate the final parameter estimates and confidence intervals.

Covariate plots

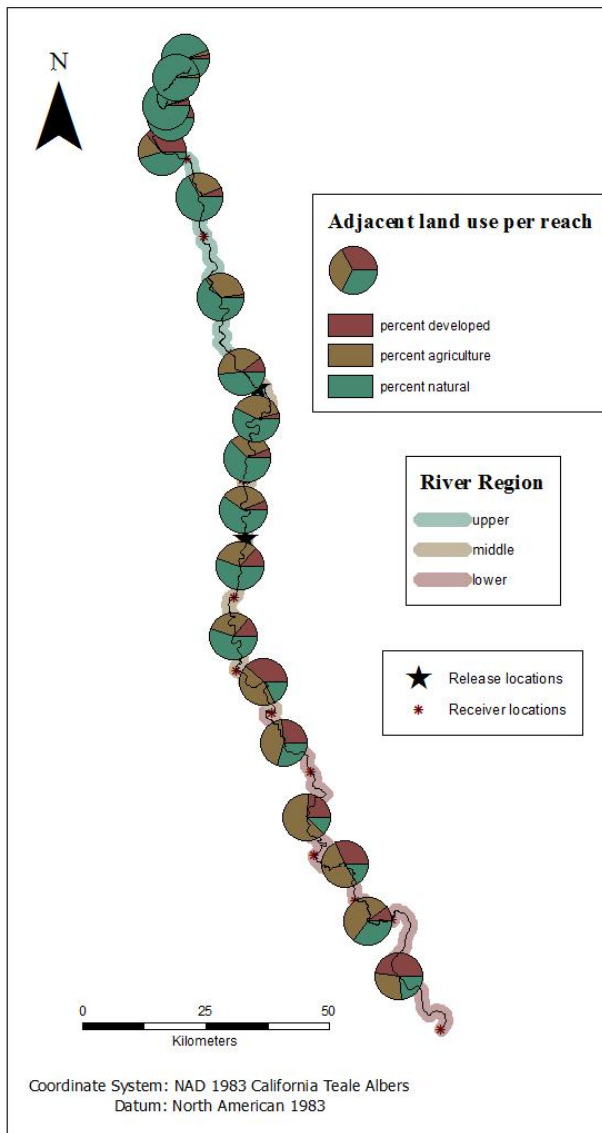
Once the relative importance of covariates had been determined from the model selection exercise, we extracted the β parameter coefficients for these covariates from the top model in which they occurred. The β parameter coefficients were then used to simulate what survival would be given a chosen covariate value, while keeping other covariates constant at their mean value. We selected regularly spaced covariate values ranging from the minimum to the maximum recorded values for that covariate, then simulated survival at each of these covariate values. The results from these simulations were then plotted, giving us a graphical representation of the relationship of flow and fish condition on survival dynamics across a reasonable range of flow and fish condition values.

Table 3: At left: covariates included in our survivorship model sets. Middle: those covariates that were not included in our analysis (excluded covariate) and at right: covariates that those excluded covariates were correlated with. Note that diversion density was collinear to depth, riprap, developed area, agricultural area and natural area.

Covariates (included)	<i>Excluded covariate:</i>	<i>Collinear with:</i>
Sinuosity	<i>Velocity</i>	<i>Flow</i>
Shaded riverine aquatic cover	<i>Depth</i>	<i>Flow + Diversion density</i>
Diversion density	<i>Riprap</i>	<i>Diversion density</i>
Off-channel habitat	<i>Developed area</i>	<i>Diversion density</i>
Fish length	<i>Agricultural area</i>	<i>Shaded riverine aquatic cover + Diversion density</i>
Fish Condition	<i>Natural area</i>	<i>Diversion density</i>
Flow		
Temperature		
Swim speed		
Released with other hatchery fish		

Results

Riverine habitat was spatially heterogeneous across the ~300 kilometers of Sacramento River that defined our study area. Although there were no major channel changes during our study period, 2011 was considered a “wet” water year, while 2007-2010 were considered “dry” years. There was a general North to South gradient in habitat features associated with human influence, with lower reaches exhibiting elevated levels of human modification concomitant to decreases in natural area (see figure 2). We compared diversion density, amount of riprapped bank, and land use area among our three river regions (upper, middle and lower) and found a general increase in the number of diversions and developed land area from the upper to lower reaches. Amount of riprapped bank also increases in the lower portions of the river compared to the upper and middle reaches. Finally, the total adjacent natural land use area decreased from the upper to lower reaches, with approximately a three-fold decrease in the total natural area in the lower reaches compared to the upper reaches (figures 2 and 3).



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Figure 2: Map depicting the percent adjacent land-use type for each of our 19 reaches along the mainstem Sacramento River. Adjacent land is defined as land within 120 meters of the mainstem Sacramento River. The categories of land use we were interested in were “natural, developed and agricultural, because adjacent land use may impact juvenile salmonid outmigration conditions. Land use data were obtained from the National Land Cover Database (NLCD) and we calculated the mean land use cover between the years 2006 and 2011.

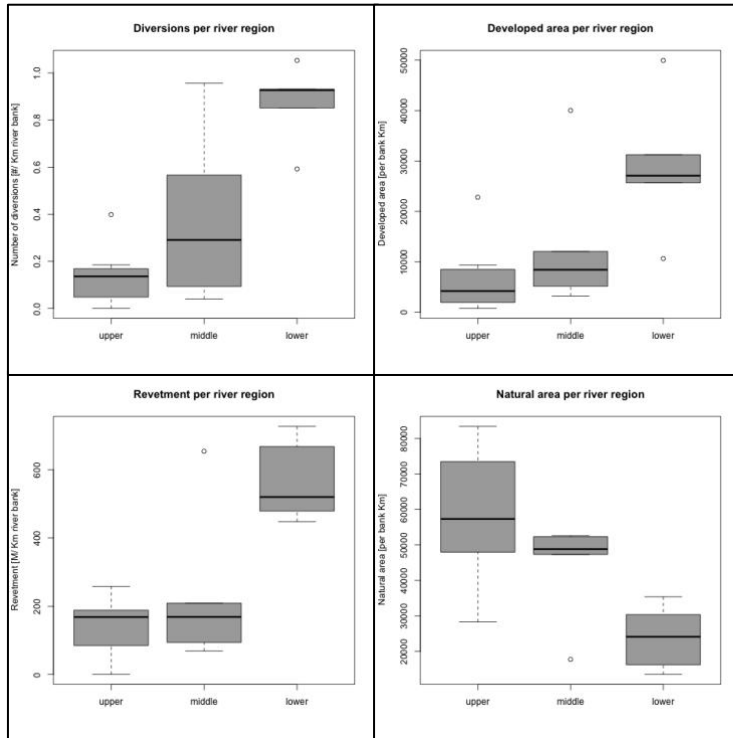


Figure 3: Upper left: mean diversion density increased from the upper reaches to the lower reaches, with a lot of variability for those reaches in the middle river region. Upper right: mean area of developed land per river region increased in the lower region. Lower left: length of riprapped bank per region, which had a clear increase in the lower reaches of the Sacramento. Bottom right: mean natural area declines from the upper to lower reaches, although the upper reaches are variable. All values were standardized by kilometers of river bank per reach.

Mark-recapture analysis- Full survival model and mortality zones

The full CJS survival model, a reach, year, interaction model, had the greatest support of all our model sets according to Akaike Information Criterion (AICc) values. We thus utilized the full model: $\phi(\sim\text{reach} * \text{year})$ $\rho(\sim\text{reach} * \text{year})$ to estimate per-reach smolt survival (per 10km). Survival per reach varied spatially and temporally. Between years, cumulative survival estimates, calculated as the product of reach specific survival rates (per 10km) within the Sacramento mainstem for the five years of our study (2007-2011) were 16.1%, 25.2%, 34.5%, 25.2% and 60.2%, respectively.

There was a general trend of decreased per-reach survival in the upper and middle reaches of the Sacramento mainstem, compared to the lower reaches (figure 4). For 2008, 2009 and 2010, reaches exhibiting the greatest estimated mortality (defined as reaches with estimated survival rates lower than 1.5 standard deviation from mean per-reach survival for that year), were not spatially consistent between years. Survival above Red Bluff Diversion Dam was inconsistent, but tended to be relatively high, while survival between Colusa and the I-80 Bridge was consistently high. In 2008, the reach adjacent to Ord Bend had the lowest survival (87% per 10 km \pm 3.8 SE), while survival was lowest in the reach above the Red Bluff Diversion Dam in 2009 (89% per 10 km \pm 3.6 SE) and near Butte City in 2010 (87% per 10 km \pm 2.1 SE), while the mean within reach survival for each of these years was \sim 96%. Thus, while there is a general trend of relatively higher survival in the lower portion of our study area, and relatively lower survival in the upper and middle reaches, the specific location with the greatest mortality risk appeared to vary between years. We were unable to generate comparable reach-specific survival estimates for

2007 due to incongruent receiver positions (6 of the 20 receiver positions were absent) and in 2011, high flows negatively impacted our detection efficiencies, rendering 12 receivers without reliable detection data (although the receivers in the lower portions of our study still produced reliable data, and thus allowed us to accurately estimate out-migration survival overall). The 2007 and 2011 years were included in the model sets that included individual and environmental covariates.

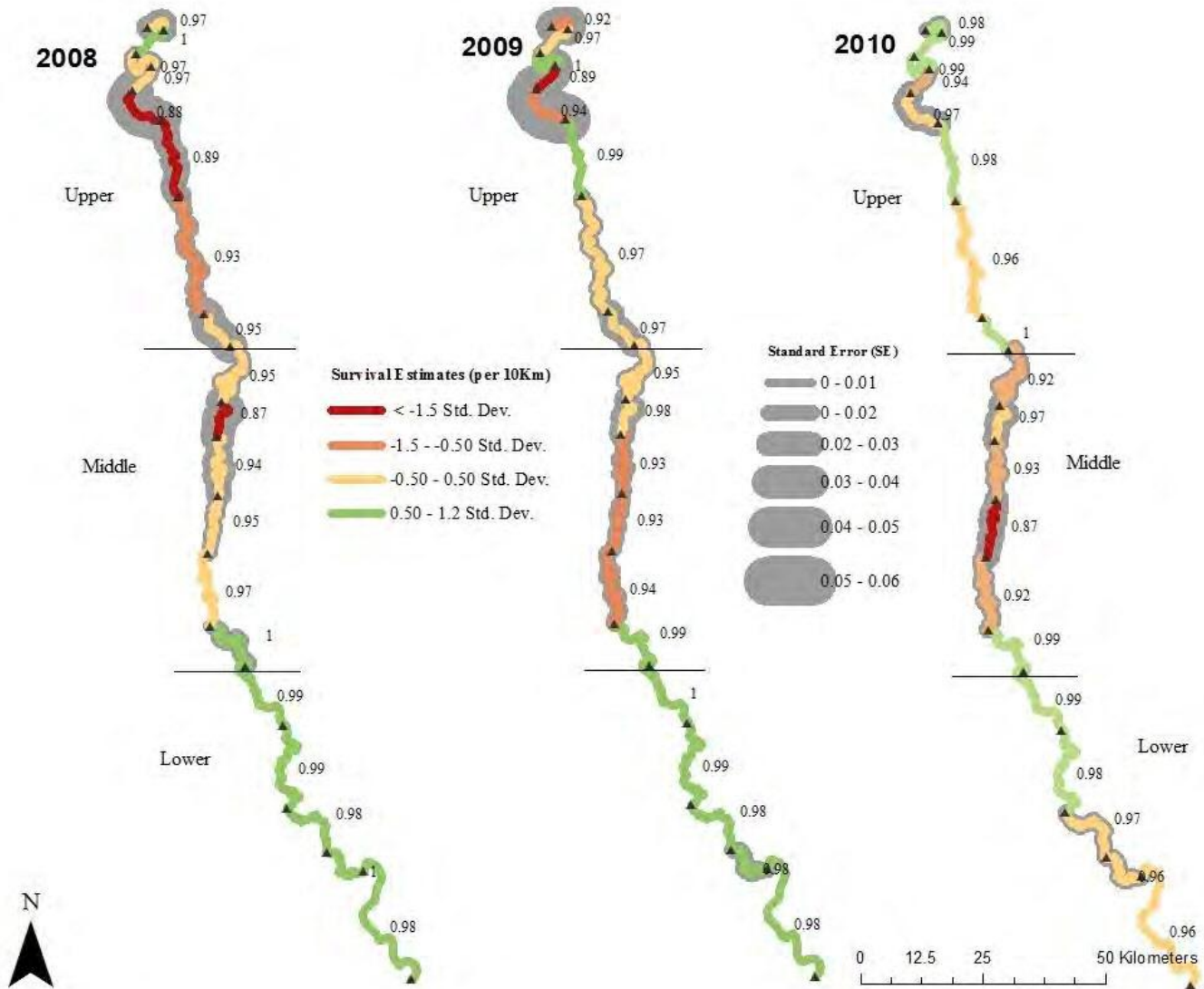


Figure 4: The following map depicts reach-specific survival estimates (per 10km) for each of our study years colored to represent per reach survival risk. Standard error is represented in this map as the grey buffer surrounding each reach. The values adjacent to each reach represent the survival estimate for a given reach (per 10 km) from our full survival model. Note that the spatial distribution of mortality zones (those areas with lower estimated survival compared to mean survival for that year) varied between reaches and years, with mortality zones occurring in the upper and middle reaches of the river. In 2010, the reach with the greatest amount of mortality (near Butte) was greater than 2 standard deviations from the mean survival of that year.

Temporal- covariates survival models

The second model set, which included reach but did not include year as a factor, did not have as much support in the data as our full model (AICc of 16239.88 compared to AICc of ~16161.47). However, we were still interested in the outcome of the temporal-covariates survival models because unlike the full model, these results allow us to investigate mechanistic hypotheses regarding the influence of the individual, habitat and environmental covariates on smolt survival. Within the temporal-covariates model set, the top model, based on Δ AIC scores, included flow, reach, fish condition, swim speed and batch release, indicating these factors were most correlated with survival (Table 4). Ten models had a Δ AIC value of four or less, when compared to the top model, indicating that all of these models had similar levels of support to the top model. Using the most parsimonious model φ (~reach + condition + flow + speed + batch release) ρ (~reach * release year), we were then able to generate β parameter estimates. Because covariate values were standardized prior to fitting, their coefficient values (β estimates) provide an indication of the relative importance of a given covariate compared to others. Standardized β coefficients can be interpreted as the estimated change in survival predicted from one standard deviation increase in the covariate value. Flow (0.53), hatchery release (0.33), fish condition (0.08) and swim speed (0.05) had an impact on smolt survival (Table 5). Flow had the greatest β estimate value, indicating that this factor had the strongest correlation with outmigration success of juvenile late-fall run yearlings. Hatchery release, specifically whether or not an individual tagged smolt was released concurrently with other hatchery fish, had the second strongest correlation with survival, followed by fish condition and swim speed. Plotting the covariates of flow and condition as a function of estimated survival (figures 5 and 6) revealed the strength of the relationships between survival and both flow and fish condition.

Spatial- temporal- covariates survival models

The final model set, which removed reach and year as covariates, did not fit the data as well as our previous model sets (AICc ~16355.62 for the spatial-temporal-covariates top model compared to a AICc of ~16239.88 for the temporal-covariates models and AICc of ~16161.47 for the full model). However, just as in our temporal-covariates model exercise; we were specifically interested in the comparative contribution of the individual, habitat and environmental covariates contained within our models to smolt outmigration survival. Including reach in the previous section allowed us to capture some of the spatial variability in survival that we were unable to explain with our habitat covariates. Modeling survival without a reach factor allowed us to explore the relationship between smolt survival spatial dynamics and spatial environmental covariates that would be otherwise explained by the reach factor. While it was beyond the scope of this study to directly test mechanistic relationships, the output of these statistical models reveals consistencies with mechanistic explanations.

The covariates of flow, hatchery release, fish condition and swim speed appeared consistently in the most parsimonious models (with Δ AICc<4). In addition to these covariates, which were also important in our temporal-covariates model set, reach length, diversion density, area of off-channel habitat and sinuosity further improved the models. The existence of multiple models with similar Δ AICc<4 indicated that several of these models support the data similarly well, and did not necessarily support the selection of only one top model. Conversely, shaded riverine aquatic cover (SRA) and temperature did not appear as consistently in those models best explaining the observed variation in smolt survival. Standardized β coefficients for the covariates occurring most frequently in our top models (φ (reach length+ sinuosity+ diversions+ off channel+ condition + flow + speed + batch release) ρ (~reach * release year)) revealed reach length to be the most important determinant of survival dynamics in this modeling exercise, with survival decreasing as reach length increased (Table 7). Flow was once again the most important environmental covariate in predicting outmigration success, with increased levels of flow correlating with increasing smolt survival. Sinuosity had a negative relationship to survival.

While there was a positive relationship between diversion structures and survival, with the higher density of diversions corresponding to increased survival estimates. Finally, we compared delta AIC values for models with and without the most explanatory covariates to give a sense for how important specific covariates, especially flow, is relative to these unexplained reach-specific differences in survival (figure 7).

Model comparison

We compared the results between the temporal covariate model and the spatial-temporal covariate model in order to visualize regions where our spatial-temporal-covariates model either over or under estimated survival when compared to the temporal-covariates models (figure 8). We assume that the better fitting temporal-covariates model (based on ΔAIC values) is the more accurate representation of the survival process. Thus, the comparison between these models provides some indication of where additional processes, beyond the covariates included in the spatial-temporal covariate model, had a significant impact on survival. Negative index values imply that the spatial-temporal-covariates model is over-estimating survival and additional mortality processes are occurring. We primarily observed these survival overestimates in the lower reaches of the river. Specifically in the reach between Butte and Colusa and the reach between Knights landing and the confluence with the Feather River.

Table 4: Model output for temporal-covariates CJS models. Note that a model that is more than 4 AIC points lower than another is generally considered to be substantially more supported than the latter (Burnham and Anderson 2002). If ΔAIC is less than 4, support of one model over another is equivocal . Lower AIC scores indicate greater relative model parsimony.

Model	num # cov	AICc	ΔAIC	Weight
$\phi(\sim\text{reach} + \text{condition} + \text{flow} + \text{speed} + \text{batch release}) \rho(\sim\text{reach} * \text{release year})$	4	16234.38	0	0.1622064
$\phi(\sim\text{reach} + \text{condition} + \text{flow} + \text{temp} + \text{speed} + \text{batch release}) \rho(\sim\text{reach} * \text{release year})$	5	16235.66	1.28	0.08553018
$\phi(\sim\text{reach} + \text{sinuosity} + \text{condition} + \text{flow} + \text{speed} + \text{batch release}) \rho(\sim\text{reach} * \text{release year})$	5	16236.36	1.98	0.0602721
$\phi(\sim\text{reach} + \text{diversion} + \text{condition} + \text{flow} + \text{temp} + \text{batch release}) \rho(\sim\text{reach} * \text{release year})$	5	16236.38	2	0.05967238
$\phi(\sim\text{reach} + \text{diversion} + \text{off channel} + \text{condition} + \text{flow} + \text{batch release}) \rho(\sim\text{reach} * \text{release year})$	5	16236.38	2	0.05967238
$\phi(\sim\text{reach} + \text{sinuosity} + \text{diversion} + \text{condition} + \text{flow} + \text{batch release}) \rho(\sim\text{reach} * \text{release year})$	5	16236.38	2	0.05967238
$\phi(\sim\text{reach} + \text{sinuosity} + \text{condition} + \text{flow} + \text{temp} + \text{speed} + \text{batch release}) \rho(\sim\text{reach} * \text{release year})$	6	16236.7	2.32	0.05084945
$\phi(\sim\text{reach} + \text{sra} + \text{condition} + \text{flow} + \text{temp} + \text{speed} + \text{batch release}) \rho(\sim\text{reach} * \text{release year})$	6	16236.7	2.32	0.05084945
$\phi(\sim\text{reach} + \text{sra} + \text{condition} + \text{flow} + \text{temp} + \text{batch release}) \rho(\sim\text{reach} * \text{release year})$	5	16237.32	2.94	0.03729538
$\phi(\sim\text{reach} + \text{diversion} + \text{sra} + \text{condition} + \text{flow} + \text{speed} + \text{batch release}) \rho(\sim\text{reach} * \text{release year})$	6	16237.68	3.3	0.03115172

Table 5: β coefficient estimates for those covariates occurring in the top model from our temporal-covariates model set. These standardized β values indicate relative importance as well as the direction of that relationship to survival. Flow, with a positive β value of 0.532 was the most correlated value to smolt outmigration survival.

Covariate and β coefficient
Flow (0.532)
Hatchery release (0.333)
Fish condition (0.084)
Swim speed (0.047)

Table 6: Model output for spatial-temporal-covariates CJS model. These 7 models have similar levels of support to the top model (as indicated by Δ AIC values). The most common covariates included in these top models were flow, hatchery releases, fish condition, swim speed (as in our temporal-covariates output), as well as the habitat variables: diversion density, off channel habitat area and sinuosity).

Model	npar	AICc	Δ AIC	weight
ϕ (reachL+ sinuosity+ sra+ diversions+ off channel+ condition + flow + speed + batch release) $\rho(\sim$ reach * release year)	123	16350.6	0	0.19938
ϕ (reachL+ sinuosity+ diversions+ off channel+ condition + flow + speed + batch release) $\rho(\sim$ reach * release year)	122	16350.8	0.24	0.17683
ϕ (reachL+ sinuosity+ sra+ diversions+ off channel+ condition + flow + temp+ speed + batch release) $\rho(\sim$ reach * release year)	124	16352.5	1.9	0.07711
ϕ (reachL+ diversions+ off channel+ condition + flow + speed + batch release) $\rho(\sim$ reach * release year)	120	16353	2.38	0.06065
ϕ (reachL+ sinuosity+ diversions+ off channel+ condition + flow + speed + batch release) $\rho(\sim$ reach * release year)	121	16353.1	2.54	0.05599
ϕ (reachL+ sinuosity+ diversions+ off channel+ flow + speed + batch release) $\rho(\sim$ reach * release year)	121	16353.9	3.32	0.03791
ϕ (reachL+ sinuosity+ diversions+ off channel+ condition+ flow + temp+ speed + batch release) $\rho(\sim$ reach * release year)	123	16354.0	3.4	0.03642

Covariate and β coefficient
Reach length (-0.566)
Flow (0.482)
Hatchery release (0.3928)
Diversion density (0.3245)
Off-channel habitat (0.1306)
Swim speed (0.0999)
Sinuosity (-0.0974)
Fish Condition (0.0721)

Table 7: Spatial-temporal-covariates model β estimates for those covariates occurring in the most parsimonious models. β values are standardized, thus allowing for comparison of relative influence on outmigration survival. Reach length had the strongest, negative correlation to outmigration survival, while flow had a positive relationship to survival (with more flow corresponding to greater survival estimates).

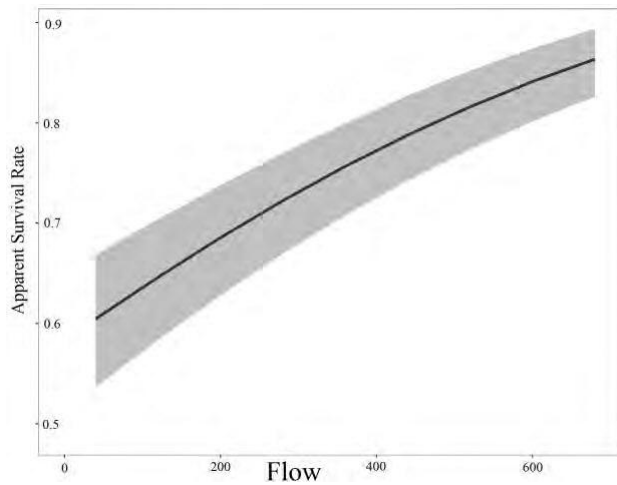


Figure 5: A plot depicting simulated survival as a function of flow (cubic meters per second) in the Sacramento River. As flow increases, apparent survival increases. Dark line indicates survival estimate, and grey area represents 95% confidence intervals.

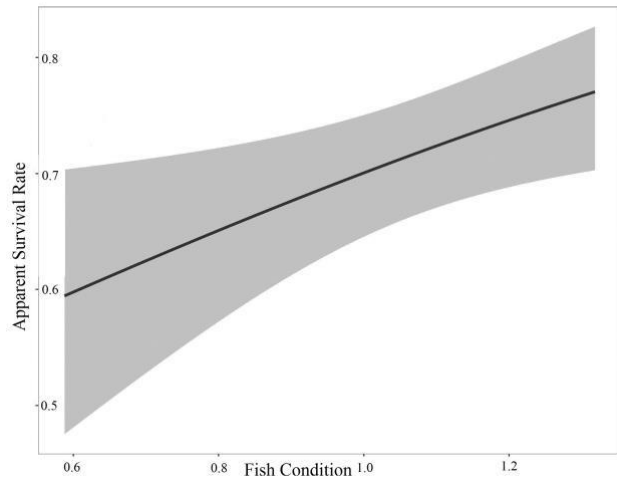


Figure 6: A plot depicting simulated survival as a function of fish condition (Fulton's K). As fish condition (an indication of fish health, calculated as a length to weight ratio) increases, so does apparent survival. Dark line indicates survival estimate, and grey area represents 95% confidence intervals.

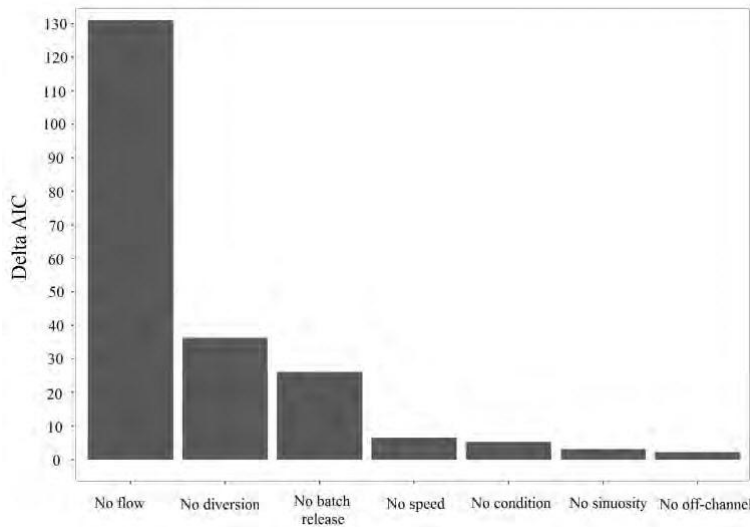


Figure 7: A plot comparing ΔAIC values for the models where only a single variable is removed. This plot demonstrates the comparative importance of flow as a correlate to apparent survival compared to the other covariates in our models.

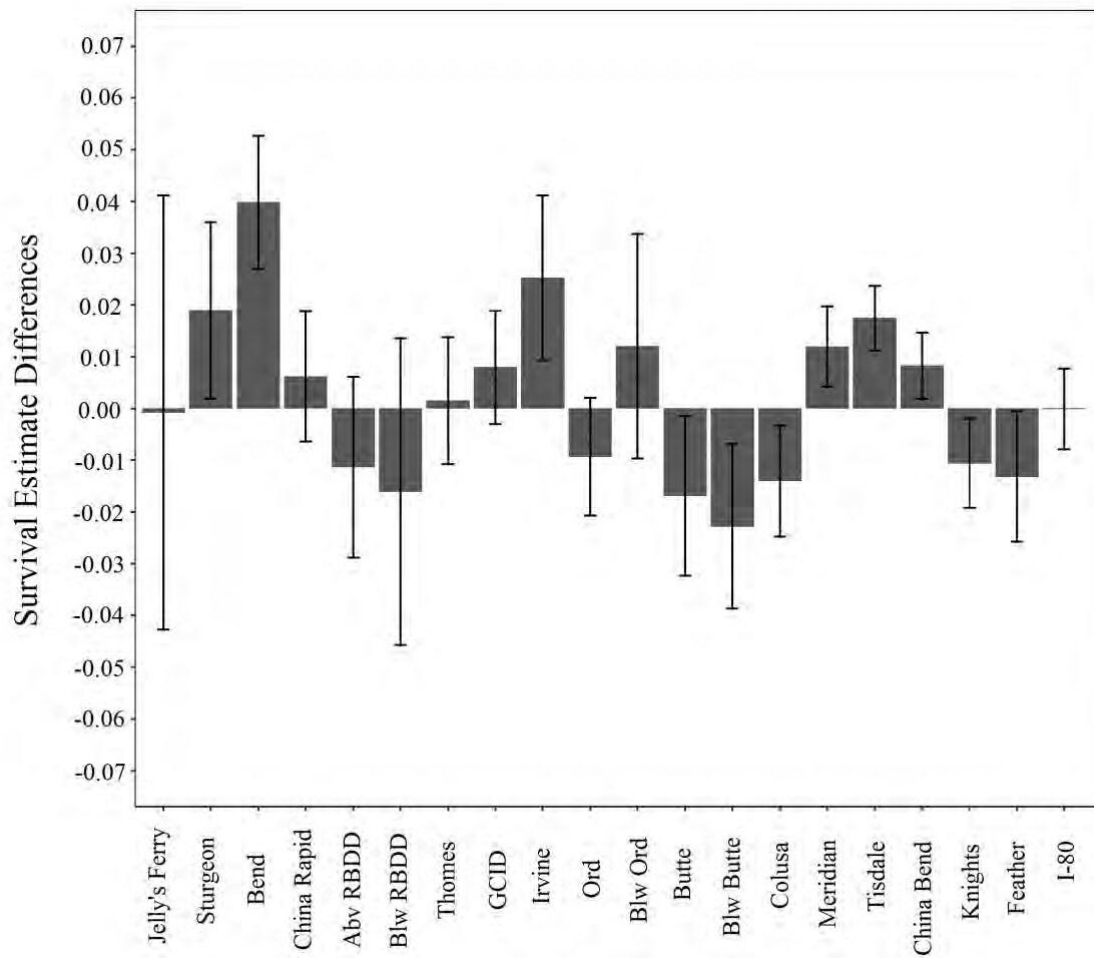


Figure 8: A plot of the differences in standardized survival estimates for the spatial-temporal-covariates model and the temporal-covariates model. We used the delta method to estimate the variance for these differences. Negative values indicate reaches where our spatial-temporal-covariates model underestimated survival. There is a slight spatial trend in the data whereby reaches in close proximity tend to be either over or under estimated with similar magnitude. This suggests that there may be some spatial correlations in mortality operating at a scale slightly larger than the reaches used in our analysis.

Fish summary

Of the 1,536 fish that entered the Sacramento River (this removed those fish released at Battle Creek that were never detected within our study area), only ~584 fish were detected at the end of our study area or beyond. Of those 584 fish that were detected at or below the southern edge of our study area, mean annual fish condition closely mirrored those values from the tagged fish population within a given year (table 8).

Finally, the majority of outmigration movement occurred at night, with most smolts leaving and arriving at night (see figure 9). We determined outmigration timing by grouping the times that fish were detected at receivers for the first and last time, and assumed that these detections were indicative of fish moving downstream. If we standardize detections by the number of hours per time of day however, and compare the number of detections per hour, night

still has the greatest percentage of departures, but the effect is muted, and the largest percentage of arrivals occur at dawn (46.7%) and dusk (38.9%) (table 9).

Release Year	# Tagged fish	# detected survivors	Mean fish condition (survivors)	Mean fish condition- all
2007	130	18	1.024 (SE±0.012)	1.033 (SE±0.004)
2008	304	126	1.072 (SE±0.005)	1.072 (SE± 0.003)
2009	300	129	1.098 (SE±0.006)	1.093 (SE± 0.004)
2010	408	130	1.085 (SE±0.007)	1.088 (SE± 0.003)
2011	394	181	1.081 (SE±0.004)	1.080 (SE± 0.003)

Table 8: The total number of fish tagged and released into our study area (Jelly’s Ferry to the I-80 bridge in Sacramento) and the number that were detected at the end of our study area or beyond. Mean fish condition for those fish that survived through our study area is contrasted to the mean condition for all tagged fish.

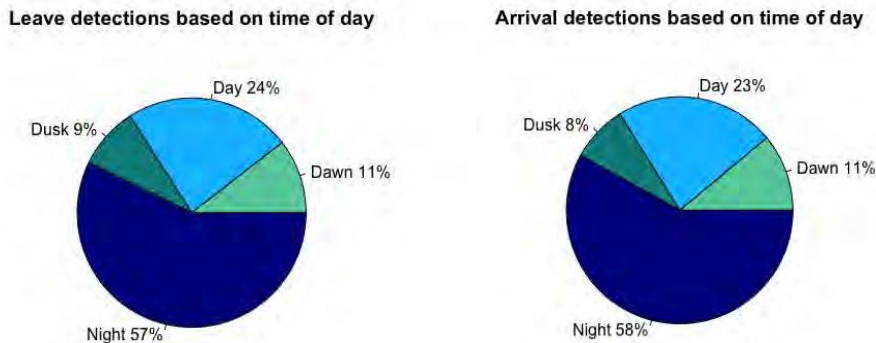


Figure 9: Out of a total of 8,967 detections for leave time and 8,860 detections for arrival time, these pie charts represent the percent of detections occurring at these specific times of day. Day represents 9am-5pm, dusk (5pm-9pm), night (9pm- 5am) and dawn (5am- 9am), both pie charts show the majority of arrival and leave times occur at night, indicating that fish out-migrate at night.

Table 9: When we standardize the number of detections by the number of hours within that time of day, night still has the greatest proportion of leave detections, but not by as great of a margin as Figure 9, and the greatest percent of arrivals occur at dawn.

Time of day	Percent of detections (per hour/time of day) leaving	Percent of detections (per hour/time of day) arriving
Dawn	29.7	46.7
Day	13.3	4.19
Dusk	24.7	38.9
Night	32.3	10.2

DISCUSSION

Conservation of beleaguered salmonid populations is currently hindered by a disparity of scale- with research commonly occurring in distinct time frames and locations, and management acting on broader scales of human disturbance (Fausch et al. 2002). In our study, we bridge this gap by examining mortality factors associated with low survival at multiple spatial scales. Examining the landscape of mortality revealed zones of elevated mortality that occurred in different locations in different years. While we could not include all possible sources of mortality in our analysis, we ascertain that even when reach-specific habitat features and individual covariates are included, flow remains the single most influential factor for determining survival of late-fall run salmon smolts.

Spatial heterogeneity of survival

Our results indicate that mortality during outmigration is spatially heterogeneous; with certain reaches exhibiting elevated levels of mortality. The severity of mortality in each reach varied between years, and is likely a result of the dynamic nature of the Sacramento system. However, our reach designations (mortality zones) were composed of large swaths of river, and it is difficult to draw conclusions about what features, specific to a given reach, may contribute to smolt mortality from survival estimates alone. Further, because survival estimates were standardized by reach length, it is possible that the larger length reaches included mortality hotspots, but the effect of these were attenuated by areas of higher survival within the same reach. Overall, we can conclude from our reach-specific survival estimates that mortality zones occurred most frequently in the upper and middle regions of the Sacramento River, while survival increased through the lower reaches, specifically below Colusa to the I-80 Bridge. One possible explanation for this is that in the upper regions, sick or weak fish which survived in hatchery conditions were picked off soon after release and only the strongest fish survived to the later reaches, at which point they had higher chances of survival. The observation that fish condition was positively correlated with survival suggests that this kind of effect is possible. Overall we can conclude that mortality risk is not evenly distributed across the outmigration corridor, and some zones may pose a greater risk to out-migrating smolts. Future work would benefit from exploring mortality zones at a finer spatial resolution, as well as investigating potential mechanisms responsible for observed decreases in survival within these zones, especially the upper regions, through time.

Environmental covariates

Based on model selection criteria, the full model had the greatest level of support, but did little to elucidate the role of environmental and individual covariates in survival. As our main priority in this study was to compare the relative role of individual, habitat and environmental covariates on outmigration success, it was imperative to examine model results without the all-encompassing factors of reach and year. Both model sets revealed flow, hatchery release strategy, fish condition and swim speed to be important factors influencing survival. Flow exerted the greatest overall effect on outmigration success, with increased flow correlated to increased smolt survival. Flow has been significantly reduced and homogenized in the Sacramento River system from historic levels (Buer et al. 1989). Flow determines the amount of habitat available for juvenile salmon (USFWS 2005), and in some cases, may be an important outmigration timing cue (Young et al. 2011). Flow has repeatedly been the most important factor affecting overall survival of Chinook salmon in the Central Valley (Kjelson and Brandes 1989, Zeug et al. 2014, Michel et al. 2015), likely as a result of concurrent temperature, velocity and turbidity conditions that influence the ability of smolts to evade predation while staying within their physiological tolerances. Further, because we included both flow and swim speed as covariates in our models,

we were able to separate the effect of flow from swim speed, suggesting that there are features inherent to flow itself, not just its effect on travel time, that correlate to survival. Finally, while we did not include turbidity as a factor in this analysis due to the current paucity of data, it is also hypothesized that higher flows increase turbidity, which in turn decreases smolt susceptibility to predation (Gregory and Levings 1998). Whatever the specific mechanism, flow was clearly the most important factor influencing the outmigration success of late-fall run Chinook smolts in 2007-2011. Future research would benefit from controlled-release studies concomitant to tagged-release investigations in the Central Valley, in order to establish possible threshold values.

Individual covariates

Our results indicate that the batch release of smolts is correlated to increased smolt outmigration survival. One rationale for why this release strategy may improve overall survival is the theory of “predator swamping;” whereby predators, inundated by prey, pose less of an individual threat for smolts. This effect has already been demonstrated for Chinook salmon in the Yakima River (Fritts and Pearsons 2008) and juvenile sockeye salmon in British Columbia (Furey et al. 2016). Furey et al. (2016) posit that outmigration timing, whereby smolts hold during the day and travel by night, may have evolved as a strategy to encourage predator swamping. One thing we were not able to account for is whether this effect persists for the whole riverine system, or is just observed within the initial reaches.

Another individual covariate that correlated strongly to improved survival rates for out-migrating smolts was fish condition. Calculated as Fulton’s k factor, which describes the relationship of weight to length for an individual fish, fish condition can be used to infer overall health of an individual fish. According to Davidsen et al. (2009), survival of post-smolt Atlantic salmon was dependent on fish size (fork length), and in the San Joaquin Basin, downstream survival during outmigration was influenced by size (and life stage) (Sturrock et al. 2015). The yearlings utilized in our study were large (only those smolts 140mm or larger were tagged due to concerns of tag burden), and may only represent the upper limit in size frequencies within natural populations. Fish condition may be of even greater importance for naturally occurring populations of Chinook salmon, who exhibit a wide range of sizes during out-migration, and could be subject to size selective mortality. There are many unknowns regarding the size and timing of outmigration of naturally occurring Chinook salmon populations in the Central Valley, and future studies should focus on the comparative outmigration success of different life-history strategies under different environmental conditions.

Predicted swim speeds were an important factor describing out-migrant survival data, with increasing swim speeds correlating to increased survival. For out-migrating yearling smolts, it is likely that swim-speed in the context of our study is a proxy for duration of exposure to mortality factors. In the Columbia River system, yearling smolt outmigration rates were not correlated with river discharge, temperature, release date or fish size (Giorgi et al. 1997), indicating that yearlings are not passive particles during outmigration, and can control their speed through the system. However, Michel et al. (2013) found that Sacramento River smolt migration rates were related to river width to depth ratio, flow, turbidity and water velocity, so the degree to which environmental factors influence the amount of time spent traversing the outmigration corridor warrants further research, especially if the duration of exposure to mortality factors during outmigration is important in overall survival during this phase. Finally, the swim speed of out-migrants may vary based on whether fish are hatchery or natural origin, at least according to Friesen et al. (2007), who found a significant difference in the outmigration rate between hatchery and natural Chinook salmon in the Willamette River. Thus, natural populations may be traveling slower and in turn exposed to a greater mortality risk based on increased duration of exposure. While the full model revealed the spatial heterogeneity of survival, and the temporal-covariates model elucidated the environmental and individual covariates most associated with mortality, it is

the outcome of the spatial-temporal-covariates model that allows us to examine a relative comparison of which habitat features are influencing these observed patterns of survival.

Physical habitat features

As revealed by the trend in the location of mortality zones, there is a general trend of relatively higher survival in the lower reaches of the Sacramento mainstem compared to the upper and middle reaches. Model selection results revealed reach length, diversion density, off-channel habitat and sinuosity to be correlated with survival. Sinuosity may have occurred in our model results as a result of its negative association with the channelized, riprapped reaches characteristic of the lower reaches. Thus, when we consider the role of finer-scale habitat features in shaping survival success, it is in the context of this larger trend of better survival towards the more modified lower reaches. It is important to note that while late-fall run yearlings tend to have lower survival in general in the upper reaches of our study area, we do not mean to imply that these habitats are not of critical importance to other life-stages and runs of Chinook salmon. Studies have shown that Chinook salmon fry, for example, have higher survival in the upper Sacramento River (Brandes and McLain 2001), suggesting that this area may provide critical habitat to other runs and life-stages. The lower reaches are highly channelized, with little available habitat. Diversions are more prevalent in this area due to greater agricultural land use, and were highly correlated to other habitat variables typical of agricultural zones; namely depth, riprapped banks and agricultural and developed land use. Because we did not wish to obfuscate the results of our analysis, we withdrew these factors from our modeling efforts because of their collinearity, but the role of “diversions” on survival could be equally viewed as the role of depth, agriculture and developed land and riprap as well.

Diversions in our study are considered only for their structural value, as water pumping is presumed to be at a minimum during the winter outmigration periods of our study (fish released in Dec-Jan 2007-2011), thus limiting entrainment risk. The inclusion of diversions in our study was mainly to test the hypothesis that diversion structures, often large, prominent features of the riverscape, were increasing mortality risk through associated predation assemblages (Sabal et al. 2016). However, the positive association of diversions to smolt survival may be a result of a size refuge in which the late-fall run yearlings used in our study evaded predation, due to their larger size. Additionally, it is possible that these structures were not concentrating predators, which target late-fall run smolts. If late-fall yearlings in our study were exempt from predation pressure at these features, it is possible that due to the lack of natural habitat in the vicinity, diversion structures provided the only available cover for holding. Friesen et al. (2007) noted that yearling smolts in the Willamette River appeared to have an affinity for pilings during outmigration, so it is not unreasonable to assume out-migrants may utilize whatever cover is available in the absence of natural habitat. Conversely, it is possible that the lack of available shallow, natural habitat in the lower reaches of the Sacramento River reduced the available predator-aggregating habitat and thus decreases overall predation.

Off-channel habitat area was the final covariate correlated to survival. Our estimate of “off-channel” habitat comes with many limitations, as it was digitized from a static DWR vegetation and land use layer and only contained permanently wetted areas within 50 meters of the mainstem; in turn omitting those ephemerally inundated areas that have been demonstrated to be important habitat for juvenile salmonids, such as floodplain (Sommer et al. 2001, Limm and Marchetti 2003, Jeffres et al. 2008, Limm and Marchetti 2009). Given the rapidity with which smolts transited our study area, it is unlikely that the availability of off-channel habitat areas dramatically improved survival. However, if smolts were indeed transiting the system via a pattern of holding during the day and moving at night (Chapman et al. 2013), it is possible that small features of off-channel area may be providing a break from the prevailing currents or enhanced feeding opportunities while holding.

The importance of side-channel habitat for juvenile salmonids has been highlighted in other locations (Decker 2002, Morley et al. 2005), and Johnson et al. (2015) note that yearling Chinook salmon utilize off-channel areas in the Colombia River, prompting the author to suggest that management efforts should prioritize the restoration of shallow off-channel areas. Blackwell et al. (1999) suggest that it is the quantity more than the quality of these habitats that will influence the number of out-migrants. At the same time, yearling Chinook salmon have been documented distributed evenly across the river channel compared to sub-yearling fish, which tend to associate closely with shoreline habitat (Friesen et al 2007 and Dauble et al 1989), so in general it is unclear how yearling smolts utilize the 2 dimensional structure of the river and whether the availability of off-channel habitat would affect survival. While habitat does not account for considerable variability in the survival of late-fall run hatchery fish, smaller juveniles may rely more on these habitat features than the large late-fall run smolts used in our study. Thus, while habitat does not account for considerable variability in the survival of the late-fall run in this study, it likely constitutes essential habitat for natural populations and other salmon life-stages.

Modeling limitations

Models are only approximations of what is actually occurring *in situ*, and there are “no true models in life (Anderson 2008).” For a complex ecosystem such as the Sacramento River mainstem, there are many limitations to the conclusions we can draw regarding the interaction of out-migrating smolts and their environment, and there is always a risk of spurious results when including numerous factors. However, each of the covariates we included were chosen *a priori* and accompanied with a hypothesized biological mechanism, although mechanisms were not directly tested in this study. While we utilized a broad range of factors, there were some very important variables for which we did not have adequate data to include in our analysis. These factors are nonetheless likely indispensable for explaining survival variability. Among others, the three factors that likely would have improved our explanatory power are: turbidity, predator densities/ predation rates and the availability of large woody debris. Turbidity can affect predator avoidance behavior of Chinook salmon (Gregory 1993), and decrease predator foraging efficiency (Sweka and Hartman 2003). Predators have been identified as a major cause of mortality for out-migrating salmonids in other systems such as the Columbia River (Schreck et al. 2006) and Beamesderfer et al. (1996) estimated that Northern pikeminnow alone consume up to 8% of migrants in the Colombia and Snake River system. In the Central Valley, the density of predators can affect the survival of acoustically tagged Chinook salmon smolts (but is also related to flow) (Cavallo et al. 2013). In a study in the Stanislaus River, an estimated 70% of tagged smolts were eaten by predators (Demko et al. 1998). Predation hotspots have been documented within the delta (Grossman et al. 2013), and it is possible that some of the heterogeneity of survival is caused by the accumulation of high predator densities in certain regions. Currently, little information exists regarding the spatial heterogeneity of predator abundance and future outmigration studies should concurrently sample predator densities and predator affects on outmigration success. If predators do play an important role in smolt outmigration survival, as is suggested by the existing literature, we must also consider that all correlations between environmental variables and smolt survival could also be occurring through the pathway of those variables influence on predator movements and densities, and ultimately the probability of smolt/predator encounters. Finally, large woody debris is routinely shown to provide vital habitat for juvenile salmon, yet available data mapping the abundance and distribution of large woody debris in the Sacramento River is currently unavailable. While SRA was used as an approximation for in-water cover in our study, it was not directly measured in the field, and likely does not serve as an appropriate proxy for large woody debris specifically. Juvenile Chinook salmon utilize areas of submerged terrestrial vegetation and woody debris, as well as undercut banks, for protection during high-flow events and as cover from predators (Jackson 1992,

Hampton 1998). Additionally, large woody debris, which has declined significantly as a result of logging and removal to prevent flooding, is important for creating pools, and providing substrate for invertebrate production (Williams 2006). The inclusion of these factors of known importance to juvenile salmon could improve our model fit to survival data, as well as better explain biological mechanisms causing mortality during outmigration.

The residuals from our model comparison plot give us an idea of what the spatial-temporal-covariates model was either over or under estimating. A negative index value implies that the spatial-temporal-covariates models are over-estimating survival. The potential spatial trend in our reaches, whereby adjacent reaches similarly over or under estimate survival, suggests that there may additionally spatial correlations in mortality operating on a slightly larger spatial scale than the reaches delimited in our analysis. The over and under estimations of survival suggest there is another source of mortality in these reaches that we have not accounted for with the covariates we included in this study. This appears to happen more downstream, in the stretch from Ord to Colusa and from China Bend to the Feather River. Thus, while our models allow inferences regarding the relative importance of the environmental covariates we included, as recounted above, we are still missing additional covariates that would explain a greater amount of the variability in survival.

Finally, any discussion regarding the survival of out-migrating Chinook salmon smolts in the Central Valley would be remiss without the context that irrevocable transformations- wrought by hydraulic mining, channelization and the construction of the state and federal water projects- fundamentally altered the natural functioning of the Central Valley ecosystem. Our results, while important for understanding the current habitat realities and requirements of Chinook salmon smolts, should be viewed within the context of severe reductions of historic flow, the elimination of access to spawning grounds and the removal of vast expanses of rearing habitat. Further, our study utilized hatchery-origin Chinook salmon, which may differ from natural-origin smolts in their behavior and vulnerabilities.

Conclusion:

Flow, smolt condition, swim speed and release strategy had the strongest correlation to survival of out-migrating, hatchery origin, late-fall run Chinook during the 2007-2011 water years. The riverine portion of the outmigration corridor receives less attention than the lower delta, and estuary regions. However, for years with high flow, gains in in-river survival can lead to a three-fold increase in total outmigration survival, while survival in the delta and estuary remain the same (Michel et al. 2015). There is limited natural habitat remaining for Chinook salmon in the Central Valley as a result of human activities. Reductions of bank erosion, channelization of river banks and massive reductions of flow resulting from land use changes (Buer et al. 1984) portend an uncertain future for Chinook salmon in the Central Valley. Here, we emphasize the importance of flow for outmigration survival of late-fall run, hatchery origin smolts in the Sacramento River. Individual covariates, specifically batch releases, fish condition and swim speed may additionally improve outmigration success. Certain habitat features, specifically off-channel areas, diversion structures and sinuosity were associated with survival, although to a lesser extent than flow and individual covariates. Although our study utilized hatchery fish, which have limitations as wild fish surrogates, and while the mechanisms through which environmental features affect the ability of Chinook salmon to rear and out-migrate successfully are largely unknown, we emphasize the importance of examining mortality factors on multiple spatial scales and in a holistic context. An individual fish experiences outmigration at a very fine scale, but both reach-specific habitat variables, and those spatio-temporal factors affecting survival on the large basin-scale, are each important considerations in maintaining Chinook salmon populations in the Central Valley.

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RESEARCH

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Real-time nodes permit adaptive management of endangered species of fishes

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Abstract

Background: Currently acoustic tag-detecting autonomous receivers must be visited periodically to download the files of tag detections. Hence, the information about the whereabouts of tagged fishes is not available to make prompt regulatory decisions to reduce entrainment. In contrast, real-time receivers can detect the signal from a transmitter on a passing fish and immediately transmit its identity and time of detection to a website, where they can be viewed on either a computer or cellular telephone. Real-time nodes can aid regulatory biologists in making important decisions. This is a powerful new tool for resource managers and conservation biologists.

Results: We describe a network of real-time, fish-tracking nodes on the Sacramento River, California. Two case studies illustrate the value of the nodes. The first entails detecting the arrival of migrating winter-run Chinook salmon near a water diversion and alerting regulatory biologists to keep the diversion closed to increase the migratory success. The second study involves the detection of green sturgeon at potential stranding sites, alerting biologists of the need to transport them from that site to the main channel of the river so they can continue their upstream migration to their spawning sites.

Keywords: Real-time nodes, Telemetry, Adaptive management, Chinook salmon, *Oncorhynchus*

Background

Individually coded acoustic tags and tag-detecting stationary receivers were developed in the 1980s to describe site fidelity of sharks at coral reefs [1] and seamounts [2, 3]. Although this technology was first used to ascertain the degree of residency of highly mobile species at biotic “hot-spots” in the ocean [4], it has been used even more frequently to determine rates of movement and reach-specific survival of adult anadromous fishes on their upstream migrations to their spawning sites within rivers and juveniles migrating downstream to the ocean [5]. By 2012, there were 378 published studies utilizing this methodology [6].

Autonomous receivers allow the collection of detection data from remote sites without personnel being present. However, the files of tag detections stored in the receivers

must be downloaded periodically, and for this reason equipment failure and the resulting loss of data are not detected until these infrequent visits are made. In contrast, real-time receivers can record the passage of tagged fish and immediately transmit their identities and times of detection at a particular location to a website, where they can be viewed on either a computer or cellular telephone. Regulatory biologists can access the data on the website to help them make important decisions. The viewer can find out whether the receiver is operating by simply checking whether a full is voltage displayed on the website. A real-time node must be distinguished from an autonomous receiver. The former is composed of a variety of receivers, a mooring within the river, a submersible cable, a circuit board, modem, and battery enclosed within a waterproof box, with a cable leading from it to an array of solar cells. This is an emerging capability, which has recently been used in remote area of the ocean to monitor the residence times and depth preferences of four species fishes at a fish aggregating device (FAD) [7].

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An acoustic receiver transmitted behavioral information to via the Argos satellite to a base station in real time.

There is a critical need for real-time detection of fishes in the Sacramento River. There are two runs, winter and spring, of Chinook salmon (*Oncorhynchus tshawytscha*) that are listed as endangered and threatened by the Environmental Protection Act (ESA). Both encounter numerous water diversions as they migrate down the river and through the delta. Furthermore, the green sturgeon (*Acipenser medirostris*) migrate to the upper river to spawn and can become disoriented and stranded within these diversions.

In response to the current extended drought conditions in California, state and federal agency regulators must balance the competing needs of endangered and threatened fish species for limited water resources with the needs of society to use water for urban, industrial, and agricultural demands. During the winter of 2015, water levels in the Sacramento–San Joaquin Delta became very low, and there was pressure to open the Delta Cross Channel (DCC) radial gates to import more water into the interior Delta to be exported to Southern California through the state and federal water diversions. However, at the same time it was imperative that this action would not jeopardize the safe passage of Chinook salmon smolts to the ocean. Perry et al. [8], using coded acoustic tags and an array of tag-detecting receivers, determined route-specific survival of the smolts through the main channel and three routes through the Delta. A higher rate of survival was recorded during December 2006 when the DCC gates were open than during January 2007 when they were closed. Furthermore, Steel et al. [9], using a 2-D tracking array, showed that juvenile salmon were diverted from the main channel of the Sacramento River into the Delta when the gates of the DCC were open. Based on these two studies, regulatory biologists recommended the closure of the DCC gates when winter-run smolts arrive in their vicinity.

In contrast, the Sacramento River during wet years will flow over the Fremont Weir at the northern end of the Yolo Bypass and move in a southerly direction through the bypass avoiding the City of Sacramento [10]. The fast moving waters in the bypass serve as a false attractant to the green sturgeon moving upstream during their spawning migrations. They become trapped at the top of the Yolo Bypass south of the Fremont Weir when the Sacramento River recedes from flood stage, and the elevation of the river falls below the crest of the weir [10]. The California Department of Fish and Wildlife (CDFW) was notified by local fishermen during 2011 that numerous sturgeon were stranded in shallow pools behind the Fremont and Tisdale Weirs after a series of rain storms. The sturgeon were trapped when the flows in the Sacramento

River subsided, consequently lowering the height of the river below the crest of the weirs. A total of 24 green sturgeon were captured, transported, and released into the Sacramento River above the weirs [11].

Fisheries biologists have advocated on an international level using real-time biotelemetry to make management decisions [12]. Real-time information about water temperature and rate of flow in the Fraser River, Canada, is currently being used to make within-season management decisions, and there is keen interest in relating these environmental drivers to the movement rates and reach-specific survival of fishes using similar tag-detection nodes [13]. Some have argued that telemetry is not relevant to conservation [14]. The approach described here alleviates this concern, providing specific examples where biotelemetric data have been used to make important management decisions.

We will first describe the components of real-time nodes that provided real-time reporting of the passage of fishes during the drought in the Sacramento River and Delta in California. Two examples will be given illustrating the value of these nodes. The first involves the two runs of Chinook salmon, winter- and spring-run. Regulatory biologists were alerted during winter 2015 of the arrival of hatchery-raised winter-run Chinook salmon near a water diversion, which was kept closed based on this information. Furthermore, the absence of the detection of tagged spring-run by a real-time node in Sacramento led regulatory biologists to increase the pulse of water coinciding with the release to enhance the survival of the smolts. The second example consisted of alerting rescue crews of the passage of adult green sturgeon (*A. medirostris*) past the Yolo Bypass, a potential stranding site, during their upstream spawning migration during spring 2016.

Methods

Architecture of real-time node

The real-time nodes contained up to three receivers with hydrophones with different frequency sensitivities (Fig. 1). Two of the receivers, which were manufactured by Vemco Ltd (Halifax, Nova Scotia), detected the interval modulated signals from 69 and 180 kHz emitting transmitters. The third receiver, produced by Teknologic Engineering (Edmunds, Washington), detected phase-shifted signals from 416 kHz emitting Juvenile Salmon Acoustic Telemetry System (JSATS) transmitters. The components of the real-time system are shown in Fig. 2. A waterproof bulk-head connector attached to each receiver. Three short cables were molded together into a single 30-m long cable ending in a bulk-head connector (SEACON, Underwater Electrical and Fiber Optic, El Cajon, San Diego) that plugged into a communication



Fig. 1 Picture of pod of receivers (a) and modem and solar cell (b) of the real-time node at the Capitol Freeway Bridge near the city of Sacramento

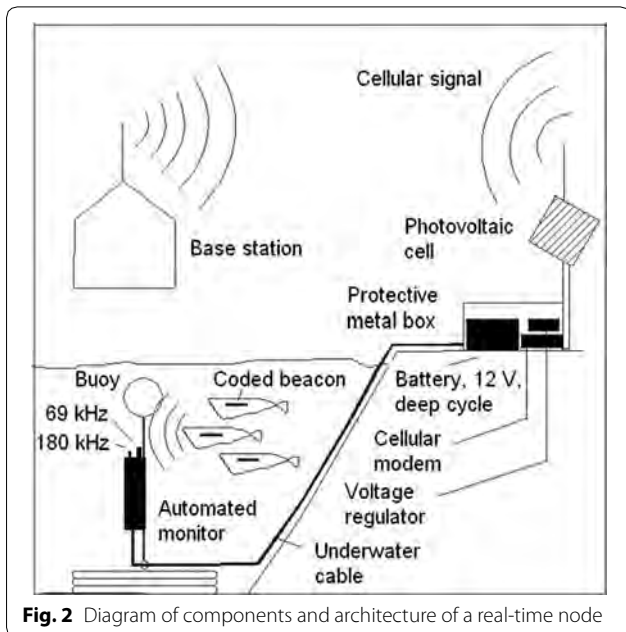


Fig. 2 Diagram of components and architecture of a real-time node

control center (CCC) on shore. The waterproof housing contained of a cellular modem, GPS, and voltage regulator. The first-generation CCC used a cellular modem with integrated GPS manufactured by Netronix Inc. (Philadelphia, Pennsylvania), which transmitted cellular packets to through a cellular tower to an in-house server. The second-generation CCC uses a microprocessor (Raspberry Pi)-controlled cellular modem interfaced both with a GPS and with a voltage regulator (Teknologic Engineering, Edmunds, Washington). It communicates with local cellular towers, delivering cellular packets to the Amazon Cloud. The cellular signals from the CCCs may not be strong enough depending upon proximity to cellar tower, and in these cases a cellular signal booster and an external antenna are connected to the unit to increase signal range. A 40-watt solar panel provided power to the CCC. The first-generation CCC could operate for 24 h without charging; the second-generation could operate 4 or 5 days without charging. Concern should be given when selecting a battery for the CCC—the larger the amp hour rating of the battery, the longer the CCC will operate

without external charge. This is an important consideration because charging may be limited when the skies are overcast, and transmission would stop upon discharge of the batteries in the CCC.

The first-generation real-time, tag-detection system was an expansion of “Environet,” a website devoted to the display of environmental data hosted by Netronix Inc. This site can be accessed at <https://environet.com> by entering the following email address: mjthomas@ucdavis.edu and password “getdata.” The second-generation real-time, tag-detection system was developed by the biologists of the Biotelemetry Laboratory in conjunction with the engineers of Teknologic Engineering and named the Biotelemetry Autonomous and Real-Time Database (BARD). To access this site, use the following address: <http://sandbox5.metro.ucdavis.edu/landingmap>.

Following is a description of the steps taken in data acquisition and processing by both the first- and second-generation real-time detection nodes (Fig. 3). The date, time, and identify of each tag detected are stored in the memories of the three receivers. Environet polls the receiver every minute for the detections recorded, whereas the BARD can poll the receivers at any time interval. A fundamental difference between the two systems is that the former assigns a GPS time stamp every minute to each tag-detection event, while the latter takes the time stamp with sub-minute temporal resolution from the receiver. It is important to have sub-minute temporal resolution for JSATS detections because these transmit phase-modulated bursts every 5 s, and error checking involves determining of six or more packets occur sequentially—and this likely occurs within a minute. Environet could provide the same minute time stamp to as many as 24 detections occurring at different times. The low temporal resolution to data acquisition at Environet is due to the large volume of data processed by the system, hosting data acquired from many nodes worldwide. Metadata taken from the JSATS receiver and CCC are also paired with the detections in the second-generation node. The data in the Netronix CCC are transmitted via modem to the cellular tower and written to the Netronix server. The uploaded information is provided in table and graphic format on the Environet website. The interface extracts from the server information based on monitor location and date range. The data transmitted from the Teknologic modem through the cellular tower to the Amazon cloud server. The Cloud is periodically queried using Python, and the data files are assimilated into the SQL database. The BARD web interface permits both tabular and graphic display of the data.

The advantages and disadvantages of the two systems are given in Table 1. The BARD has greater temporal resolution to tag detection. If Environet does not operate

or reception is lost to the node, all of tags detected over the intervening period of time are given the time stamp when the website goes online again. The time resolution of the second-generation node is greater since the time stamps are those of the receivers not the Netronix cellular server. The space on the Amazon cloud exceeds that of the Netronix server, and the latter is limited to 20 detections per minute, whereas the BARD can upload many more detections per polling. Finally, a convenience to the BARD is that a list of specific IDs can be entered into the website and the detections will be displayed with color coding for the different nodes when detections are plotted over time. Again, the ability to display multiple locations by the BARD in contrast to the single location of Environet is a plus for the former node.

Website of real-time node

The home page of the BARD website displays the locations of all of the monitors in the Sacramento–San Joaquin watershed (Fig. 4). You can zoom in on particular areas by using the mouse wheel or the plus symbol in the lower right of the map. If one positions the cursor over a symbol, the name of the location and geographical coordinates of the receiver will be displayed with river kilometer (from Golden Gate span). The color of the symbol indicates the types of receivers present on the nodes, 69, 180, or 416 kHz, the shape, circle or triangle, whether it is autonomous or real time. Note the triangle, indicating the real-time monitor at the Capital City Freeway Bridge leading to the city of Sacramento slightly above the cluster of receivers in the Delta. A rectangle can be drawn around a particular area, and then, a button become available in the upper left just above the map. If it is selected, a page is displayed with the recent detections for those monitors within the area.

If you select the tab, “RECENT DETECTIONS,” on the site navigation panel, this will bring up a page, which permits you to specify a range of time and choose locations by clicking on them once (Fig. 5). A bar to the right of the window enables you to select the receivers, from which detections are to be displayed both in a table and in a graph. Once you select locations, they will appear in the box in the right. These lists of detections at particular locations can be saved and the names of the lists shown below the selected locations list. Below these two menus are displayed a plot of detection events and a table of the detection events. The total number of detections can be plotted over specified time period. Shown is a plot of the detections from three receivers, located at Antioch Bridge, Benicia Bridge, and the North Fork of the Mokelumne River time of year in Pacific Standard Time (Fig. 5). A stacked histogram is displayed, in which the number of detections at each location is specified by

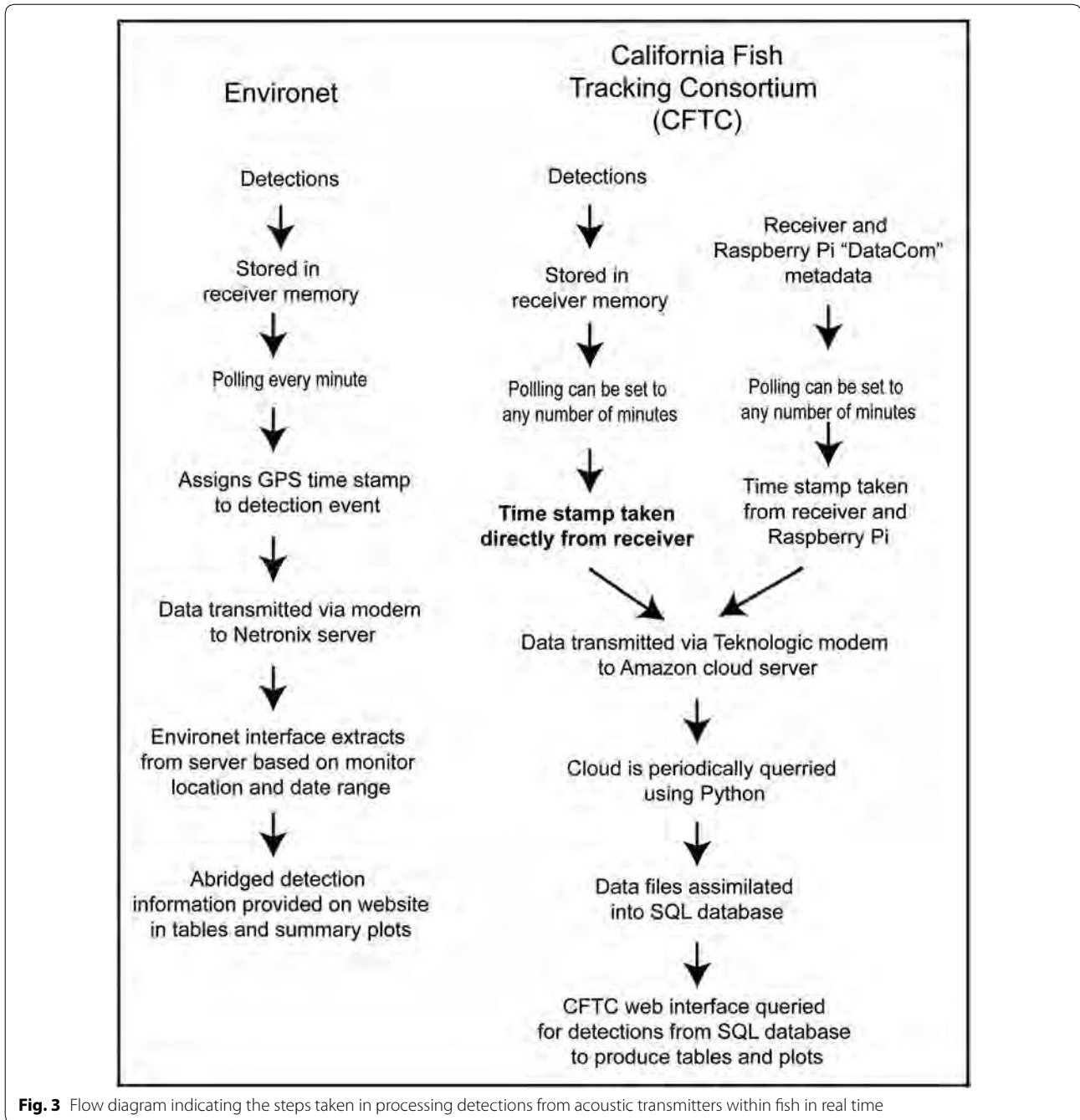


Fig. 3 Flow diagram indicating the steps taken in processing detections from acoustic transmitters within fish in real time

a different color with the height of the cumulative total being the total count of detections at all three sites.

If you select “TRACK A FISH” on the site navigation panel, more can be learned about the movements of tracked fish (Fig. 6). If you enter a date range and a list of tags on individual fish, the identities of tags with detections are displayed as buttons below the “Results” header. If a particular tag of interest is selected, the detection events will be listed in chronological order at the different

receivers detecting the traveling fish. Each record displays the date and time of detection along with the name of the location detected. To the right of this table is a map that displays the track as a series of line segments and the locations detected with “balloons.” Note that there is an “S” at the start of the track and an “E” at the last location detected. Below is graph of the locations of the fish over time, given in river kilometer. The graph shows the movement of tag 4331, a green sturgeon carrying a 69-kHz

Table 1 Advantages and disadvantages of the first- and second-generation real-time stations

Environet	Biotelemetry Autonomous and Real-Time Database (BARD)
Detection times stamped by node GPS (m/d/y hh:mm)	Detection times stamped by receivers (m/d/y hh:mm:ss:ms)
If offline, all detections are stamped with time of next successful polling	If offline, all detections get original time stamp from receiver at time of detection
Polling limited to minute polling rate due to cellular node time stamping	Greater temporal resolution, since time is independent of cellular node
Netronix server space limited	SQL space permits 4 tBytes; “unlimited” space with Amazon cloud
Limited to 20 detections per minute	Unlimited detections per polling interval; 196 kByte limit, which equals about 2000 detections per polling
Web interface not adaptable	Web interface with SQL database is adaptable to visualize any query
Displays single monitor location	Displays multiple locations for comparison
Unable to input a list of unique IDs	Can provide list of specific IDs
	Current database, 101 gBytes with 52.7 million detections



Fig. 4 Home page of Biotelemetry Autonomous and Real-Time Database (BARD) website that displays the detections of fish carrying acoustical tags from both autonomous and real-time nodes in the Sacramento–San Joaquin watershed. The *circular symbols* indicate autonomous nodes; *triangles* designate the real-time nodes. The frequencies of receivers are indicated by *orange* for a node with only a 69-kHz-sensitive receiver, denoting the addition of a 180-kHz-sensitive receiver, a *green color* informing of the presence of a JSATS receiver

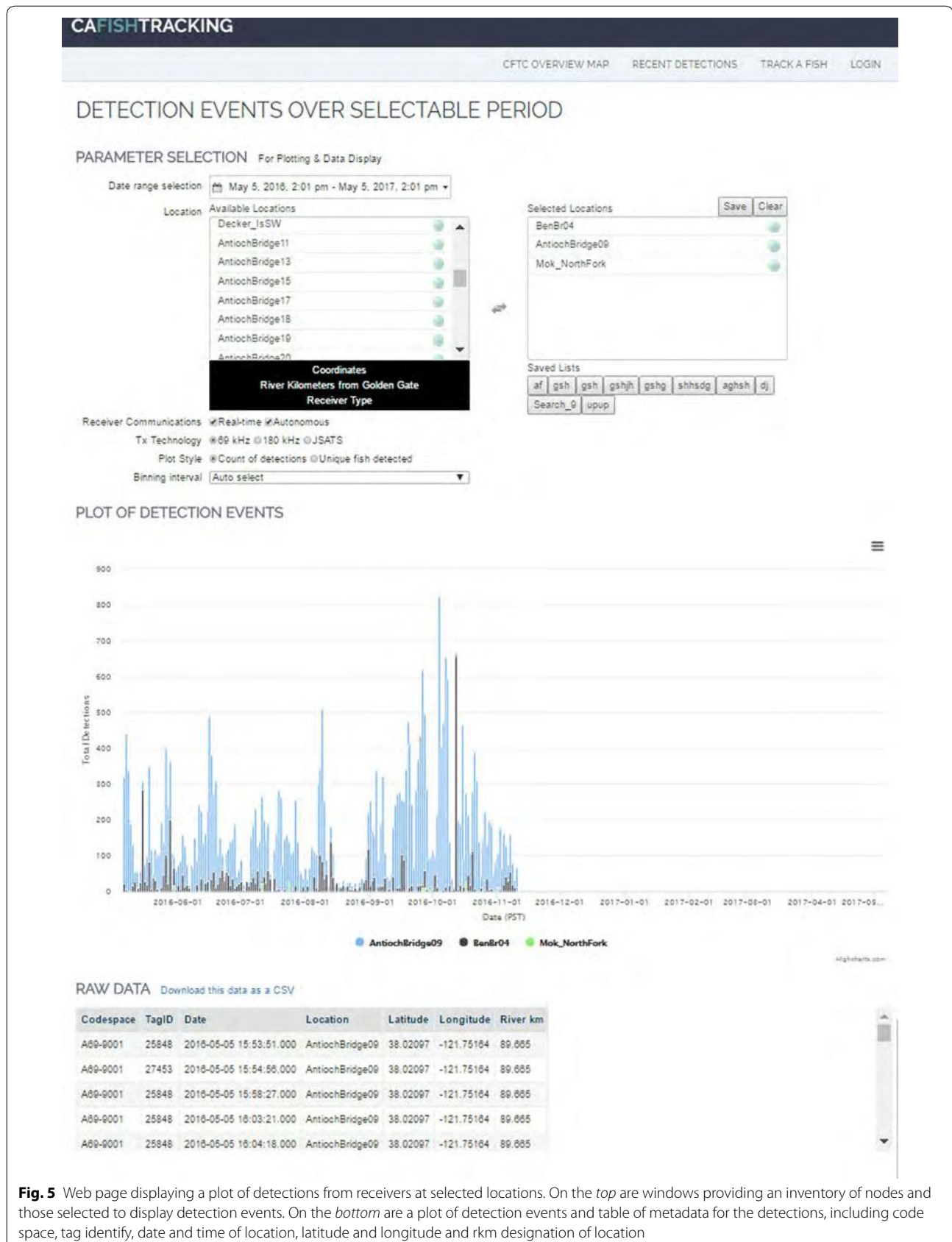


Fig. 5 Web page displaying a plot of detections from receivers at selected locations. On the top are windows providing an inventory of nodes and those selected to display detection events. On the bottom are a plot of detection events and table of metadata for the detections, including code space, tag identify, date and time of location, latitude and longitude and rkm designation of location

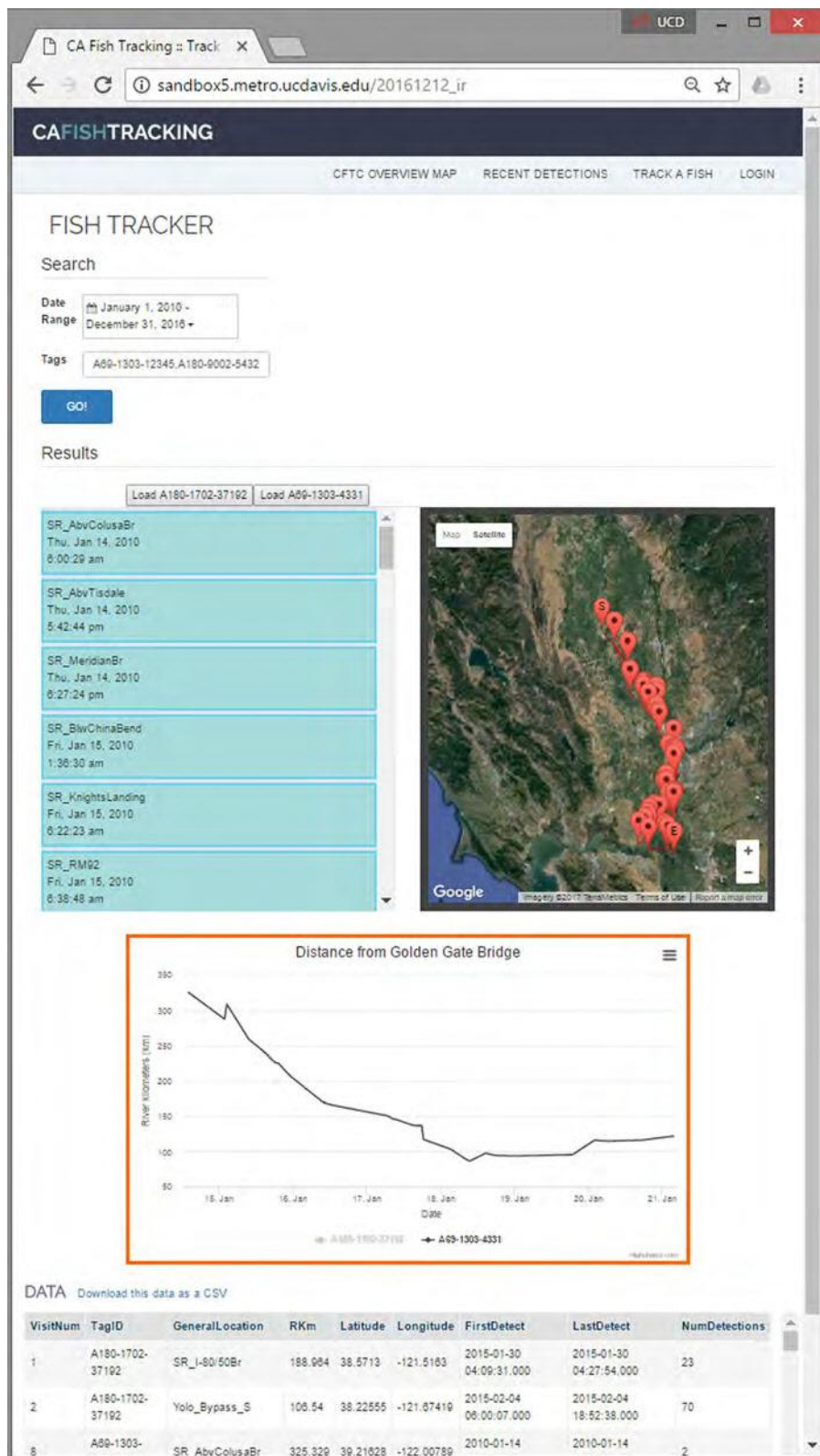


Fig. 6 Web page displaying a map with the location indicated where fish have been detected by receivers. Note that the letter “S” indicates the start of the track and the letter “E” the end of the track. At the left of the map is a table listing entries in chronological order giving the identity of each tag detected with the date and time of detection as well as the location of detection

beacon, beginning on the 13th of January as it migrated downstream from its summer and fall spawning region at 340 rKm to arrive at the Delta at the 18th the confluence of the Sacramento River and the Delta. It stayed in this region through January 21, 2010. The specific information for this tag is displayed under visit number 8 on the table below the graph.

Further development of this telemetric portal is ongoing. We would like to add additional capabilities. We will be deploying an environmental sonde from Eureka Sensors, which has sensors of temperature, salinity, pH, dissolved oxygen, turbidity, and chlorophyll A. It is our intention to eventually display these data upon the website. Also addition diagnostic metadata will be displayed such as the voltage of the communication control center in order to know that the battery is charged and the solar panel is connected and functional.

Real-time node geographical distribution

The staff of the Biotelemetry Laboratory maintains the array of autonomous and real-time receivers as a service for many researchers in private and state universities, consulting companies, and state and federal agencies (Fig. 7). Two hundred and five receivers (VR-02, Vemco Ltd, Halifax) are distributed at 50 locations in the Sacramento–San Joaquin watershed. The receivers are deployed at 20-km intervals along the length of the Sacramento River, stretching from the confluence of Battle Creek to the Delta. Receivers are distributed throughout the Delta at water-way junctions. There have been cross-bay arrays at the Carquinez, Benicia, and Raccoon Straits as well as across the Richmond, Bay, and Golden Gate Bridges. Scientists from these organizations can not only access detections of their fish from a large array of autonomous monitors by contacting the database manager at the Biotelemetry Laboratory, but also obtain records of the detection of fish at the real-time nodes by logging on to Environet or BARD. There is an Array Maintenance Committee, composed of one scientist from each organization that meets twice annually. The Biotelemetry laboratory provides an update of the status of the array at these times, and the committee can request the deployment of additional receivers, either autonomous or real time in nature.

During the winter of 2015, six real-time nodes were deployed along with the much larger array of autonomous receivers (see red triangles, Fig. 7). Five of the real-time receivers were deployed to detect the passage of winter- and spring-run smolts on their downstream migration. The real-time nodes at Tisdale, Sacramento, Hood (see nodes 4, 3, and 2), would detect when salmon smolts were approaching the location of the DCC (see Node 1, Fig. 8). The station at Middle River is located

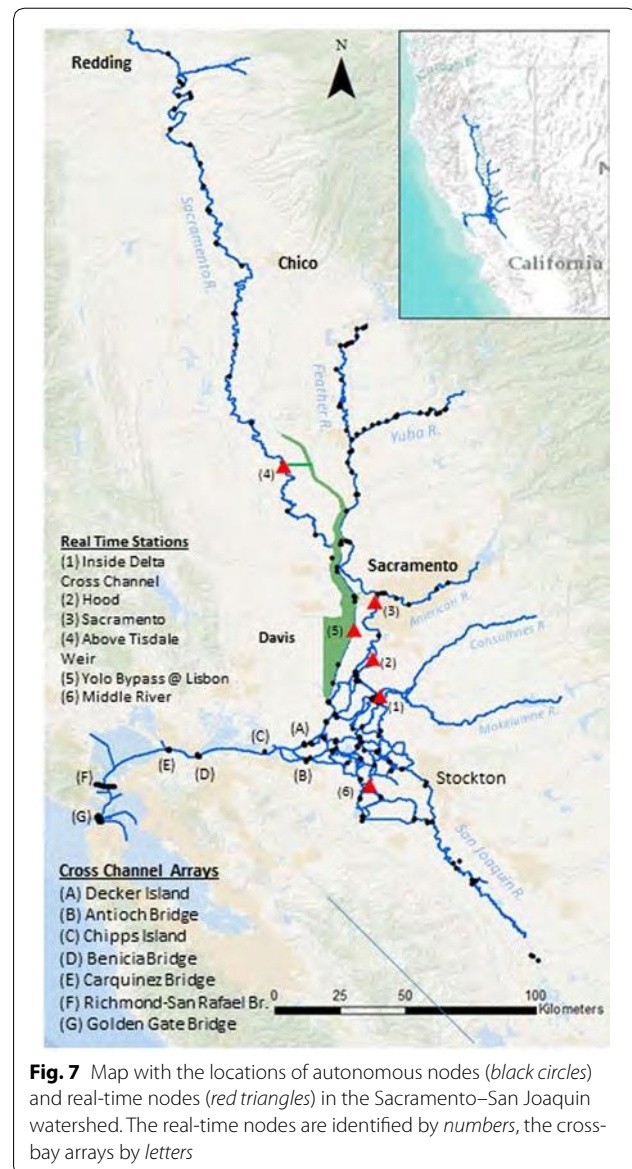


Fig. 7 Map with the locations of autonomous nodes (black circles) and real-time nodes (red triangles) in the Sacramento–San Joaquin watershed. The real-time nodes are identified by numbers, the cross-bay arrays by letters

downstream of the two major state and federal water export facilities [State Water Project (SWP) and Central Valley Project (CVP)] that pump Delta water to the southern San Joaquin Valley and Southern California (see node 6). Net water movement is typically “upstream” in this tidally affected area under the influence of the export actions and tides, moving toward the SWP and CVP facilities. This node was deployed to detect individuals approaching the SWP and CVP. Movement rates of juvenile winter-run Chinook salmon could be calculated based on the difference in the time of arrival at the three real-time stations on the Sacramento River above the DCC (Tisdale, City of Sacramento, and Hood to estimate when these smolts would arrive at the two diversions and

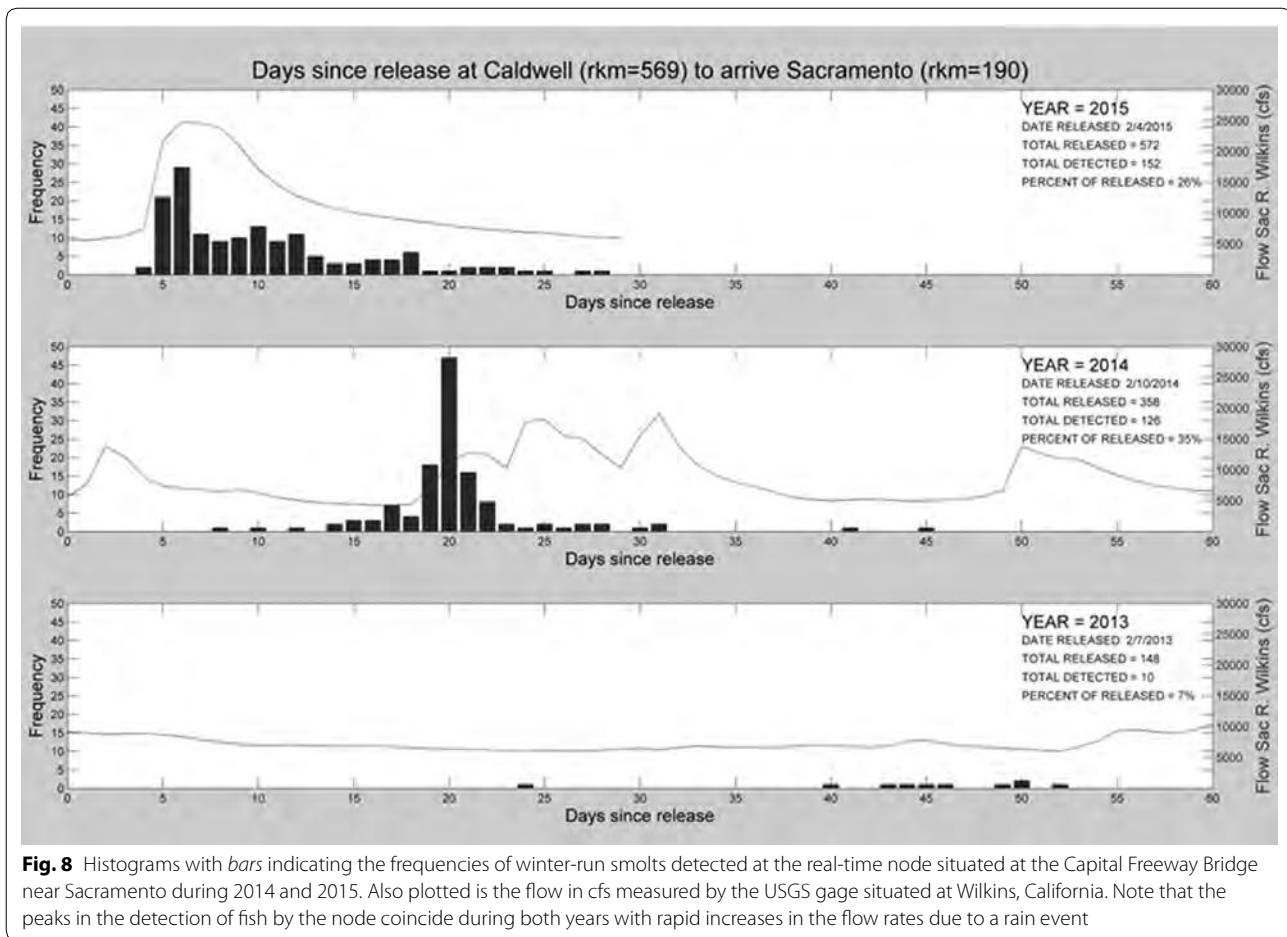


Fig. 8 Histograms with *bars* indicating the frequencies of winter-run smolts detected at the real-time node situated at the Capital Freeway Bridge near Sacramento during 2014 and 2015. Also plotted is the flow in cfs measured by the USGS gage situated at Wilkins, California. Note that the peaks in the detection of fish by the node coincide during both years with rapid increases in the flow rates due to a rain event

become entrained within them. A sixth real-time node was deployed in the Yolo Bypass to detect whether any green sturgeon might become stranded below the Fremont Weir.

During the winter of 2016, 16 real-time nodes were established at a ten sites in the watershed. On the Sacramento River upstream to downstream, paired nodes were set up at Colusa, Tisdale Weir, Knights Landing, Feather River, The I-80 and Tower Bridges near the city of Sacramento. The last two paired nodes were less than a kilometer apart, permitting a final determination of probability of detection. Those winter-run that migrated this far downstream were detected at both paired nodes, providing a 100% detection efficiency, and this facilitated the estimation of the rate of survival between the successive paired upstream real-time nodes. Arnold Ammann gave sixteen biweekly updates with the percentage of fishes reaching the successive pairs of nodes downstream of the release site ending on March 3, 2016. These nodes are currently being upgraded to the second-generation architecture.

Results

We will now present two examples where information about tagged fish from the real-time nodes proved useful to resource managers. It is not our intent in this communication to present the detailed scientific results from the studies of these fish but to illustrate how the real-time detection of fish can be used by managers in making regulatory decisions. This same approach could be used with terrestrial species that aggregate at sites.

Detecting winter- and spring-run smolts in real time

The timing of the arrival of the smolts at the gates depends on river conditions. These can change rapidly, and the timing of the changes varies among years. The nodes enabled the gates of the DCC to be closed prior to the arrival of fish in 2015. In early February 612,056 hatchery produced winter-run Chinook salmon were released from the Livingston Stone National Fish Hatchery into the upper Sacramento River at Caldwell (rkm = 569) near Redding, California, in advance of an approaching winter storm. There were two releases of

fish, one on the 4 and another on 6 February. Acoustic tags were placed within the body cavities of a subsample of these fish—250 fish in the first release and 322 fish in the second release. The subsamples of tagged fish gave resource managers an additional way of tracking the downstream movement of the larger hatchery releases in addition to the fyke nets operated within the river. Arnold Ammann of the National Marine Fisheries Service (NMFS) queried the real-time nodes at Tisdale, Sacramento, Hood, and DCC real-time nodes daily to provide updates of the number of tagged smolts that were detected at these sites. The salmon winter-run smolts were first detected at Sacramento on February 8, 2015, 4 days later than the first release date. The peak numbers of fish passed by Sacramento on 9 and 10 February with steadily decreasing numbers passing over the next 24 days (Fig. 9). A total of 50 tagged fish were detected during those 2 days, which coincided with a 20,000 cfs increase in the flow in the Sacramento River from 5000 to 25,000 cfs, measured at the USGS flow gage at Wilkins, California. One hundred and fifty-two smolts were detected of the 572 tagged smolts released at Caldwell at rkm 569. Ammann alerted regulatory managers in Sacramento on 8 February, only 4 days after the first release, that tagged winter-run smolts had been detected at the Sacramento real-time node, not far from the DCC that connects the Sacramento River with the Delta.

The regulatory biologists did not anticipate the rapid arrival of the hatchery fish at the Sacramento. The winter-run hatchery releases during 2014 took a much longer

time to reach Sacramento. These smolts were released at Caldwell on February 10, 2014, in anticipation of a pulsed flow that increased 5000 cfs from 5000 to 10,000 cfs measured 2 days later. However, the peak of 48 smolts did not occur until 20 days on March 2, 2014, coinciding with a second 6000 cfs increase from 4000 to 10,000 cfs. Based on this prior information, resource agencies planned to open the gates throughout February to divert water into the interior Delta to improve water quality. The agencies believed that the fish would take 3 weeks to a month to reach the DCC gates. The prompt arrival of winter-run smolts at Sacramento on February 6, 2015, convinced the agencies to keep the DCC closed through March 2015, reducing additional mortality to the 2015 hatchery winter-run releases due to diversion into the Delta. During winter 2016, we deployed 16 real-time nodes at a ten sites in the watershed. On the Sacramento River upstream to downstream, paired nodes were set up at Colusa, Tisdale Weir, Knights Landing, Feather River, The I-80 and Tower Bridges near the city of Sacramento. Ammann gave sixteen biweekly updates with the percentage of fishes reaching the successive pairs of nodes downstream of the release site ending on March 3, 2016.

Real-time reporting proved useful also in monitoring downstream migration of the spring-run smolts during 2015 and 2016. The Feather River Fish Hatchery released smolts at two locations, Gridley and Boyds Pump Boat Ramps, on the Feather River late March 2015. A subsample of 75 acoustically tagged fish accompanied each release of hatchery fish to permit immediate monitoring

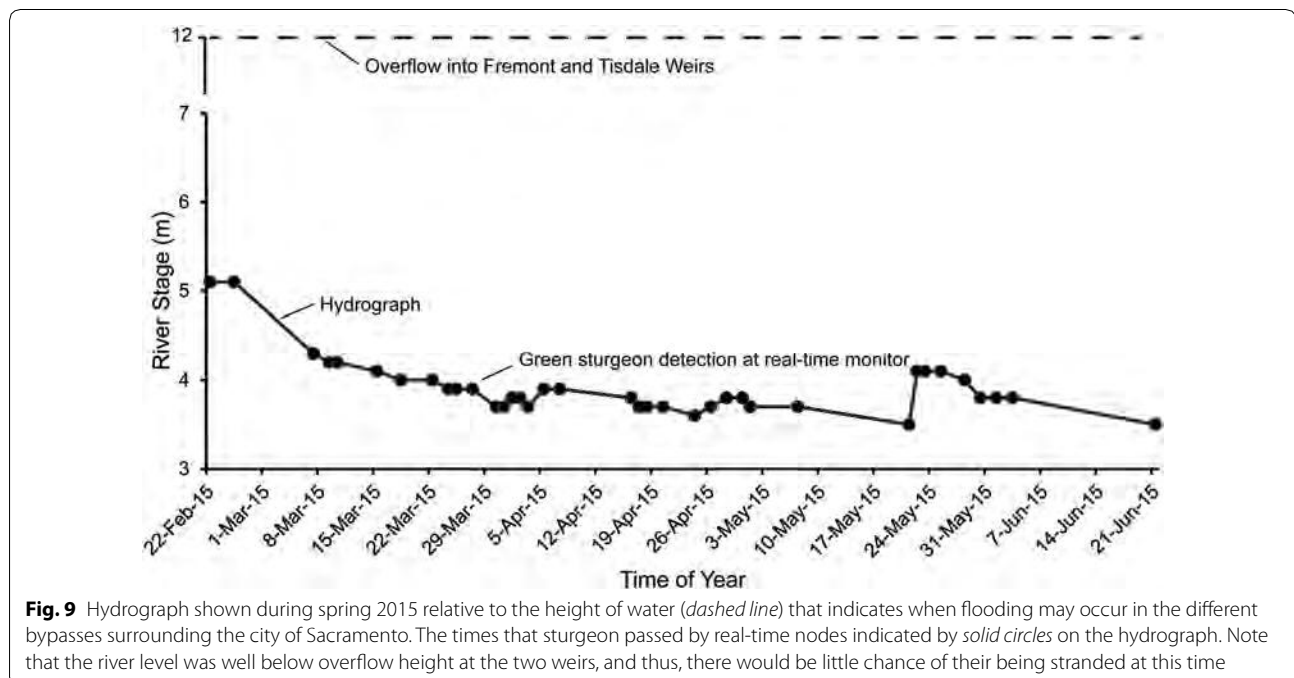


Fig. 9 Hydrograph shown during spring 2015 relative to the height of water (dashed line) that indicates when flooding may occur in the different bypasses surrounding the city of Sacramento. The times that sturgeon passed by real-time nodes indicated by solid circles on the hydrograph. Note that the river level was well below overflow height at the two weirs, and thus, there would be little chance of their being stranded at this time

of their downstream migration success. A supplemental pulse of water of 440 cfs was released from Oroville Reservoir to stimulate downriver migration. Only one tagged individual from the upstream release at Gridley and seven from the downstream release site at Boyds Pump, or 5.3% of the total, reached the single real-time node near the city of Sacramento (Arnold Ammann, NMFS, unpub. data). The Feather River Hatchery Oversight Team decided to release the rest of the hatchery-raised spring-run on 2 April rather than the traditional mid-April date and to accompany them with a larger release of water of 1400 cfs (Jeffrey Stuart, NMFS, pers. commun.). A total of 12 (8.0%) of the 150 tagged smolts released at the two sites were detected at the Sacramento node (Arnold Amman, NMFS, unpub. data.). During the El Niño conditions of spring 2016, 54 (27%) of 200 tagged smolts were detected at the Sacramento nodes (Colin Purdy, CDFW, pers. commun.). These smolts not only exhibited higher migratory success but also moved downstream faster than smolts during spring 2015. This higher survival and faster movement coincided with the higher flows in the Sacramento River during 2016.

Detecting green sturgeon in real time

Researchers in Washington and California have pleased long-term coded tags beacons within the abdominal body cavities of nearly 400 Green Sturgeon over the past 10 years. The information on sizes, weights, timing of tagging and release are contained in the California Fish Tracking Consortium database. The batteries with lives ranging from 3 to 10 years have made it possible to monitor repeated upstream migrations of green sturgeon in the Sacramento River system. Adults return to spawn in the Sacramento River approximately every 2–5 years (unpub. data, Michael Thomas).

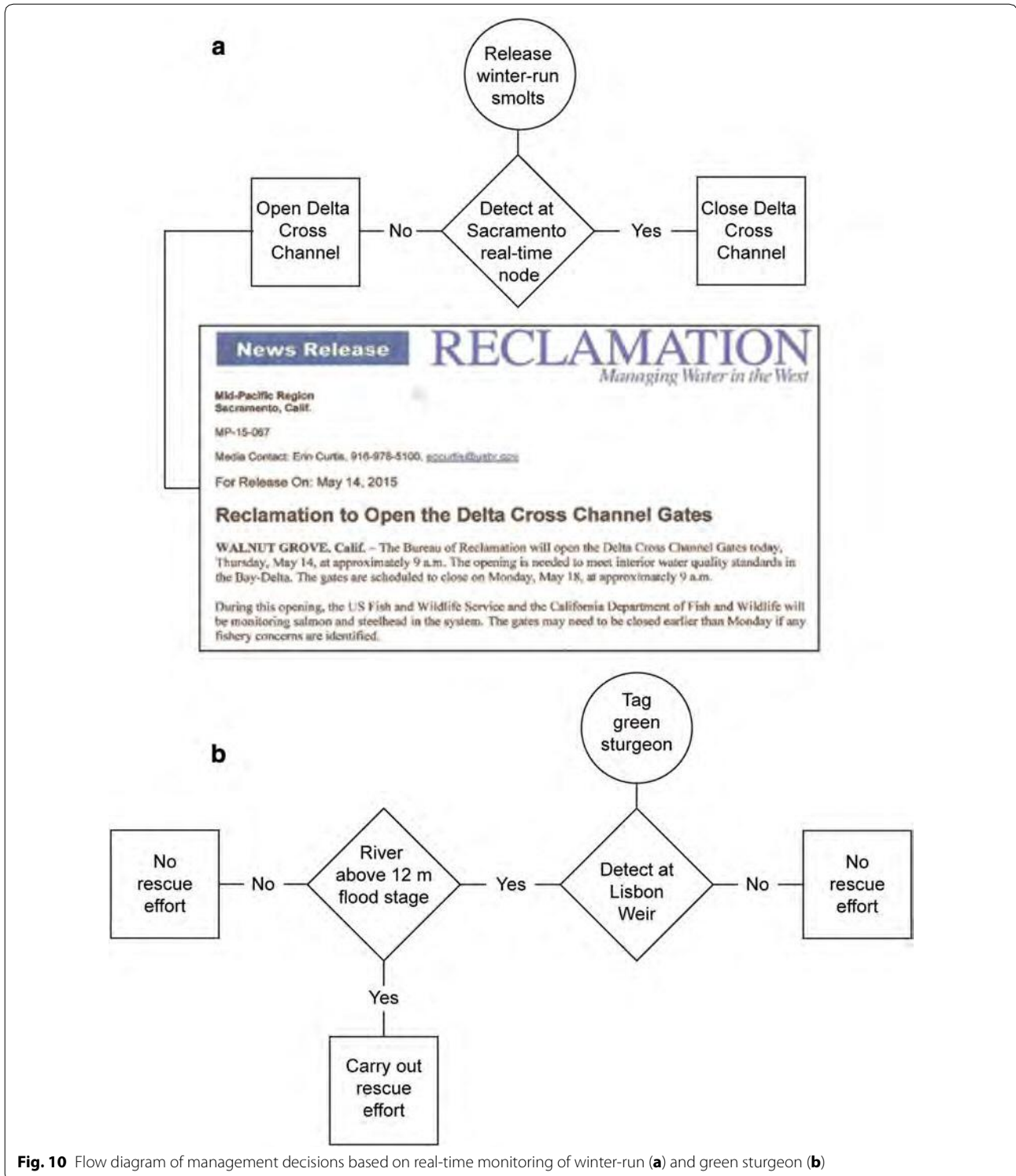
This success led CDFW to support the development of the real-time node. One real-time node was immediately situated in the Yolo Bypass downstream of Lisbon Weir and one on the main stem of the Sacramento River downstream of the Tisdale Weir, where green sturgeon might strand (nodes 5 and 4 in Fig. 5). These two nodes enable CDFW now to better respond to sturgeon stranding at the two bypasses. The nodes detected 23 green sturgeon during their spawning season from late February to late June 2015. The passage of tagged fish are indicated by solid circles superimposed on a hydrograph of the river stage, or height in meters (Fig. 5). The river height, measured at the Fremont gage, ranged from 5.2 m from the end of February to 3.5 m by the end of June, well below the 12 m height that would result in flooding. Regulatory biologists concerned with the protection of this species were given weekly alerts by Matt Pagel, the

Database Manager in the Biotelemetry Laboratory, during the spawning season.

Discussion

The winter-run race is classified as endangered under the Endangered Species Act. Winter-run adults migrate up river from December through July, with a peak during the period between January and April. Adults hold in a section of the Sacramento River between Keswick Dam and approximately the location of the Red Bluff Diversion Dam until they commence spawning. They spawn between late-April and mid-August, with a peak in June and July as reported by CDFW annual escape-ment surveys. Young of the year winter-run Chinook Salmon begin to emigrate downstream from their natal river reaches in fall into the lower Sacramento River and typically reach the area of the DCC gates starting in late winter (mid-January and February). Elevated river flows associated with storm events stimulate this downstream movement.

The decision to keep the DCC closed was based upon information passed on to the managers of the state and federal resource agencies, including the Assistant Regional Administrator of the California Central Valley Office of National Marine Fisheries Service (NMFS). NMFS is responsible for the protection of anadromous species listed under the ESA in the Sacramento River. During the drought operations in the winter of 2015, the resource managers from the different state and federal agencies met frequently to coordinate operations of the water infrastructure of California to provide water for both public and environmental demands. These managers cooperated to ensure safe fish passage past federal, state, and private water diversions and manage appropriate releases of water from dams to support fisheries. A flow diagram is presented showing the consequences of either detecting juvenile winter-run at the Sacramento real-time node or not detecting them (Fig. 10a). In the first case, the resource agencies recommended that the Delta Cross Channel remained closed based on the detection of hatchery-raised, winter-run smolts at the Sacramento node. However, later that year, the gates were opened on May 14, 2015, to May 18, 2015, “to meet the water quality standards in the Bay-Delta,” a week earlier than would have been allowed under present operating criteria. The resource managers determined that the level of risk to listed fish was sufficiently low to allow flexibility in the DCC gate operations. The alerts were provided on a daily basis during 2015–2016. After getting daily updates, Maria Rea, Assistant Regional Administrator, NMFS, wrote the following email to emphasize the importance of real-time reporting.



Thank you so much for all your daily reporting. I want to let you know how helpful it is to get this kind of “real-time” information, as the Directors of the five agencies continue to meet by conference call

every morning at 8 am to go over all information and decide on the best balance of water exports and fish protection for the day. ...I really appreciate you accommodating the management needs in the con-

tinuing drought (Maria Rea, pers. communication).

In conclusion, real-time information about the whereabouts of winter- and spring-run smolts is enabling resource managers to make more timely decisions with regard to the closure of a water diversion and the magnitudes of supplementary water releases.

The nodes enabled rescue workers to know when to search for stranded green and white sturgeon. The process that leads to rescuing sturgeon stranded downriver of major weirs is also shown in a decision tree (Fig. 10b). In periods of no or negligible risk, search efforts for stranding sturgeon can be curtailed as in 2015. Alternatively, the CDFW can quickly begin monitoring and performing rescue efforts during years or months when flood stage is reached, weirs are overtopped, and tagged fish are detected entering the lower ends of the bypasses. In addition to pre-rescue monitoring, the array permits agency biologist to get routine updates on whether the rescued sturgeon move upstream or downstream in the Sacramento River. The value of this information can be appreciated in an email sent by Mr. Colin Purdy, the lead biologist on the rescue team to Mr. Pagel, the Database Manager in the Biotelemetry Laboratory, who furnished biweekly updates.

Thanks again for these detailed updates and apologies for the confusion on metadata. The white sturgeon rescued on 31 March 2016...is moving downstream (~40 river miles). We believe this was a spawned out female so this downstream behavior seems appropriate. I am always glad to get reports of fish moving around after being rescued as it shows they survived and our efforts were not in vain (Colin Purdy, pers. commun.).

The two case studies presented within illustrate a real success story of researchers from the resource agencies working closely with researchers in academia to utilize conservation-based information in protecting listed species. In the first case, the information was rapidly transmitted to the regulatory division of NMFS, which quickly disseminated it to the other federal and state resource agencies for timely management decisions. In the second case, the information was relayed to the lead biologist of a sturgeon rescue crew at CDFW. This real-time technology permits resource managers to take an adaptive approach to balancing the public's need for water with the needs of migratory fishes. The success of the case studies presented here relied heavily on a mutual cooperation among researchers and resource managers during this period of drought in Central California.

Authors' contributions

APK obtained the funding, oversaw the development and deployment of the real-time nodes, and wrote the paper. AJA provided the detection data for winter- and spring-run Chinook smolts. TVA led the team deploying and maintain the array of real-time detection nodes. RDB deployed and maintained the real-time monitors. MDP maintained a SQL database of tag detections, provided weekly updates of sturgeon detections during their spawning season, and edited a draft of the paper. MJT developed a prototype real-time node working closely with engineers from VEMCO-Americx, Netronix, and Teknologic Industries, and helped in their deployment and maintenance. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The records of spring-run Chinook smolt detections plotted in Fig. 8 are available from Mr. Arnold Ammann, Research Scientist at the Southwest Fisheries Center, Santa Cruz. The records of green sturgeon presented in Fig. 9 are available from Mr. Matthew Pagel, Database Manager at the Biotelemetry Laboratory at UC Davis.

Consent for publication

All of the authors consent to this role in the preparation of this article.

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Statement of ethics approval

The implantation techniques used for JSATS beacons used in this study were reviewed by the veterinarian staff of UC Davis and are covered by UC Davis Animal Care Protocols #16819, "Migration and Movement of Fall and Spring Run Chinook Smolts" and #18744, "Spring Run Chinook Salmon Smolt Movement in the San Joaquin River."

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UNIVERSITY OF CALIFORNIA

SANTA CRUZ

**OUT-MIGRATION SURVIVAL OF WILD CHINOOK SALMON
(*ONCORHYNCHUS TSHAWYTSCHA*) SMOLTS FROM MILL CREEK
THROUGH THE SACRAMENTO RIVER DURING DROUGHT
CONDITIONS**

A thesis submitted in partial satisfaction
of the requirements for the degree of

MASTER OF SCIENCE

in

OCEAN SCIENCES

by

Jeremy Notch

June 2017

The thesis of Jeremy Notch
is approved:

Professor Christopher Edwards,
Chair

Professor Eric Palkovacs

Nate Mantua, Ph.D.

Tyrus Miller
Vice Provost and Dean of Graduate Studies

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ABSTRACT

OUT-MIGRATION SURVIVAL OF WILD CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) SMOLTS FROM MILL CREEK THROUGH THE SACRAMENTO RIVER DURING DROUGHT CONDITIONS.

by

Jeremy Notch

Once emerged from the gravel after being spawned in natal streams, Chinook salmon spend many months rearing and growing in freshwater before undergoing smoltification and out-migrating to the ocean. This relatively short period of time is considered to be the most vulnerable and dangerous phase in the life cycle of a Pacific salmon. It is during this phase when smolts navigate around many anthropogenic structures and experience environmental stressors while making their way to the ocean. In California's Central Valley, the few remaining wild populations of Chinook salmon (*Oncorhynchus tshawytscha*) out-migrate through a highly modified riverine and estuary landscape characterized by leveed banks, altered flow and temperature regimes, transformed food webs, and limited floodplain and rearing habitat. Juvenile salmon smolts migrate through these landscapes within a relatively short period of time, requiring them to quickly adapt to changing water conditions and habitat types. Understanding the survival rates of wild smolts from source tributaries to the Pacific Ocean is essential in protecting and restoring these

populations from the low abundances currently observed. When faced with drought conditions out-migrating smolts experience low flows, elevated water temperatures and high densities of predators while out-migrating to sea. In order to assess smolt survival during drought conditions in late spring (April-May), 304 wild smolts were acoustically tagged and tracked from Mill Creek (Tehama County) to the Pacific Ocean between 2013 and 2016. Total outmigration survival to the ocean was 0.3% during these years, with only one fish making it to the Golden Gate and the Pacific Ocean. These survival estimates are some of the lowest ever recorded for salmon out-migrating to the Pacific Ocean, with much of the mortality occurring within Mill Creek and the Sacramento River. Cumulative survival through Mill Creek (rkm 452-441) was 68% (± 12 S.E.), and cumulative survival through the Sacramento River (rkm 441-203) was 7.6% (± 16 S.E.) These low survival rates are likely attributed to low flows in Mill Creek and the Sacramento River resulting from critically dry winters between 2013 and 2015, which were reduced even further by water diversions for agriculture in both Mill Creek and the Sacramento River. During periods of higher flow in 2016 survival rates dramatically increased, suggesting that more water in Mill Creek and the Sacramento River is necessary to improve in-river smolt migration survival during the late spring.

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Chapter 1

Introduction

California's Central Valley historically supported some of the largest runs of Chinook salmon in the world. Native American tribes throughout the region relied heavily on these fish, and harvested an estimated 8.5 million pounds annually (Yoshiyama et al. 1998). Similar catch rates were documented by commercial fishing fleets based in San Francisco during peak operations in the mid-late 1800's. The engine behind these enormous runs was the network of rivers draining off the Sierra Nevada mountain range, as well the productive marine waters of the Gulf of the Farallones and the northeast Pacific Ocean. Salmon historically had unimpeded access from the ocean to headwater streams which were fed by cold water from melting springtime snowpack and abundant springs, providing optimum spawning and rearing conditions nearly year-round. Four runs of Chinook salmon - spring, fall, late-fall and winter - evolved within Central Valley watersheds to take advantage of the unique hydrology and habitat available in the Sacramento and San Joaquin River basins. The timing of freshwater entry from the ocean gives each run its name, which have evolved distinct life history strategies to exploit the diverse habitat available in the Central Valley.

Spring-run Chinook salmon enter freshwater during March-June as sexually immature adults, and time their upstream migration during periods of high water discharge from snowmelt. Once reaching elevations > 2,000 ft. they over-summer in deep pools where they mature before spawning in the early fall. Juveniles emerge

from gravel nests approximately 2 months after being spawned and feed off their yolk sac before foraging in the stream as fry. Juvenile spring-run out-migrate from natal streams as fry (≤ 55 mm), parr (>55 to ≤ 75 mm), smolts (>75 to ≤ 100 mm) and yearlings (≥ 100 mm). This range of sizes diversifies the timing of downstream migration and reduces the chances of collapse of a particular life stage in the event of poor survival conditions for a given life-history strategy under varying climate and related freshwater habitat conditions while also helping to avoid density-dependent mortality (Williams 2006). Before entering the ocean all juvenile salmon must begin smoltification; a process that prepares the salmon's osmoregulation system for salt water and changes their coloration to silver and black to help camouflage them in the ocean.

Fall-run Chinook salmon enter freshwater during August – October and spawn shortly after entering natal streams. They are relatively larger fish compared to other runs of salmon because of the extra time spent at sea, where they mature and grow rapidly throughout the summer. Fall-run salmon typically spawn in the lower reaches of rivers near the valley floor during the onset of fall freshets and decreasing water temperatures. After emerging from the gravel fall-run juveniles out-migrate as fry, par and smolts but do not exhibit a yearling life history (Moyle 2002). Juveniles enter the ocean during the same time as other runs, typically April-May when upwelling along the California Coast sets-up nutrient and food rich marine waters.

Late-fall Chinook salmon enter freshwater during November-January and spawn shortly after entering natal streams. Historically late-fall run salmon were

found exclusively in the upper reaches of the Sacramento and San Joaquin Rivers, where high winter flows allowed them access to productive spawning and rearing habitat. Late-fall salmon were regarded as the biggest of all salmon returning to spawn in the Central Valley, typically returning as four year old adults (Moyle 2002). After emerging from gravel nests juveniles over summer in natal streams before migrating to the ocean as yearlings (Vogel and Marine 1991).

Winter-run Chinook salmon evolved exclusively in the upper Sacramento River Basin and are found nowhere else on earth (Healey 1991). The McCloud River was the primary spawning tributary for these fish, a river regarded by many historians as one of the greatest salmon rivers in the world and the location of California's first salmon hatchery (Yoshiyama and Fisher 2001). Winter-run salmon enter freshwater during January – March and spawn in July and August. Their sole occurrence in the upper Sacramento River basin is due to the cold water which is supplied all summer by springs off Mount Shasta. Stable cold-water flows made egg incubation and juvenile rearing possible during the hot summer months, a time of year when most Central Valley streams are too warm to support salmon. After emerging from the gravel in late summer/early fall, juveniles migrate downstream as fry and rear in the lower Sacramento River and Delta, or remain in their natal stream before migrating to the ocean as smolts or yearlings.

Natal homing and the diversity in freshwater entry and spawn timing created spatial and temporal segregation between these runs, allowing each to evolve specific traits unique to the habitat types they occupied; winter and spring-run ascending to

headwater streams while fall and late-fall run occupied lower elevation stream reaches. This diversity also enabled salmon to spawn and juveniles to rear nearly year-round in over 26 tributaries to the Central Valley (Yoshiyama et al. 2001). Connecting these rivers to the sea was the Sacramento-San Joaquin River Delta - a massive estuary that historically provided over 800,000 acres of rearing habitat for juvenile salmon before they entered the Pacific Ocean (Whipple et al. 2012). This habitat was a critical component in the life cycle of Central Valley salmon, because fry and parr which out-migrate earlier in the year are typically too small for ocean entry, so they use the Delta as a nursery for additional growth before migrating to sea in April-May.

The abundant runs of Central Valley salmon began to slowly fade beginning in the late 1800's, when gold mining took its toll on spawning streams and over-fishing exploited adults in the ocean and rivers. Further collapse of the runs continued into the 1900's as dam construction began in many/most Central Valley tributaries. Impassible dams became migration barriers that removed much of the spawning and rearing habitat for spring-run and winter-run Chinook salmon, and land reclamation in the Delta transformed the productive floodplain rearing habitat into agriculture fields. Most recently the construction of the State and Federal water projects has diverted a large amount of the mainstem Sacramento and San Joaquin river flow coming into the Delta to the Bay Area and southern California via the California Aqueduct for agriculture and municipal uses. What currently remains for Chinook salmon in the Central Valley is 47% of their historic habitat (Yoshiyama et

al. 2001) and 50% of the natural stream flow exiting the Delta (Yates et al. 2008).

The cumulative effect of these alterations on river flow and habitat has been the decimation of the Central Valley's natural-origin Chinook salmon populations, which are now largely supported by hatchery production. The remaining wild populations of Chinook salmon exist in just a few tributaries to the upper Sacramento River, where pristine spawning and rearing habitat persists and spatial segregation limits them from breeding with hatchery-origin salmon.

In an effort to study the dwindling numbers of Central Valley Chinook salmon, coded wire tagging (CWT) experiments began in the 1960's which aimed at understanding juvenile survival, ocean distribution and harvest rates of primarily hatchery produced salmon (Nandor et al. 2010). These studies inject a small wire (0.25×1.1 mm) containing a unique ID into the nasal cartilage of juvenile salmon and couple the procedure with clipping the adipose fin, which indicates the fish is of hatchery origin and contains a coded wire tag. When the marked salmon is captured in the ocean or river, the CWT is extracted and the unique ID is read under a microscope which relates the hatchery of origin, release group and brood year of the fish. These studies have produced some of the foundational knowledge regarding freshwater habitat usage, timing of ocean entry, ocean distribution and proportion of wild vs hatchery salmon returning to spawn in the Central Valley. The CWT studies are still in operation today and currently mark 50 million salmon annually along the west coast of North America (Nandor et al. 2010). While these studies have helped our understanding of hatchery salmon survivorship at large spatial and temporal

scales, understanding specific areas where juvenile salmon experience mortality has been widely speculated until recently.

Advances in technology and the need to track salmon at finer scales of space and time led to the invention of miniature acoustic tags, which are surgically implanted into the stomach cavity of juvenile salmon and emit a uniquely coded signal detected by underwater hydrophones. Since its inception in the early 2000's in the Columbia River system, acoustic tagging studies have provided movement and survival rates of juvenile salmon at fine scales through areas of interest containing hydropower dams, large water diversions and known predator hot spots (Harnish et al. 2012; Rechisky et al. 2013; Welch et al. 2008). These tags offer many benefits that CWT studies lack, primarily the fine scale resolution of movement and survival rates of individual fish, as well as real-time detection capabilities of receivers linked to the internet. Currently this technology is the most advanced way of tracking Central Valley salmon smolts across space and time throughout their migration pathway to the ocean. With the growing need to understand survival rates of naturally produced salmon smolts in the Central Valley, my thesis reports on the use of this technology to track the movement and survival rates of wild Chinook salmon smolts originating in Mill Creek.

Mill Creek is a tributary to the upper Sacramento River that supports some of the last remaining populations of wild Central Valley spring-run Chinook salmon; a population that is part of an evolutionary significant unit (ESU) listed as threatened under the federal Endangered Species Act (ESA) since 1999. The pristine spawning

and rearing habitat accessible to this population allows for their continued existence, and makes this watershed unique in a landscape dominated by large dams, degraded habitat and hatchery produced salmon. With only three tributaries in the Central Valley continuing to support established runs of wild spring-run salmon (Mill, Deer, Butte Creeks), understanding the dynamics in juvenile out-migration survival is critical to support effective recovery actions for these endangered populations.

In this study I acoustically tag and track out-migrating salmon smolts from Mill Creek to the Golden Gate and the Pacific Ocean during a period of four years (2013-2016), and estimate movement and survival rates throughout different regions of interest. The data collected in this study comes from natural-origin Chinook salmon smolts that are migrating downstream in April and May at sizes >80mm fork-length, which is historically the peak out-migration window for Mill Creek smolts. These fish are representative of the smolt life history, one in which juveniles rear for extended periods of time in the upper watershed before out-migrating to the ocean during late spring. However, juvenile Chinook salmon out-migrate from Mill Creek throughout much of the year as sub-yearlings and yearlings, and downstream migrants that either migrate from June-March or at different sizes (<80 mm) from those tagged in my study most likely have different movement and survival rates compared to the smolts tagged and tracked in this study. In addition, the data collected throughout much of this study was during a series of unprecedented drought conditions (2013-2014-2015) that most likely affected smolt out-migration movement and survival as a result of exceptionally low flows and elevated water temperatures.

Chapter 2 describes the results from this study and includes statistical analysis relating survival to key biological and physical variables.

In an effort to tease apart the low survival rates with potential side effects related to trapping, handling and surgically implanting acoustic tags in juvenile salmon, a tagging effects study was conducted in Mill Creek during spring of 2016. This study was designed to test two assumptions made when conducting survival studies using acoustic telemetry: (a) the tagged fish are representative of the population, and thus the surgical procedure has no effect on their behavior; and (b) the acoustic tag stays inside the fish for the duration of the study. If these assumptions are violated then the data collected during the study are potentially biased and corrections must be made. In order to test these assumptions an experiment was conducted in Mill Creek where three experimental groups of fish were either captured by a rotary screw trap (RST) and acoustic tagged, captured by the RST and not tagged, and a control group. After 30 days the effects of each treatment were analyzed and the rate of tag retention was monitored throughout the study. Chapter 3 describes this study, which allowed us to examine the effects of acoustic tagging on the growth, survival and tag retention in juvenile salmon and helped address concerns about the surgical procedure which juvenile salmon undergo.

The results from this study have implications for future management and recovery actions related to threatened populations of Central Valley spring-run Chinook salmon. As the number of returning adults to Mill Creek continues to decline, more attention is being focused on the factors influencing juvenile and adult

survival rates. The data collected in this study can help shed light on specific reaches and regions where Chinook salmon smolts are experiencing low survival rates within a relatively long out-migration corridor. In addition, survival rates estimated over a range of environmental conditions can better inform resource managers of how changes in stream flow and temperature affect the survival dynamics of out-migrating salmon smolts. An improved understanding of survival dynamics in relation to flow and temperature is especially important during drought conditions, as the limited amount of available water should be utilized in a way that promotes both ecosystem and agricultural needs.

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Chapter 2

Out-migration survival of wild Chinook salmon (*Oncorhynchus tshawytscha*) smolts from Mill Creek through the Sacramento River during drought conditions

Introduction

Wild stocks of Chinook salmon (*Oncorhynchus tshawytscha*) were historically abundant in all rivers draining into in California's Central Valley (CCV), with population estimates of over two million adults returning to spawn each year (Yoshiyama et al. 1998). Today these populations have severely declined, due in large part to the loss of over 53% of historic spawning and rearing habitat behind large dams (Yoshiyama et al. 2001) (Fig. 1). To mitigate the affects of lost and degraded spawning and rearing habitats hatcheries are now operated on major CCV rivers. Hatcheries currently produce the majority of Chinook salmon returning to spawn in California's CCV as well as those harvested in the ocean fishery (Satterthwaite et al. 2015). The remaining wild populations of Chinook salmon in the Central Valley are isolated in just a few tributaries to the upper Sacramento River where pristine spawning and rearing habitat persists, and spatial segregation limits them from breeding with hatchery-origin salmon.

Despite the pristine spawning and rearing habitat available for wild populations their numbers have severely declined, and in 1999 the CCV spring-run Chinook salmon ESU was listed as threatened under the federal Endangered Species Act (ESA). It is presumed that poor out-migration survival is a proximate cause for

the declining populations, due in part to a highly modified river and estuary environment that has reduced rearing potential, combined with altered flow and temperature regimes in the Sacramento River and Delta which has increased populations of non-native predators that benefit from the altered ecosystem. The short window of time during the downstream migration of smolts to the ocean is the most vulnerable phase in the life cycle of a Pacific salmon, and is believed to account for much of the mortality the species experiences (Bradford 1995; Clark et al. 2016; Healey 1991; Rechisky et al. 2012). As a result of water projects in the CCV which create artificially low flows in the winter and spring, simulating drought conditions, smolt survival to the ocean is reduced even further resulting from the effects of elevated water temperatures, reduced flows, decreased turbidity and increased interactions with predator fish (Baker et al. 1995; Becker 1971; Cavallo et al. 2012; Gregory 1993). Without significant habitat improvements in the river and estuary environments, as well as improved instream flows, these effects will likely intensify as the climate in California becomes more extreme as a consequence of anthropogenic climate change, resulting in prolonged droughts which will impair the out-migration survival of juvenile Chinook salmon even further (Yates et al. 2008).

Several studies have found low hatchery smolt-migration survival rates throughout many rivers in the CCV, Delta and estuary (Baker and Morhardt 2001; Brandes and McLain 2001; Buchanan et al. 2013; Michel et al. 2015; Perry et al. 2010). However, little data has been collected on the survival rates of naturally produced Chinook salmon smolts in the CCV, due in large part to the difficulty in

capturing these fish as the few remaining wild populations are severely depleted. Wild salmon smolts out-migrate to the ocean across many weeks during the spring compared to hatchery salmon which are typically released in a few large groups. Inferring survival rates for wild smolts based on acoustic telemetry data of hatchery salmon can be misinforming due to differences in fish size, fitness and environmental conditions encountered while out-migrating. In order to manage wild populations for future recovery, understanding the movement and survival rates of naturally produced smolts is necessary to devise effective management strategies.

In this study, I measure the movement and survival rates of acoustically tagged Chinook salmon smolts from a tributary to the upper Sacramento River which supports some of the last populations of wild spring-run Chinook salmon in the CCV. Utilizing an extensive network of acoustic receivers, the movement and survival rates of acoustically tagged juveniles were calculated at fine scales throughout the migratory pathway to the Pacific Ocean. Data collected over four consecutive years (2013-2016) examines survival and movement rates throughout a range of environmental conditions, most notably three consecutive years of drought, and provides insight into how these conditions affect juvenile salmon out-migration survival. I develop and test a series of mixed-effects models to evaluate the potential roles for varying fish size, stream flow and stream temperature on downstream migration survival rates.

Methods

Study Area

Mill Creek is a free flowing tributary to the Sacramento River containing pristine spawning and rearing habitat for Chinook salmon and steelhead trout (*Oncorhynchus mykiss*). Its headwaters originate in Lassen National Park at an elevation over 8,000ft where numerous springs feed into high elevation meadows. Mill Creek continues to flow south-west through protected land in Lassen National Forest before transitioning into a rugged and deep canyon while flowing through the Ishi Wilderness. During its 100 kilometer course Mill Creek drops over 5,000ft in elevation, providing salmon and steelhead access to some of the highest elevation anadromous fish spawning habitat in the United States. Downstream of the canyon on the valley floor there are two water diversion dams on Mill Creek operated by Los Molinos Mutual Water Company (LMMWC), both of which provide salmon upstream access with fish ladders.

Mill Creek joins the Sacramento River, the largest river in California draining an area of 70,000 km², near the town of Los Molinos (Fig. 1). The Sacramento River flows for 289 river kilometers (rkm) downstream of Mill Creek before transitioning into the Sacramento-San Joaquin River Delta. The Sacramento River has two distinct regions, noted as the upper (rkm 441-344) and lower (rkm 344-203) Sacramento River in this study. The upper Sacramento River is in a relatively natural state with expansive gravel bars, riparian habitat and braided channels, whereas the lower Sacramento River is highly modified by agricultural practices and becomes

channelized, straightened and its banks covered with cobble to lessen erosion. This study focuses on the movement and survival rates of wild juvenile salmon smolts captured, tagged and released below the upstream diversion dam on Mill Creek.

Fish collection and Tagging

Approximately 10 km upstream from the Sacramento River and directly below the upper diversion dam, a rotary screw trap (RST) was operated to capture migrating salmon smolts. The location is downstream of much of the juvenile rearing habitat, and the smolts captured are more likely to be migrating downstream to the ocean. The 5' diameter RST was deployed in early April each year and operated continuously until catch rates diminished and out-migration ceased as a result of elevated water temperatures (typically late May-early June). Each morning the trap was checked for salmon and cleaned of debris using a long handled dip net. Salmon were placed in a 5-gallon bucket before being transferred to a 100 quart cooler where oxygen was provided with bubblers.

Before undergoing surgery, all salmon were anesthetized in MS-222 buffered by 120mg L^{-1} sodium bicarbonate prior to being weighed to the nearest tenth of a gram and measured to the nearest mm of caudal fork length. Acoustic tags were surgically implanted into the peritoneal cavity of the anesthetized fish as described by Deters et al. (2010). The tag weight did not exceed 5% of the fish's body weight, which Brown et al. (1999) found did not affect the growth or swimming performance of hatchery salmon implanted with acoustic tags. Following this guideline allowed smolts as small as 6 grams and 80 mm fork length to be acoustic tagged.

During 2013-2014 fish were released in Mill Creek below the RST approximately 1 hour after recovery. Because these smolts were actively migrating we believed that holding them for extended periods may disrupt their migratory cue, and releasing them soon after recovery was the best option to avoid additional stress. To monitor the salmon after release, periodic snorkel surveys were conducted to ensure that no predators such as Sacramento pikeminnow (*Ptychocheilus grandis*) and smallmouth bass (*Micropterus dolomieu*) were aggregating around the release location and preying on the tagged juveniles. The snorkel surveys were also conducted to observe smolt behavior after recovery and release, revealing that all fish appeared to have functional swimming performance and appeared to school together before finding shade to hold and rest.

After reconsidering our release protocol due to low survival rates observed within Mill Creek during 2013 and 2014 and the possibility that smolts were not fully recovered from surgery, we employed an automated release hamper for 2015 and 2016. This allowed smolts to rest for 12 hours before being released at 10pm and potentially avoid predation while migrating at night. The release hamper also allowed us to observe if smolts had died after surgery when checking it the following morning, which revealed no smolts had died as a result of surgery. We continued to conduct snorkel surveys around the release site to ensure no predators were aggregating around the release hamper.

Acoustic Telemetry

This study uses the Juvenile Salmon Acoustic Telemetry System (JSATS) (McMichael et al. 2010) to track survival and movement rates of migrating smolts from Mill Creek. The acoustic tags (300mg, 10.7mm long x 5mm diameter, Advanced Telemetry Systems) emit a uniquely coded signal at 416.7 KHz programmed with a 5-second pulse rate, giving the tag a 32 day battery life expectancy. JSATS technology is favored over other types of acoustic technology because of the high performance of the tags in noisy environments, with an on-board processor in the receiver which filters out false detections. The acoustic receivers (made by Advanced Telemetry Systems) are positively buoyant, autonomous devices containing a hydrophone that detects and decodes the tag signal to produce a unique ID for each tagged fish. The receivers are equipped with 120 day lithium ion batteries which power the hydrophone, temperature and tilt logger.

Over 140 acoustic receivers were deployed each spring throughout the migration pathway of juvenile Chinook salmon from Mill Creek to the Pacific Ocean (Table 1, Fig. 2). For this study I included 14 reaches between Mill Creek and the Golden Gate Bridge, simplifying the Delta into one reach. Reaches are classified as 20-30 kilometer sections of river where survival rates are of interest, allowing the long migration corridor to be broken into smaller sections which enables small scale patterns in movement and survival rates to be observed over time. The receivers were left in place for 30 days after the last smolt was tagged and released. The receivers were secured to a tree, bridge or structure using ¼” stainless steel cable and fastened

by a sleeve which crimps the connection. Between 30 and 100ft of cable is extended from the shore anchor to a location in the channel where the receiver can detect pinging tags. To anchor the receiver on the river bottom, 20-30lbs of weight is secured to the cable and a ~20" cable allows the receiver to float above the weights. The receiver is equipped with a fin to keep it from swaying under water and to keep the hydrophone pointed towards the surface.

Data Analysis

Data analysis was performed using a Cormack-Jolly-Seber (CJS) model for live recaptures (Cormack 1964; Jolly 1965; Seber 1982) using the program MARK (White and Burnham 1999) within the RMark package (Laake and Rexstad 2013) which is written in the R programming language (version 3.0.1). This model works particularly well for juvenile salmon because they tend to exhibit a strict downstream movement behavior once smoltification has begun (Healey 1991). This behavior is advantageous for acoustic telemetry studies in riverine environments due to the linear nature of these systems, which require the fish to pass specific reaches. As the tagged fish are migrating toward the ocean, we assume if no detections are recorded downstream of its last location, that the fish died between its last detection and the next downstream receiver.

When calculating mortality rates, we have to take into consideration detection efficiency of the receiver (how accurate the receiver is at detecting acoustic tags), which can become problematic under certain environmental conditions. High water flows and noise associated with these events can impair the efficiency of the receiver

and allow fish to pass undetected, creating uncertainty in its accuracy. To calibrate these estimates the CJS model takes into account the number fish detected at downstream receivers to estimate the accuracy of the upstream receiver, and then uses maximum-likelihood estimates for detection efficiency of all monitor locations (p), all survival estimates (Φ), and 95% confidence intervals for both (Lebreton et al. 1992). With the exception of 2015, we had relatively small sample sizes throughout this study which led to increasing uncertainty in the survival estimates going downstream as fewer fish remained in the system.

Several covariates were considered in an effort to determine which physical and environmental factors were most influential in smolt survival. Specifically, I considered Mill Creek flow at release (cubic feet per second (CFS)), Mill Creek temperature at release (degrees celsius), upper Sacramento River flow (CFS), lower Sacramento River flow (CFS) and fish length (millimeters). The influence of these factors on survival was assessed by allowing each group (year, $n=4$) and fish released within each group, to have its own set of parameters based on the in situ water conditions throughout each region. In order to compare these covariates against other models, a null model (constant survival through space and time), a base model (reach \times year) and a series of models using environmental and physical covariates were constructed to see which were best supported. The purpose of using a base model is to include all sources of mortality that should not be attributed to the environment. The model selection criterion used was Akaike's Information Criterion (AIC)(Akaike 1981), which ranks each model by assigning a score according to how accurate the

model is relative to the given data, and penalizes models with more parameters

(Eqn.1):

$$1. \text{ AIC} = 2K - 2(\log\text{-likelihood})$$

where K is the number of parameters included in the model, and the log-likelihood of the model reflects the overall model fit (a smaller value indicates worse fit). This equation and the score it assigns allows each model to be compared based on parsimony and not simply goodness-of-fit, with a lower AIC value indicating a better fit. To determine the best model given the data, the Δ AIC, which is the difference in AIC score relative to the top model, is used; as suggested by Burnham and Anderson (2002), AIC values were corrected for small sample sizes (AICc).

In total 16 models were used in the survival analysis which tested a combination of group (year), release flow, release temperature, regional flow (upper Sacramento River, lower Sacramento River) and fish size. Fish length was used rather than weight because both are strongly correlated. Release flow and temperature were allowed to vary for each fish in Mill Creek, but once entering the Sacramento River these values were removed from the models as flow and temperature values change dramatically. Specific flow values for the upper and lower Sacramento River were used for fish during the time they were migrating through these regions. In order to account for the large variations in reach distances survival estimates were standardized by reach length (kilometers). Within the program MARK, survival was transformed using a logit function and related to reach length and a number of environmental and physical parameters (Eqn. 2), while detection efficiency was fixed

(i.e., independent of reach). One coefficient (β) for each environmental and physical variable quantifies the linear relationship between that variable and survival. By standardizing the environmental and physical parameters (subtracting the mean value from each raw data point and dividing by the standard deviation), calculated beta coefficients offer a straightforward interpretation across different models and environmental variables. For a change in one standard deviation unit of the environmental variable, survival will change by the amount specified by that model's standardized beta coefficient.

2.
$$\text{Logit}(\Phi) = \beta_0 + \beta_1[\text{Reach Length}] + \beta_2[\text{Env. Variable}] + \beta_3[\text{Env. Variable}]$$

Survival estimates were calculated using separate reach-specific and regional approaches, respectively. The reach-specific analysis included all 14 reaches in the study from Mill Creek to the Golden Gate (rkm 450 – 1.7), and the regional analysis simplified the pathway by using 3 regions for the analysis; Mill Creek (reach 1, rkm 450-441), the upper Sacramento River (reach 2-5, rkm 441-344) and the lower Sacramento River (reach 6-10, rkm 344-203). These regions were chosen because they exhibit different habitat types and each contain different flow values as a result of water diversions which remove increasingly more water going downstream. I excluded the Delta and San Francisco Bay from the analysis due the small sample size in those reaches. Survival rates per 10 kilometers, hereafter referred to as survival rates, were calculated in order to standardize estimates between reaches of varying distances; this allows patterns to be detected where survival is relatively

higher or lower between years and indicates where mortality hot-spots may be occurring.

Results

Total survival for wild smolts emigrating from Mill Creek to the Pacific Ocean was 0.3% during the four years of the study. Of the 304 fish tagged and released, only one was detected at the Golden Gate in 2013. Cumulative survival from Mill Creek to the Sacramento River was 68% (± 12 S.E), cumulative survival from Mill Creek through the upper Sacramento River was 23% (± 19 S.E) and cumulative survival from Mill Creek through the lower Sacramento River was 7.6% (± 16 S.E)(Fig. 3).

Region specific survival rates were relatively consistent in the upper and lower Sacramento River, but varied within Mill Creek (Fig. 4). Survival rates in Mill Creek ranged from 86% (± 7 S.E) in 2016 to 58% (± 3.5 S.E) in 2015. Survival rates in the upper Sacramento River ranged from 94% (± 5 S.E) in 2013 to 86% (± 7 S.E) in 2014 and survival rates in the lower Sacramento ranged from 94% (± 7 S.E) in 2013 to 86% (± 7 S.E) in 2014. In 2016 no smolts survived past reach 3 in the upper Sacramento River to allow for survival estimates through the region.

Survival rates between individual reaches followed a similar pattern each year. The lowest survival rates were observed in Mill Creek (reach 1) between 58-86%, followed by increasing survival rates in the first upper Sacramento River reach (reach 2) between 95-100%. Downstream of reach 2 survival rates progressively decreased, with the lowest survival rates observed in reach 6 between 79-89%.

Downstream of reach 6 survival rates generally increased, with estimates in reach 7 between 90-97.5% and reach 8 between 96-100%. Downstream of reach 8 survival rates generally decrease, but the large error bars resulting from the few remaining fish create uncertainty in these estimates (Fig. 5).

Tagged fish fork length varied significantly among years ($P < 0.02$) but fish weight did not vary significantly ($P = 0.24$). Sample sizes of tagged smolts were relatively small each year ($n=23-186$; Table 2), with the exception of 2015 when 186 smolts were tagged and released. The small sample sizes were likely attributed to limited numbers of smolts available due to low numbers of spawning adults the prior year. The capture efficiency of the RST was also an issue because of the large volume of water going around the trap, with the exception of 2015 when flows were so low that most of the remaining water below the upper diversion dam flowed directly into the RST.

Due to severe drought conditions in 3 of 4 years of this study (2013-2014-2015), study-period flows were significantly lower and water temperatures higher in Mill Creek relative to the historic average (Fig. 6). Flows increased substantially in 2016 resulting from an above average snowpack. Water temperature remained above the historic mean for all study years, but was especially high in 2015 compared to other years. Water flow and temperature were indicative of survival in Mill Creek; higher flows corresponded to higher survival rates (Fig. 7), and lower water temperatures corresponded to higher survival rates (Fig. 8). The interaction of water temperature and flow in Mill Creek in relation to survival found that both have an

effect, but flow has greater influence on survival compared to temperature given the values observed during this study (Fig. 9). In the upper and lower Sacramento River this finding remained consistent, with smolts experiencing higher cumulative survival rates during years of higher flow (Fig. 10-11). Models used to estimate survival according to flow alone in the upper and lower Sacramento River were not well supported ($\Delta \text{AICc} = 16.3, 18.3$ respectively), indicated by the large discrepancies between the predicted survival confidence intervals and the actual survival data.

Movement speeds were correlated with survival rates among all reaches, with slower movement speeds resulting in lower survival rates and faster movement speeds resulting in higher survival rates (Fig. 12). The slowest average movement speeds were observed in Mill Creek ($10.3 \text{ km/day} \pm 3.1 \text{ S.D}$), followed by relatively high movement speeds in reach 2 upon entering the upper Sacramento River ($64 \text{ km/day} \pm 9.5 \text{ S.D}$), and the slowest movement speeds through the Sacramento River in reach 4 ($43 \text{ km/day} \pm 13.4 \text{ S.D}$). Downstream of reach 6 movement speeds generally increased, and obtained a maximum in the lower Sacramento River in reach 8 ($81 \text{ km/day} \pm 7 \text{ S.D}$). This peak in movement speed is likely attributed to faster water velocities resulting from channelization and a decrease in sinuosity in the lower Sacramento River.

In the analysis of survival as a function of physical and environmental covariates, the top model indicates that group (year), in addition to flow in Mill Creek and fish size (length) was a better model than the null model (constant survival) and base model (year x reach). Both the reach specific and regional analysis included 16

different models that tested a combination of physical and environmental covariates, release year and reach length. By running both a reach-specific and regional analysis the effects of each covariate could be evaluated separately to see if they have different levels of influence at fine scale vs. larger spatial scales. Each model returned similar results (Table 3), both indicating that flow at release in Mill Creek in addition to fish size and year best explain the variation in survival at both the reach specific and regional scale. The second best supported model for both analyses included flow and temperature in Mill Creek in addition to fish length and release year, with a $\Delta AIC < 2$ for both analyses.

Discussion

This study provides the first estimates of wild Chinook salmon smolt survival from Mill Creek through the Sacramento River. Survival estimates during this study were very low relative to other telemetry studies conducted in the Sacramento River (Michel et al. 2015; Perry et al. 2010), and were most likely influenced by three consecutive years of drought. Water flow in Mill Creek was significantly lower than the historic average spring flow during the three drought years, and water temperatures were slightly above historic spring averages as well (Fig.6). Throughout the study period flows were impaired even further by water diversions for agriculture, which diverted up to 50% of the natural flow and resulted in the lowest spring flows ever recorded in Mill Creek in 2015.

Survival rates within Mill Creek were very low relative to other reaches in the study. In total approximately 70% of the 304 tagged smolts appeared to have survived

through Mill Creek and entered the Sacramento River. The lowest survival rates were observed in 2015 when 58% of the 186 smolts tagged and released survived the Mill Creek reach to the Sacramento River. Spring flows in 2015 were some of the lowest on record, due to the combination of an exceptionally low snowpack resulting in decreased runoff, and water diversions which removed all but 50 CFS from lower Mill Creek. Water rights granted to LMMWC allows the water district to divert 130 CFS from Mill Creek throughout the year, but during drought conditions an agreement with the California Department of Fish and Wildlife (CDFW) requires them to leave 50 CFS in-stream for fisheries and ecosystem needs. This amount of water appears to be insufficient for the survival of out-migrating juvenile salmon in April-May, as lower flows and warmer water temperatures resulted in lower survival rates (Fig. 7-8). A similar relationship was documented on Idaho's Snake River, where increased flows resulted in higher survival rates for juvenile Chinook salmon migrating to the ocean (Connor et al. 2003). In addition to flow, higher water velocities were shown to increase survival rates, likely because it promotes rapid downstream migration of juvenile salmon which reduces the exposure time to predators, resulting in higher survival rates (Tiffan et al. 2009).

The low survival rates in Mill Creek may also suggest that the surgical procedure negatively impacts the survivorship of acoustic tagged smolts. When conducting survival studies using acoustic telemetry two assumptions are made: one is that the fish are representative of the population, and thus the surgical procedure has no effect on their behavior; and the second is that the acoustic tag stays inside the

animal for the duration of the study. In order to test these assumptions a tag effect study was conducted in Mill Creek during 2016, which is described in more detail in Chapter 3. 50 hatchery smolts were acoustically tagged using the same surgical procedures and held in tanks for 30 days on the bank of Mill Creek. In addition, 50 smolts were sent through the RST to test any effects the trap may have on survival, and 50 smolts were placed in the tanks as controls. The tanks were checked daily for shed tags and dead smolts, and the survival and overall condition of the fish were noted. After 30 days, 10 out of 50 (20%) acoustic tags were shed from the smolts, with the first shed tag occurring after day 10. No tagged smolts died post-surgery from tag implantation, but tagged smolts did grow significantly less than the RST and control group after 30 days.

In this study, only 3 of 304 tagged smolts were detected for more than 10 days. This suggests that tag shedding is not likely an issue in this analysis (Fig. 13). These short survival durations are most likely due to predation, and suggest that Mill Creek and the Sacramento River are exceptionally hazardous regions for out-migrating smolts under the conditions experienced in 2013-2016. In addition, smolts which are tagged and released may experience delayed physical impacts from the tagging procedure, as was seen in the low growth rates for tagged smolts in the tag effects study. This could imply that a proportion of the smolts being studied are experiencing lower survival rates early in the study compared to otherwise healthy smolts, and the survival estimates towards the end of the study area may be biased high because the unfit individuals have already been removed by predators. These

predators, which include Sacramento Pikeminnow and smallmouth bass, migrate into Mill Creek during the spring to spawn, and during low flow conditions with relatively warm water temperatures their effectiveness at capturing juvenile salmon can be greatly increased (Cavallo et al. 2012). Warmer water increases the metabolism in predatory fish, and clear water resulting from reduced run-off impairs the predator avoidance behavior of juvenile salmon (Gregory 1993). Compounded with these stressors are anthropogenic structures in Mill Creek such as water diversions, bridge pilings and low-head dams which increase the effectiveness of ambush predators (Sabal et al. 2016). These structures create unnatural locations where predators can lie and wait, striking naïve juvenile salmon as they pass by potentially disoriented after swimming through these obstacles (Brown and Moyle 1981; Sabal et al. 2016).

Another possible reason for the low survival rates in Mill Creek is the amount of time smolts spend in this reach compared to reaches in the Sacramento River (Fig. 12). Movement rates were between 8-14 kilometers per day in Mill Creek compared to 40-80 kilometers per day in the Sacramento River. The slow movement speeds through Mill Creek increases their exposure time to potential risks such as predation and the effects of water diversions, which can both significantly impact survival; water diversions reduce flow which diminishes habitat, resulting in increased predator densities (Mussen et al. 2012). During drought conditions smolt movement speeds were relatively slow compared to 2016 when flow was higher, increasing from 8 to 14 kilometers per day. As a result higher survival rates were observed when

movement speeds increased within Mill Creek (58% in 2015 with exceptionally low flow (mean=72 cfs), and 86% in 2016 with near average flow (mean=268 cfs)).

Once smolts leave Mill Creek they experience rapidly changing water conditions in the highly modified habitat and managed flows of the mainstem Sacramento River. Large changes in April-May mainstem flows are experienced because of water diversions that take up to 50% of the river flow before joining the Delta (Fig. 14). Water diversions for out of stream uses by agriculture typically increase during April-May, the same time Mill Creek smolts out-migrate through the Sacramento River (Fig. 15), which is relatively late in the spring compared to other salmon in the CCV (Vogel and Marine 1991) as a result of the high elevations at which they are spawned and rear. The effect of these artificially low flows, which were significantly lower than the historic average during the study period (Fig. 16), can have implications for predator abundances and their prey capture efficiency. Low flows lead to more favorable spawning conditions for alien fish species (Larry and Marissa 2009), which leads to established populations over time if more natural flow regimes are not implemented (Marchetti and Moyle 2001). In addition, low flows are correlated with low turbidity levels (Feyrer and Healey 2003) which can influence the rate of predation on migration juvenile salmon, with predators more effective at capturing salmon in clear water (Gregory and Levings 1998).

The lowest survival rates in the Sacramento River were in the first lower Sacramento River reach (reach 6, rkm. 308), which contains large populations of striped bass (*Morone saxatilis*) and other predatory fish throughout the year. Every

spring striped bass migrate upstream from the San Francisco Bay and Delta to spawn, and aggregate in this reach due to favorable water temperatures and flow required for spawning (Chadwick 1967). Depending on the population size of striped bass and the number of salmon smolts present, striped bass have been estimated to significantly impact juvenile Chinook salmon populations (Lindley and Mohr 2003) while only accounting for a fraction of their bio-energetic demands (Loboschefskey et al. 2012). The combined exposure time to predators coupled with the long distances that Mill Creek smolts transit through the Sacramento River may lead to significant mortality in the smolt population (Anderson et al. 2005).

The results from this study have implications for future restoration and management actions aimed at threatened and endangered populations of wild Chinook salmon in the CCV. This study shows that juvenile salmon out-migrating as smolts relatively late in the spring experienced very low survival rates from 2013-2016, most likely resulting from flow-mediated predation in a period of drought conditions from 2013-2015 and substantial water diversions in all study years. Data collected over a range of flow and temperature values indicate that survival improves with higher flows and lower temperatures, and during drought conditions a large proportion of smolts may perish within natal streams or shortly after migrating into the Sacramento River. To remedy this situation, especially during drought conditions, supplying enough water instream for smolts during their critical migration window can lead to higher out-migration survival, a situation that may be necessary to support increased returns of spawning adults (Berggren and Filardo 1993; Giorgi et

al. 1997; Raymond 1968). Using the data collected in this study, in order to sustain a 90% survival rate for smolts through Mill Creek a minimum of 250 CFS should be maintained during April-May when these fish are actively migrating downstream. This outcome can be accomplished through managing water flows for both agriculture and fisheries needs, and maintaining adequate water flows during critical stages of the salmon life cycle. As the few remaining wild salmon populations in the CCV remain threatened and endangered with extirpation, understanding how habitat and environmental conditions influence their survival is critical to support effective recovery planning and actions.

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Location Name	Reach Number	River Km
MillCk_RST		451
Mill_Ck_Conf	1	441
Abv_WoodsonBr	2	425
Blw_IrvineFinch	3	395
BlwOrd	4	362
ButteBr	5	344
AbvColusaBr	6	308
AbvTisdale	7	269
BlwChinaBend	8	241
Knights	9	224
Blw_FRConf	10	203
I80_Br	11	171
Freeport	12	152
Benicia	13	52
GoldenGate	14	2

Table 1. Receiver location name, reach number, and distance in kilometers from the Pacific Ocean.

Year	Sample Size	Fork Length \pm SD (mm)	Weight \pm SD (g)
2013	59	84.2 \pm 11.4	7.3 \pm 3.3
2014	36	83.5 \pm 2.9	6.7 \pm 0.9
2015	186	86.9 \pm 6.2	7.4 \pm 2.1
2016	23	85.7 \pm 4.0	7.7 \pm 1.1
ALL	304	85.9 \pm 7.2	7.4 \pm 2.2

Table 2. Sample size, weight and length for smolts tagged and released each year.

Reach Specific Model	#Parameters	Δ AICc
year + reach + mill:flow.z + length.z	21	0
year + reach + mill:flow.z + mill:temp.z + length.z	22	0.46
year + reach + mill:temp.z + length.z	21	10.49
year + reach + mill:flow.z	20	11.14
year + reach + lowersac:flow.z + length.z	21	18.5
year + reach + uppersac:flow.z + length.z	21	18.5
reach + year	19	19.94
year + reach + mill:temp.z	20	21.99
year + reach + lowersac:flow.z	20	29.5
year + reach + uppersac:flow.z	20	29.8
reach * year	61	36.83
reach	16	55.45
length.z	3	148.69
temp.z	3	166.68
constant (null)	2	176.94
flow.z	3	177.16
Regional Model	# Parameters	Δ AICc
year + reach + mill:flow.z + length.z	12	0
year + reach + mill:flow.z + mill:temp.z + length.z	13	1.76
year + reach + lowersac:flow.z + length.z	12	7.71
year + reach + mill:flow.z	11	9.44
year + reach + uppersac:flow.z + length.z	12	9.69
year + reach + mill:temp.z + length.z	12	11.34
year + reach + lowersac:flow.z	11	16.3
year + reach + uppersac:flow.z	11	18.3
reach + year	10	20.6
year + reach + mill:temp.z	11	21.89
reach * year	25	25.8
reach	7	38.2
length.z	3	144.6
temp.z	3	163.01
flow.z	3	171.39
constant (null)	2	171.54

Table 3. Survival models for different study design factors, ordered from best to worst according to AIC scores. Parameters were standardized for the analysis, thus the .z notation (z score). The Δ AICc statistic represents the distance of that model from the best supported model.

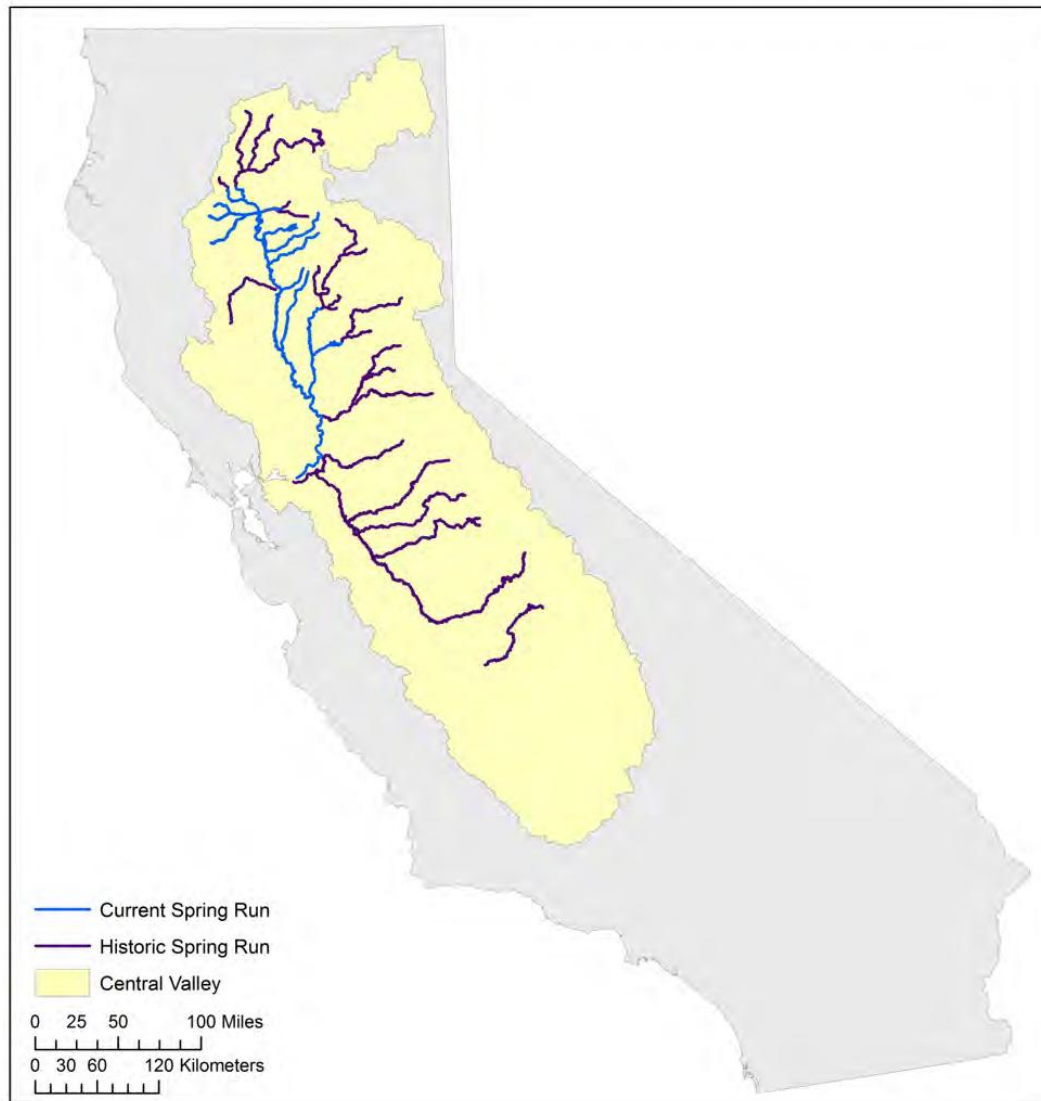


Figure 1. Current (blue) and historic (purple) distribution of spring-run Chinook salmon in California's Central Valley

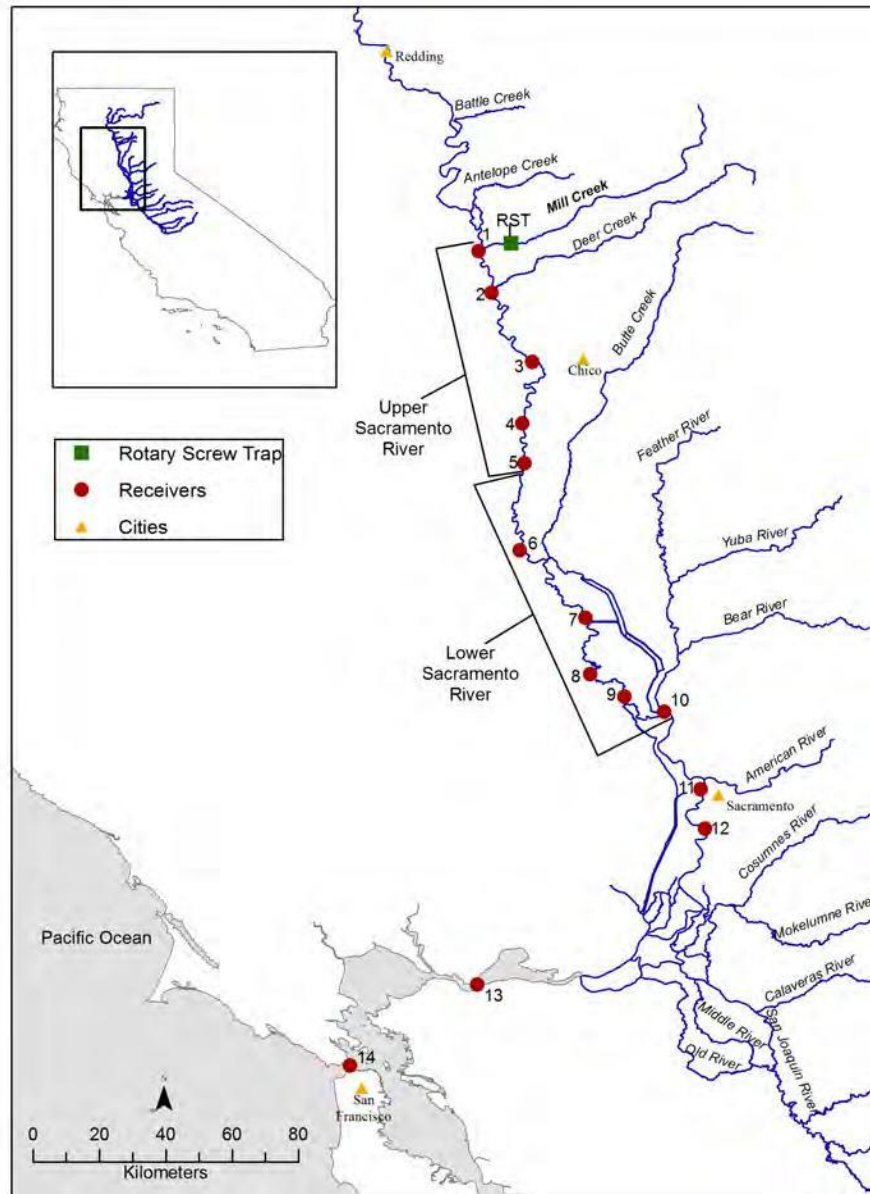


Figure 2. Location of all 14 reaches used for this study, including Mill Creek, the lower Sacramento River and upper Sacramento River. Each red dot indicates where acoustic receivers were placed to detect out-migrating smolts.

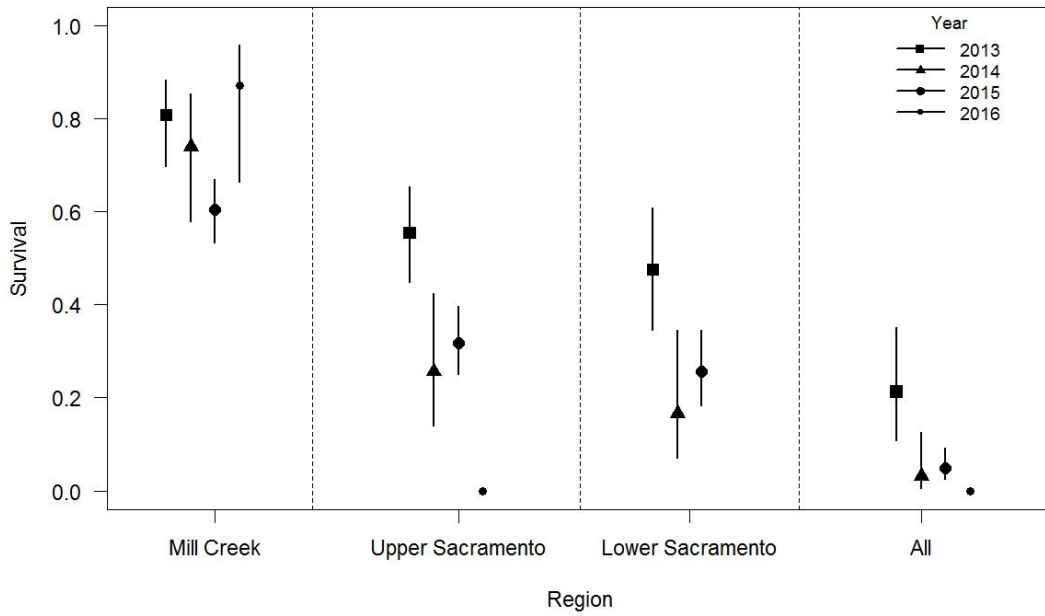


Figure 3. Cumulative survival estimates within each region and total survival throughout all regions for each study year. Error bars represent 95% confidence intervals.

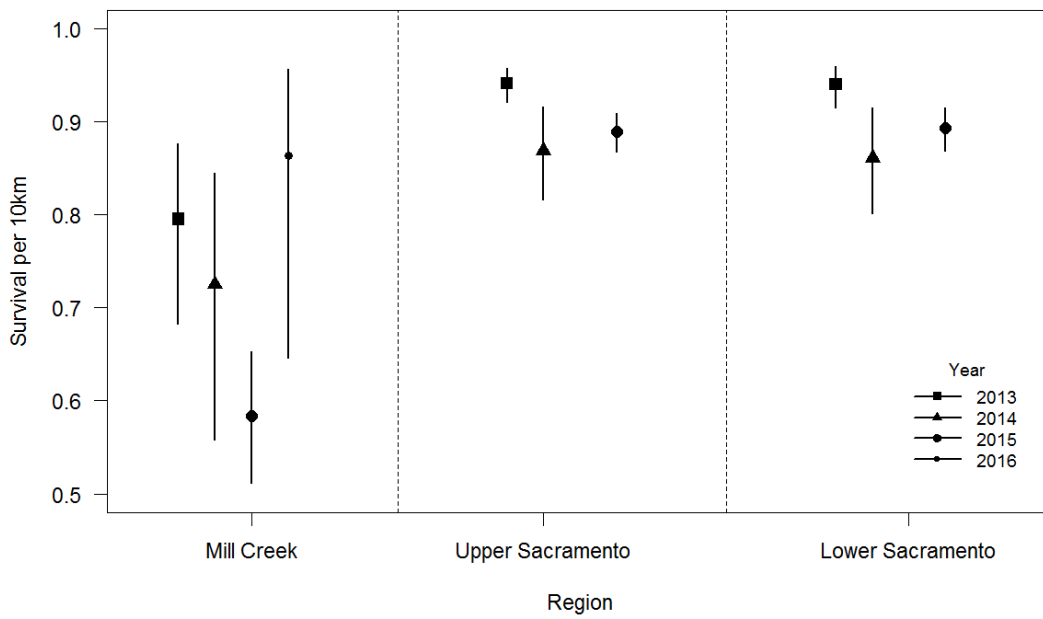


Figure 4. Region specific survival calculated per 10 kilometers in Mill Creek, the upper Sacramento River and lower Sacramento River. Error bars represent 95% confidence intervals. In 2016 no fish made it through the second reach of the upper Sacramento River.

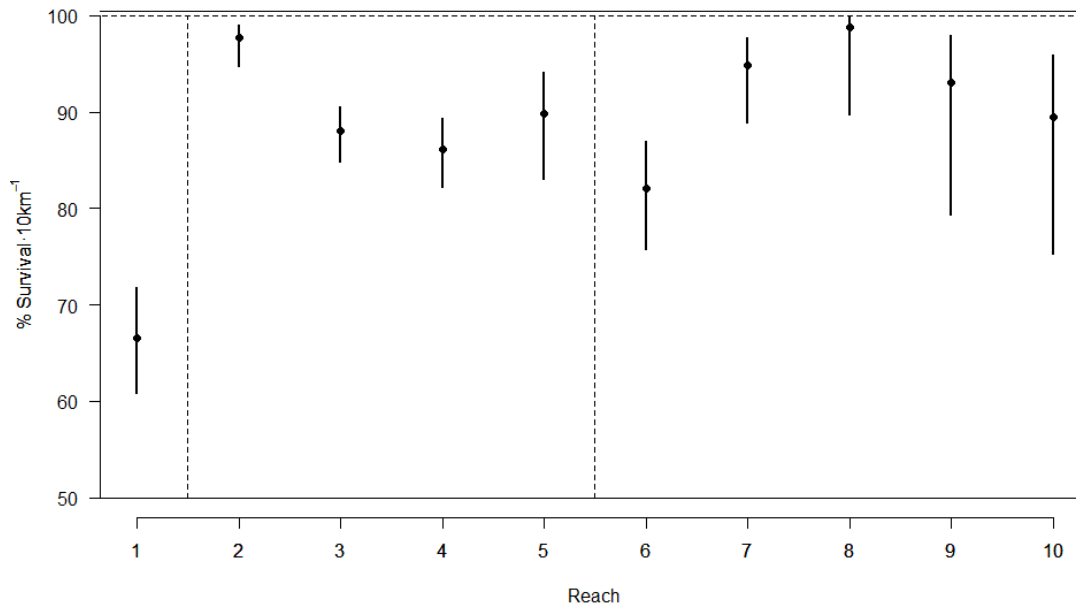


Figure 5. Reach specific survival rates through Mill Creek (reach 1), the upper Sacramento (reaches 2-5) and lower Sacramento River (reaches 6-10) averaged for all years of the study. Dashed vertical lines separate each region. Error bars represent 95% confidence intervals.

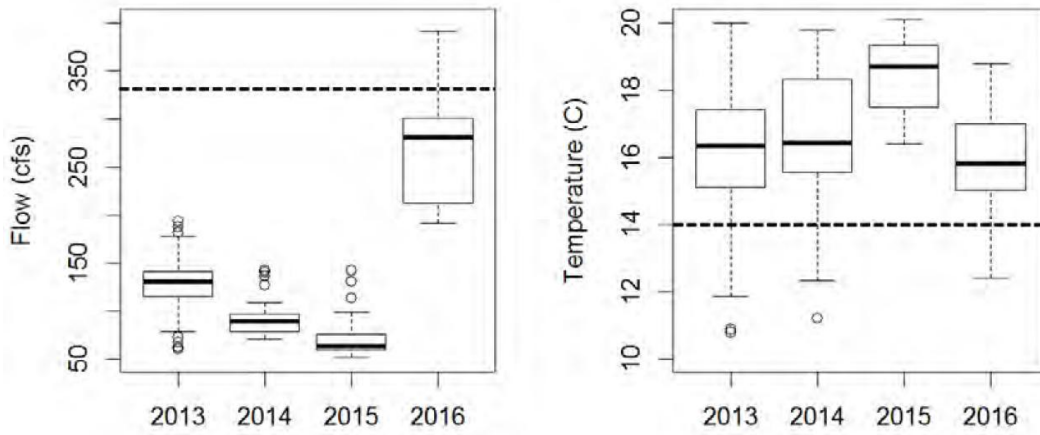


Figure 6. Stream flow (left) and water temperature (right) measured downstream of water diversions in Mill Creek during the study period for each year. Water flow is measured in cubic feet per second (CFS). The dashed line represents the historic mean flow and temperature downstream of water diversions during the study period.

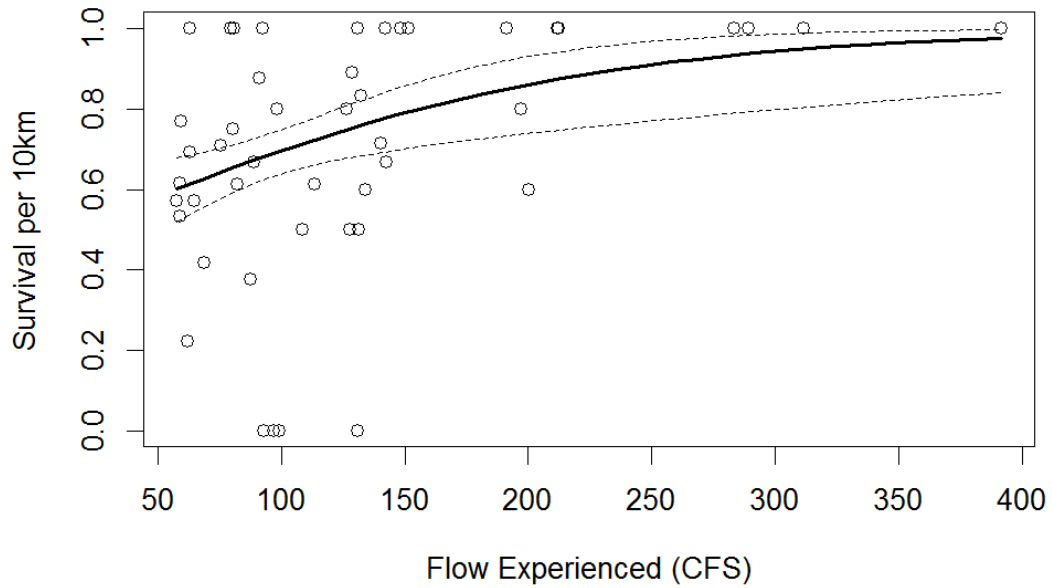


Figure 7. Smolt survival predicted in Mill Creek (solid line) during 2013-2016 as a function of flow at release, including upper and lower 95% confidence intervals (dashed lines). Dots represent the actual survival rates observed through Mill Creek for groups of fish released at the specified flow value. Note that historic April/May stream flow in Mill Creek (1987-present) is 352 CFS \pm 190 CFS.

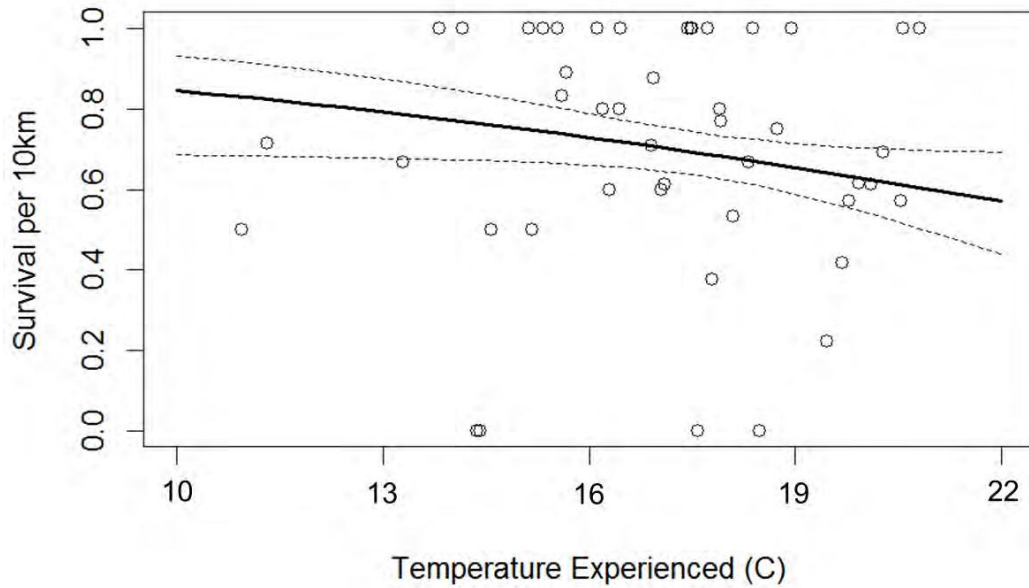


Figure 8. Smolt survival predicted in Mill Creek (solid line) during 2013-2016 as a function of water temperature at release, including upper and lower 95% confidence intervals (dashed lines). Dots represent the actual survival rates observed through Mill Creek for groups of fish released at the specified temperature. Note that historic April/May stream temperature in Mill Creek (1987-present) is $13^{\circ}\text{C} \pm 5^{\circ}$.

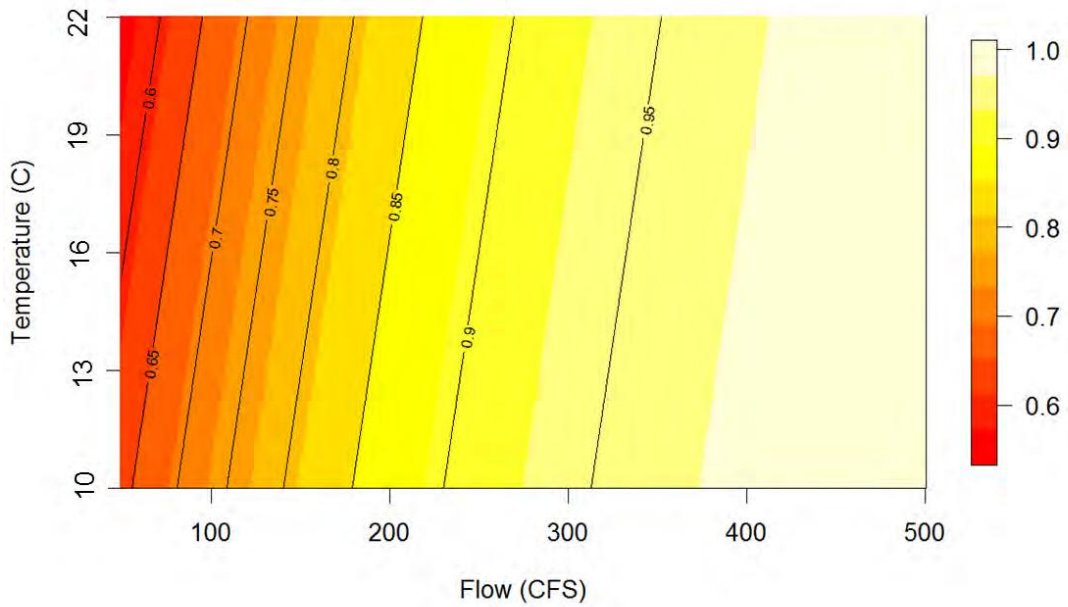


Figure 9. Contour plot of survival rates per 10km predicted in Mill Creek as a function of flow and temperature. The changes in color and black lines indicate the various survival rates predicted at each flow and temperature value. This graph shows that survival rates depend upon both parameters, but flow has more influence in survival compared to temperature.

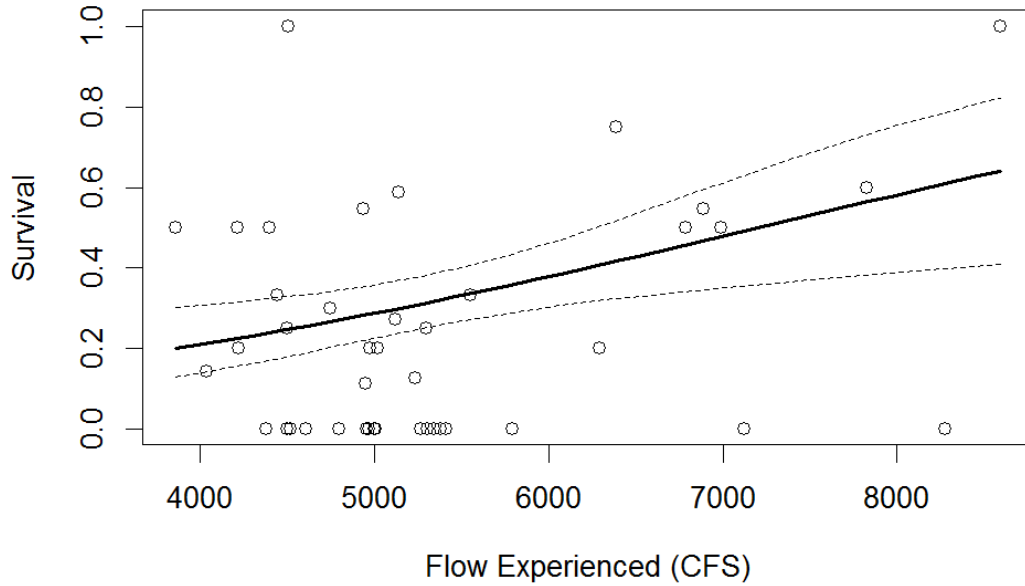


Figure 10. Cumulative survival predicted through the upper Sacramento River (solid line) during 2013-2016 as a function of flow at Butte City Bridge (reach 5, rkm. 344), including upper and lower 95% confidence intervals (dashed lines). Dots represent the cumulative survival rates for groups of fish through the upper Sacramento River at the specific flow values.

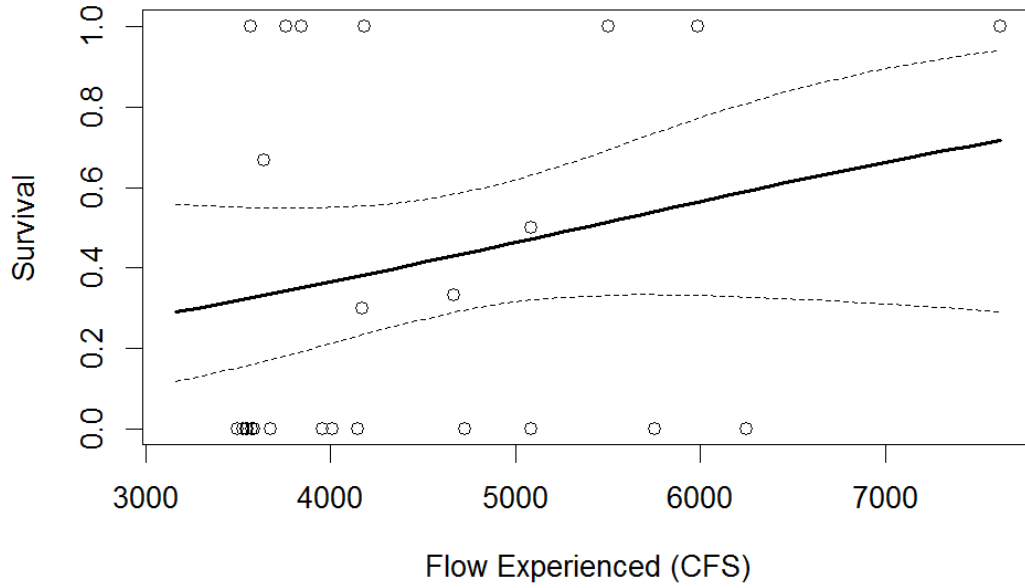


Figure 11. Cumulative survival predicted through the lower Sacramento River (solid line) during 2013-2016 as a function of flow at Wilkins Slough (reach 8, rkm. 241), including upper and lower 95% confidence intervals (dashed lines). Dots represent cumulative survival rates for groups of fish through the lower Sacramento River at the specific flow values.

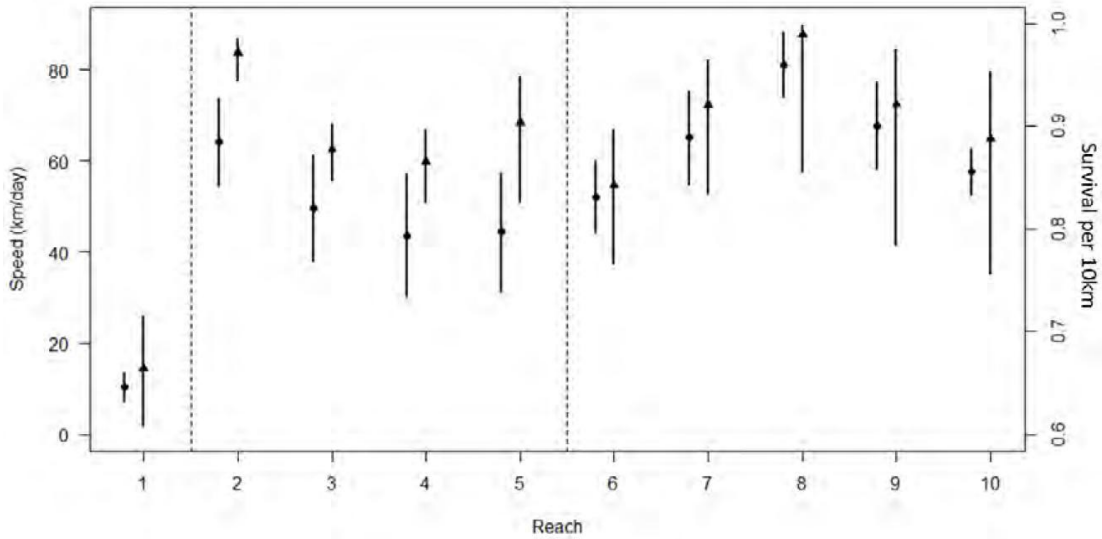


Figure 12. Movement speeds (kilometers per day, dots) and survival rates (per 10km, triangles) averaged for all years through Mill Creek, the upper and lower Sacramento River. The dotted lines are breaks between Mill Creek, the upper Sacramento River and lower Sacramento River. Error bars for movement speeds and survival rates represent one standard deviation from the mean and the upper and lower 95% confidence intervals, respectively.

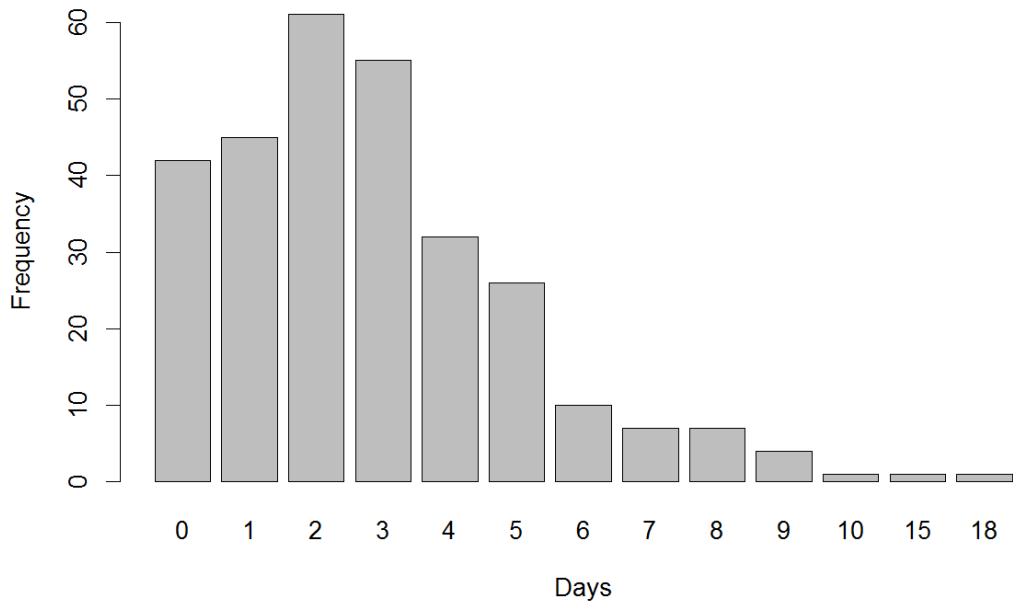
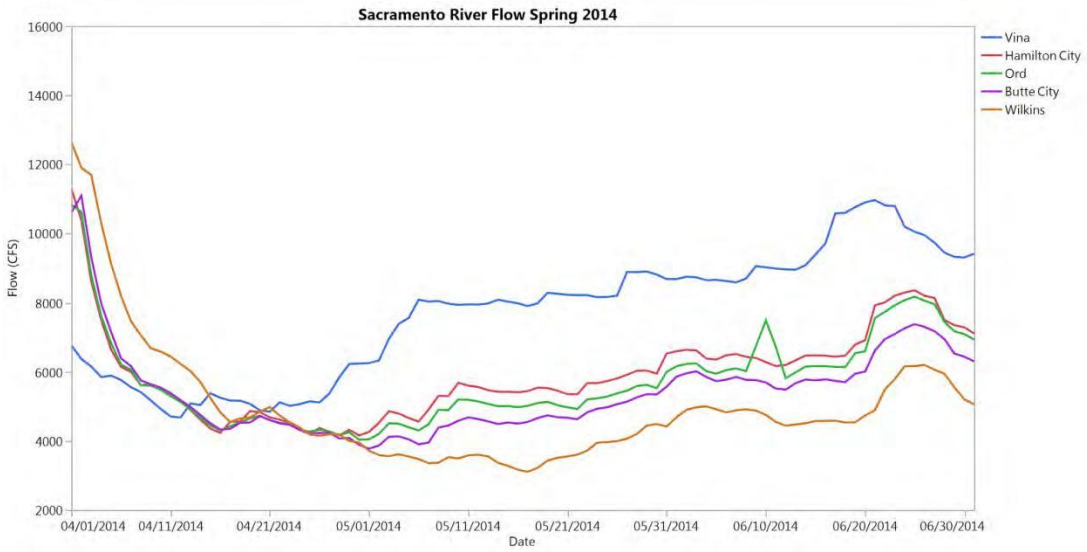
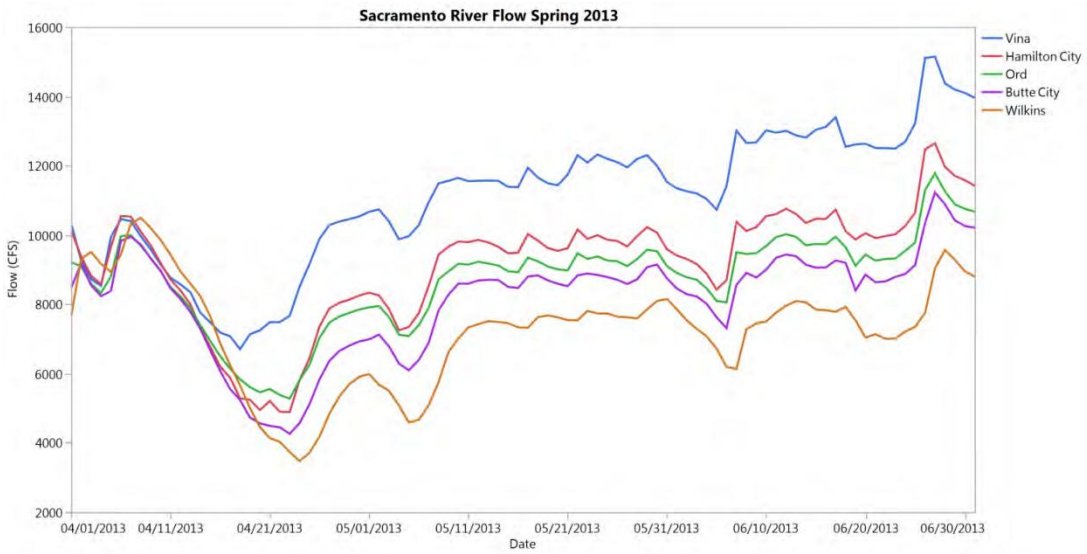


Figure 13. Number of days all 304 tagged Mill Creek smolts were detected after release, and before they were assumed to have died. Day 0 represents smolts that were detected < 24hrs.



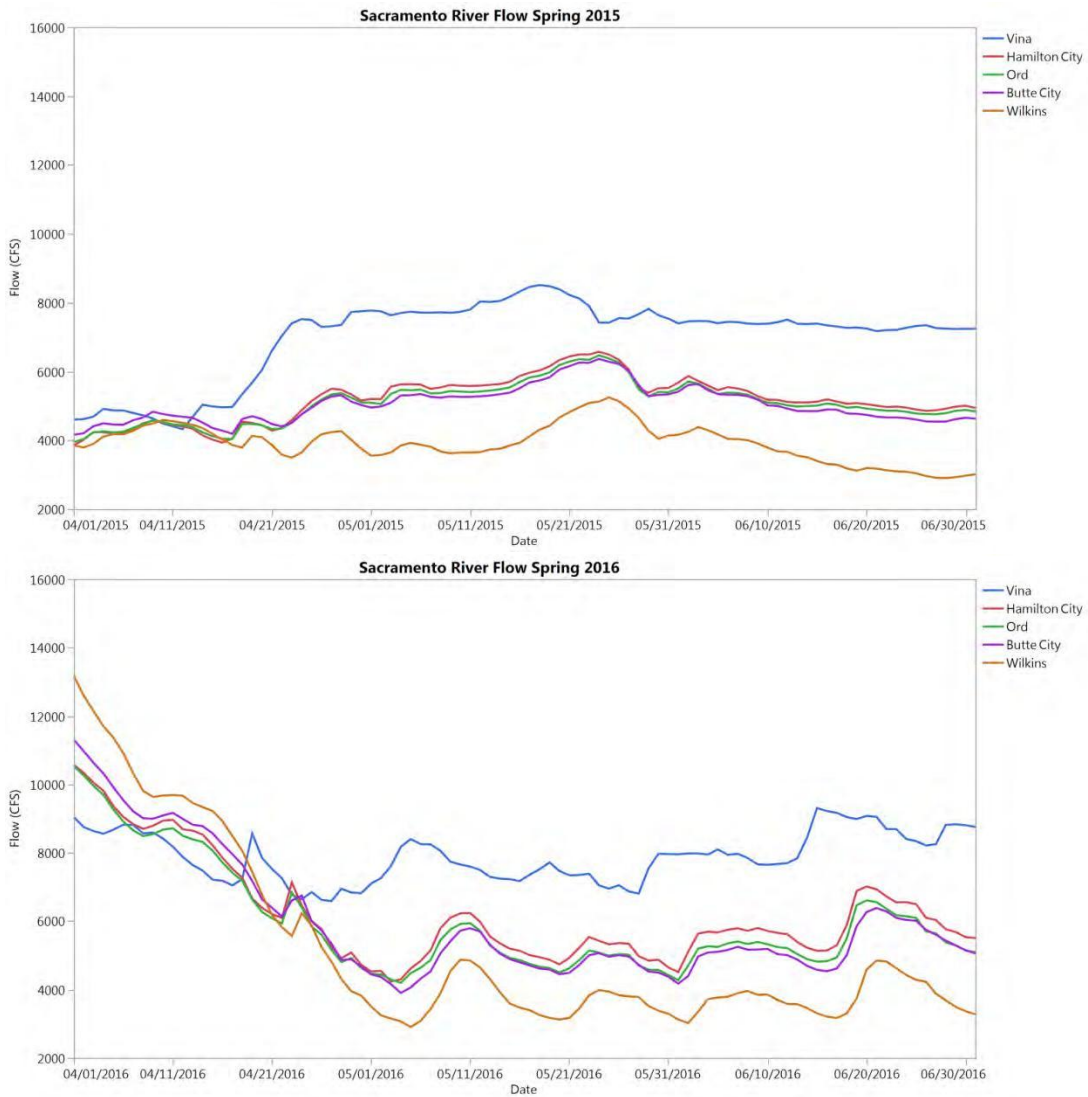


Figure 14. Flows measured at gauging stations in the upper and lower Sacramento River between 2013-2016. Vina is the beginning of the upper Sacramento River, Butte City is the end of the upper Sacramento River/beginning of the lower Sacramento River, Wilkins Slough is near the end of the lower Sacramento River. The area under each line represents the amount of water diverted in that reach. After water diversions begin mid-April, approximately 50% of the flow is diverted between the beginning of the upper Sacramento and end of the lower Sacramento River.

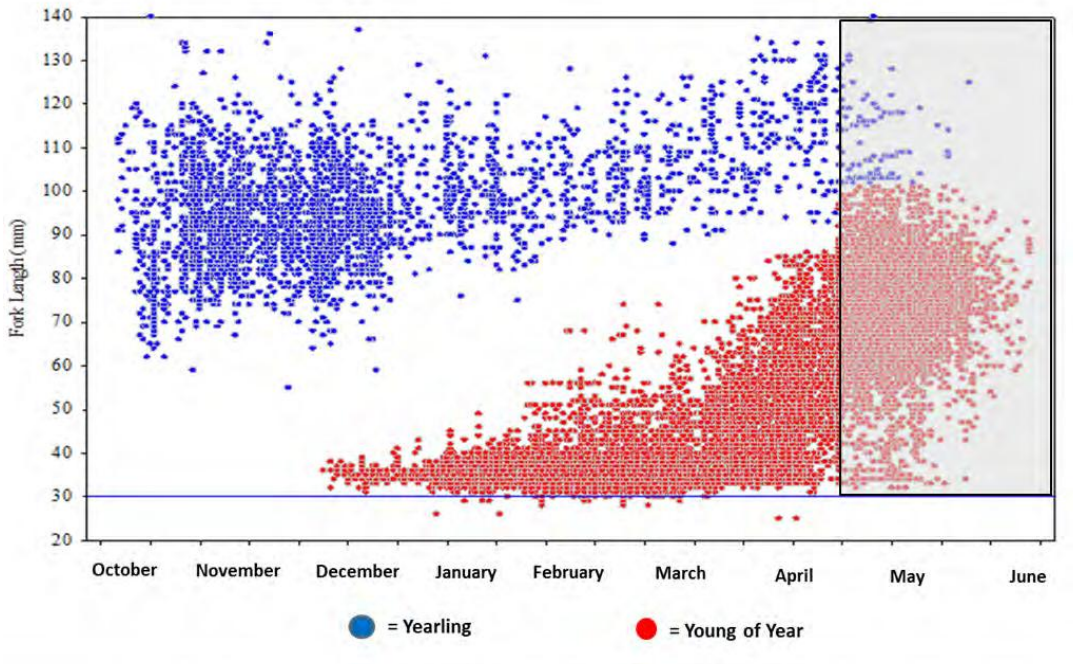


Figure 15: Length at date of out-migrating juvenile salmon from Mill Creek between 1995-2010. Smolts tagged in this study >80mm tend to leave relatively late in the spring compared to hatchery reared salmon and natural origin yearling-type Chinook salmon. Mill Creek smolts typically out-migrate during the timeframe when water diversions are operating in Mill Creek and the Sacramento River, which is indicated by the shaded box.

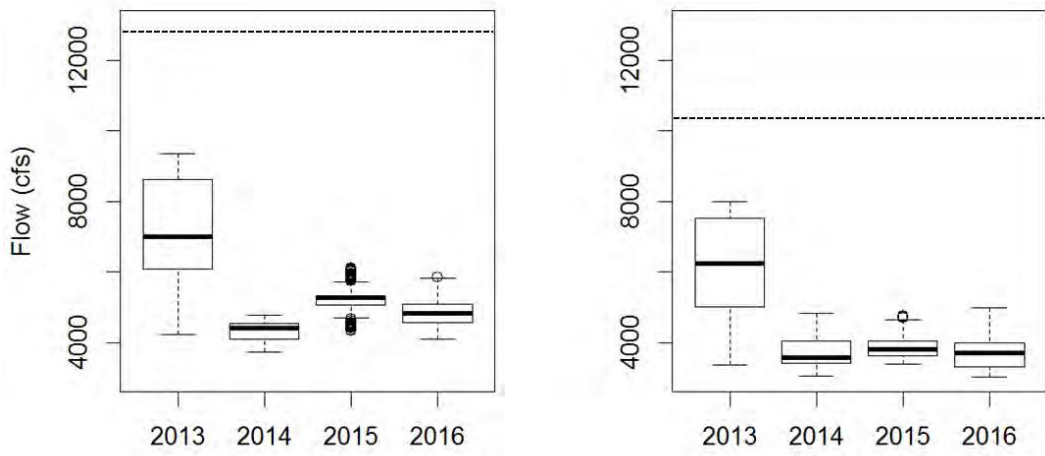


Figure 16. Flow values for the upper (left) and lower (right) Sacramento River during the study period for each year. Flow values are measured in cubic feet per second (CFS). The dashed lines indicate the historic average flow values for each region during the study period (1987-present).

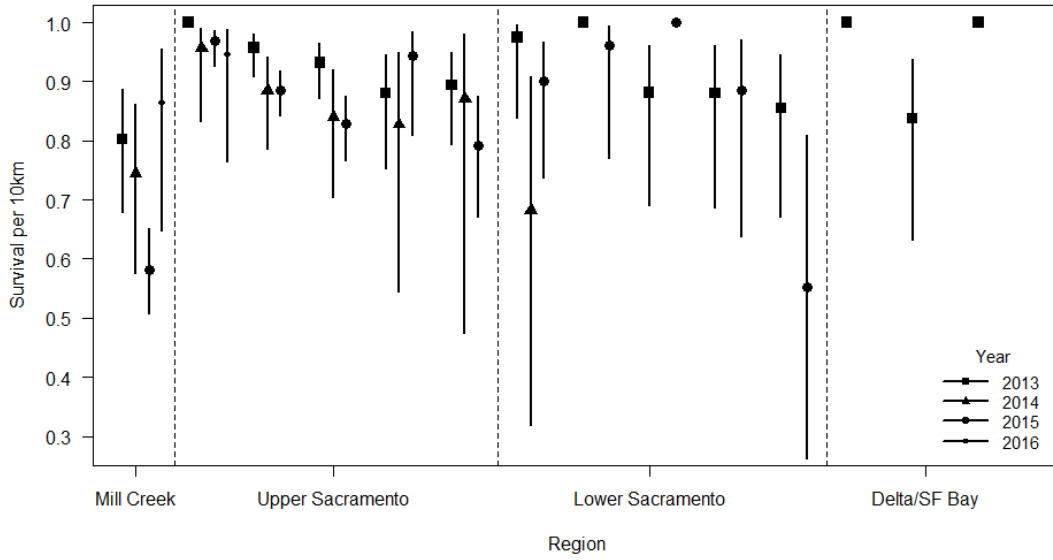


Figure 17. Reach specific survival rates per year throughout each study region, including the Delta and San Francisco Bay.

Chapter 3

Acoustic Tag Retention and Growth Rates in Juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) Exposed to Changing Environmental Conditions

Introduction

Acoustic telemetry is a widely-used tool to study the movement and survival rates of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) emigrating to the Pacific Ocean (McMichael et al. 2010; Michel et al. 2015; Perry et al. 2010). To perform these studies acoustic tags are surgically implanted into the peritoneal cavity of the juvenile salmon and closed using dissolvable sutures. Once recovered the salmon is released into the river and is assumed to retain the tag and behave naturally for the duration of the study. With the advent of JSATS (Juvenile Salmon Acoustic Telemetry System) miniature acoustic tags it is now possible to tag and track salmon as small as 80mm. This makes it possible to monitor the movement and survival rates of young of year salmon migrating downstream throughout rivers in California's Central Valley. This study measures the rate of tag shedding and the potential side effects of being captured by a rotary screw trap (RST) and undergoing surgery to implant the acoustic tag in hatchery Chinook salmon smolts.

Since 2013 we have been capturing and tagging wild juvenile Chinook salmon smolts from Mill Creek in Northern California (Tehama County) and tracking their movement and survival rates to the Pacific Ocean over a distance of 450 river kilometers. Once fish are tagged and released we are assuming they exhibit a strictly

downstream migration behavior. Underwater hydrophones detect the acoustic tags inside the salmon throughout their migration route at approximately every 20 river kilometers. When the acoustic tag is not detected at the next downstream receiver it is assumed that the salmon has died. An additional reason for the salmon not being detected is tag shedding. Tag shedding occurs when the salmon expels the acoustic tag through the surgical incision or body cavity, making it appear the fish has died when in fact it may not have. Many studies have researched tag retention and growth rates in juvenile Chinook salmon (Ammann et al. 2013; Anglea et al. 2004; Lacroix et al. 2004; Moore et al. 1990; Sandstrom et al. 2013; Tyus 1988) but all of these have been in a laboratory where water conditions are controlled and do not mirror the natural conditions which migrating smolts experience.

This study examines tag retention, survival and growth in juvenile salmon exposed to natural conditions while being held in tanks placed in Mill Creek, as well as examining the effects of being captured and held overnight in a RST. Throughout the study changing weather patterns and diurnal variations in solar radiation caused fluctuations in water temperature, stream flow and turbidity. These changing environmental conditions, as well as increasing photoperiod during the spring are some of the cues juvenile salmon use to begin smoltification and downstream migration (Wedemeyer et al. 1980). We held juvenile salmon in large tanks for 30 days after being captured by the RST and surgically implanting them with an acoustic tag. Growth and tag retention rates were measured at the end of the study to infer the likely impacts on natural fish we have tagged and released in Mill Creek since 2013.

Methods

Mill Creek is a tributary to the Sacramento River containing pristine spawning and rearing habitat for Chinook salmon and steelhead trout (*Oncorhynchus mykiss*). It originates on Mount Lassen and flows south-west for 33 miles before joining the Sacramento River near the town of Los Molinos. Its watershed drains 435 square miles and is only accessible at two road crossings, with most of its watershed protected within the Ishi Wilderness and Lassen National Forest. It is one of 5 streams currently supporting self-sustaining spring-run Chinook salmon populations in California's Central Valley, a life-history type that requires high elevation habitat in order to over-summer and mature in deep, cold pools. From 1995-2010 a RST was operated by California Department of Fish and Wildlife (CDFW) below Upper Dam on Mill Creek at river km 9 to study the outmigration timing of juvenile Chinook salmon and steelhead trout (Figure. 1). Since April 2013 I have used the same site and RST to capture and tag wild juvenile salmon and steelhead smolts emigrating out of Mill Creek and studied their movement and survival rates through various reaches downstream to the Pacific Ocean.

Hatchery-raised fall-run Chinook salmon smolts were used as surrogates for wild spring-run Chinook salmon juveniles because this population is part of the ESU that is listed as threatened under the ESA and the numbers of wild juveniles captured in the Mill Creek RST is very low. In order to examine RST effects on survival, we designated three treatment groups for this study: RST/untagged, RST/acoustic tagged, and control. The RST/acoustic tagged group experienced capture by the RST

and handling associated with it, followed by a surgical procedure to implant the acoustic tag in the peritoneal cavity of the fish. The RST/untagged group experienced capture by the trap and handling associated with it, and the control group was only weighed and measured. Each treatment group consisted of 50 juvenile salmon.

In total 150 juvenile salmon (body mass = 6.4 ± 0.5 g [mean \pm SD]; fork length = 81.7 ± 1.9 mm) were taken from Coleman National Fish Hatchery (CNFH) in Anderson, California and transported to upper dam on Mill Creek near Los Molinos, California. Upon arrival the smolts were divided into three groups for the RST/acoustic tag, RST/untagged, and control treatment. For the RST/acoustic tagged and RST/untagged groups, 100 smolts were released upstream of the RST and washed downstream into the trap, where they were exposed to entrainment by the trap followed by holding overnight in the trap. The control treatment was set aside in coolers with aerators and processed the following morning. The two RST groups were collected with dip nets the following morning and then anesthetized in MS-222 buffered by 120mg L^{-1} sodium bicarbonate prior to being weighed to the nearest tenth of a gram and measured to the caudal fork. An upper caudal fin-clip marked the RST/acoustic tagged fish, while the RST/untagged fish were marked by a lower caudal fin-clip. These caudal clips are similar to what wild smolts experience after being tagged and released in Mill Creek (for the purpose of collecting a tissue sample for DNA analysis).

The surgery procedure on the 50 RST/acoustic tagged smolts was consistent with the surgeries conducted on wild smolts captured in Mill Creek (see Deters et al.

(2010) for details). The Juvenile Salmon Acoustic Telemetry Systems (JSATS) tags used in this study were manufactured by Advanced Telemetry Systems (ATS), with a tag weight in air of 300mg and size of 10.7 x 5.0 x 2.8mm. After the tagged smolts recovered from surgery all fish were placed into two 490 liter plastic tanks (0.88 m tall x 0.9 m diameter) along the bank of the creek and held for 30 days. Water was supplied to the tanks at a rate of 13.6 liters per minute from a neighboring irrigation canal 0.25 meters above the tank. Two 1.2 cm hoses siphoned water from the canal to the bottom of the tanks and created a current for the salmon to swim in. Half of the smolts from each treatment were placed into each tank (each tank contained an equal number of RST/acoustic tagged, RST/untagged and control smolts).

Each morning the tanks were cleaned, temperature recorded and checked for shed tags using a large magnet to sweep the bottom. In both tanks a temperature logger recorded water temperature every 15 minutes near the bottom and (Figure. 2). Due to technical difficulties in the upstream tank the temperature logger only recorded data for approximately half of the study, which was in general consistent with temperatures in the downstream tank. Dissolved oxygen was recorded intermittently throughout the study, but difficulties with the instrument prevented us from having reliable measurements to analyze. After cleaning and checking the tanks for shed tags the smolts were fed a #2 crumble feed provided by CNFH at a ratio of 2% bodyweight per day, which is the standard feeding protocol for salmon reared in hatcheries (Iwama and Tautz 1981).

The tag retention study lasted for 30 days, which is equivalent to the battery life expectancy of acoustic tags implanted into wild smolts emigrating from Mill Creek. After the study all smolts were euthanized and processed on site. Length and weight measurements were recorded and all acoustic tagged smolts were checked with a metal detector to see if the tag was still present. For salmon that shed their tag it was noted if the tag had been expelled through the incision site or if the tag was pushed through the body wall at another location. Incision healing, inflammation rate, tag bulge and suture absence/presence were also noted.

In order to determine which factors were significant in relation to tag shedding a logistic regression was used to analyze various parameters which were measured throughout the study. The mean daily water temperature, maximum daily water temperature, fish length and weight before surgery were all factors used in the analysis. Data collected during this study allows us to factor in tag shed rates and any surgery-related mortality observed into the previous three years of outmigration survival for smolts tagged in Mill Creek. In addition we measure the growth rates of smolts from different treatment groups to examine growth effects related to the RST and RST/acoustic tag treatments.

Results

After 30 days in the holding tanks, the acoustic tagged salmon shed 10 (20%) of the original 50 tags implanted into the group. The first tag was shed after 9 days, and tag shedding continued for the remainder of the study except for a six day period

from day 17-23 (Figure 3). No salmon in this study died as a result of the surgical procedure or from being entrained by the rotary screw trap.

The growth rates of acoustic tagged salmon over the course of 30 days was significantly lower than that of the RST/untagged and control groups (ANOVA, p value = 0.0001). This finding is consistent with other studies that found an initial low growth rate for tagged salmon during the first 30 days, followed by compensatory growth after 30 days where the salmon catches up in weight and length compared to other groups (Adams et al. 1998; Ammann et al. 2013; Sandstrom et al. 2013). Additionally there was no significant tank effect (p value = 0.65) and no significant interaction between tank and treatment group (p value = 0.28). The body weight and length of the acoustic tagged smolts was initially higher than the other two groups because of the 5% tag to body weight ratio we follow for telemetry studies (Table 1); requiring the smolts to be a minimum of 6 grams in weight for JSATS tags using criteria recommended by Brown et al. (1999).

Average daily water temperature (p value = 0.43), maximum daily water temperature (p value = 0.45), and fish length before surgery (p value = 0.41) were all found to be insignificant in the analysis, and the only factor explaining variation in tag shedding was the weight of the smolt prior to surgery (p value = 0.05), which found that smaller smolts were more likely to shed their tags. Fish that shed their tag weighed on average 6.2 grams (SD = \pm 0.33 g), compared to the mean group weight of 6.5 grams. The predicted rate of tag shedding was highest for smolts near 6 grams, and declined continuously for larger fish (fig. 4).

Discussion

Acoustically tagged juvenile salmon tracked in biotelemetry studies experience a wide range of environmental conditions as they migrate downstream to the ocean. This novel experiment placed acoustic tagged juvenile salmon in changing water temperatures and turbidity levels and measured the rate of tag shedding, growth and mortality over a 30 day period. The water conditions these fish experienced were similar to the conditions experienced by smolts tagged and released in Mill Creek during the 2016 study. Downstream of Mill Creek in the Sacramento River and Delta, water conditions change as a result of increased solar radiation which warms the water and could potentially increase the rate of tag shedding. This factor, as well as other changing environmental variables such as flow and salinity, should be examined further to see if they also influence the rate of tag shedding.

After 30 days all tagged salmon survived effects from the rotary screw trap and surgical procedure, but shed 20% of the original 50 tags by the end of the study. The first tag was shed after 9 days, which is consistent with other studies that found a delayed start in tag shedding (Lacroix et al. 2004; Welch et al. 2007), and shedding continued for the duration of the study except for a seven day period (fig. 5). This rate of tag shedding is higher compared to other studies which have been conducted in hatcheries or laboratories where water temperatures are relatively cold and stable. Warm water temperatures have been shown to decrease the rate of incision healing after surgery in tag retention experiments, and in some cases prevent wound healing completely compared to fish which experience cold water temperature (Walsh et al.

2000). The water temperatures during this study were relatively warmer compared to other tagging studies (Ammann et al. 2013; Sandstrom et al. 2013; Tyus 1988), but were not consistently high due to diel fluctuations in temperature as well as temperature swings due to changing weather patterns.

While previous studies find warmer water temperatures are associated with increased tag shedding rates (Cooke et al. 2011; Walsh et al. 2000), we found that smolt weight before surgery was the only significant factor impacting tag-shed rates, with smaller fish more likely to shed their tag. Smaller fish naturally have a smaller peritoneal cavity where the acoustic tag is placed, and when the tag is inserted their stomach may put more outward pressure on the tag compared to a larger smolt with a bigger peritoneal cavity. This effect in turn may cause additional pressure on the sutures which hold the tag in place and could ultimately result in the tag being extruded. In addition to fish size, the amount of food in their stomach may be a factor in tag shedding, where higher feeding rates would lead to a more full stomach and cause more pressure on the tag and sutures. All salmon were fed a 2% body weight ration per day, which is consistent with other tag effect studies (Adams et al. 1998) and much lower than feeding rations for salmon rearing in the wild where consumption rates could be as high as 8% bodyweight per day (Sagar and Glova 1988). Given the fact that most smolts tagged and released in Mill Creek exhibit a strictly downstream migration behavior, the amount of time spent rearing and feeding is limited and in turn should lead to lower consumption rates. Additionally smolts tagged in Mill Creek migrate downstream through the Sacramento River, where the

natural channel has been replaced with rip rap and primary production has been severely impacted compared to neighboring flood plains (Sommer et al. 2001), resulting in lowered feeding opportunities.

Another finding during this study is that juvenile salmon implanted with acoustic tags grew significantly less than the control and RST/untagged groups in the same tanks. After 30 days the acoustic tagged group weighed on average one gram less than the other groups (Figure 6). This finding suggests that acoustic tagged smolts may not be as fit as control smolts or smolts only captured by the RST, and therefore may experience lower survival rates in the wild. Smolt survival rates in Mill Creek and the Sacramento River have been very low for wild smolts compared to those from other watersheds, and may be attributed to physical effects of tagging combined with the late outmigration timing of these smolts which coincides with greater predator densities in the Sacramento River and Delta (Nobriga 2007). More data needs to be collected in experiments where tagged and untagged smolts are exposed to predators to measure potential differences in predation rates on salmon which are acoustically tagged.

These findings have implications for biotelemetry studies where juvenile salmon survival is based on acoustic tag detections at receiver arrays located throughout a river system. These studies assume the juvenile salmon exhibits a strictly downstream movement behavior, and the absence of detections at subsequent receivers concludes that the fish has died. This study shows that after a certain period of time acoustic tags are being expelled by juvenile salmon, leading to the false

assumption that the fish has died. With this data it is possible to calibrate survival estimates for acoustic tagged salmon which are detected for longer than nine days. Travel times for smolts tagged in the upper Sacramento River at CNFH took on average 18.7 days (± 2.3 SE) to reach the Golden Gate over a distance of 534 river kilometers (Michel et al. 2013). According to these travel rates approximately 10% of the tags could have been shed from these smolts between 9 and 18 days, which would result in underestimating survival towards the end of their out-migration. For salmon remaining in the system for longer periods of time tag shedding could potentially be much greater, and the data collected in this study may be used to calibrate these estimates to show that survival rates may in fact be higher.

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Treatment	n	Before		After		Growth	
		Weight (g)	Length (mm)	Weight (g)	Length (mm)	Weight (g)	Length (mm)
Control	50	6.4 (5.5-7.8)	81.1 (80-86)	12.5 (9.8-15.5)	100.2 (94-106)	6.1 (3.5-9.7)	19.1 (11-24)
Tagged	50	6.5 (6-8.4)	82.3 (79-89)	11.4 (9-15.4)	97.9 (92-106)	4.9 (2.4-9)	15.5 (5-23)
RST	50	6.2 (5.5-7.5)	81.5 (79-87)	12.3 (9.5-14.9)	100.1 (94-107)	6.1 (3-9.1)	18.6 (10-28)

Table 1. Before, after and growth weight and lengths for all treatment groups. Values represent the group mean, range in parenthesis.

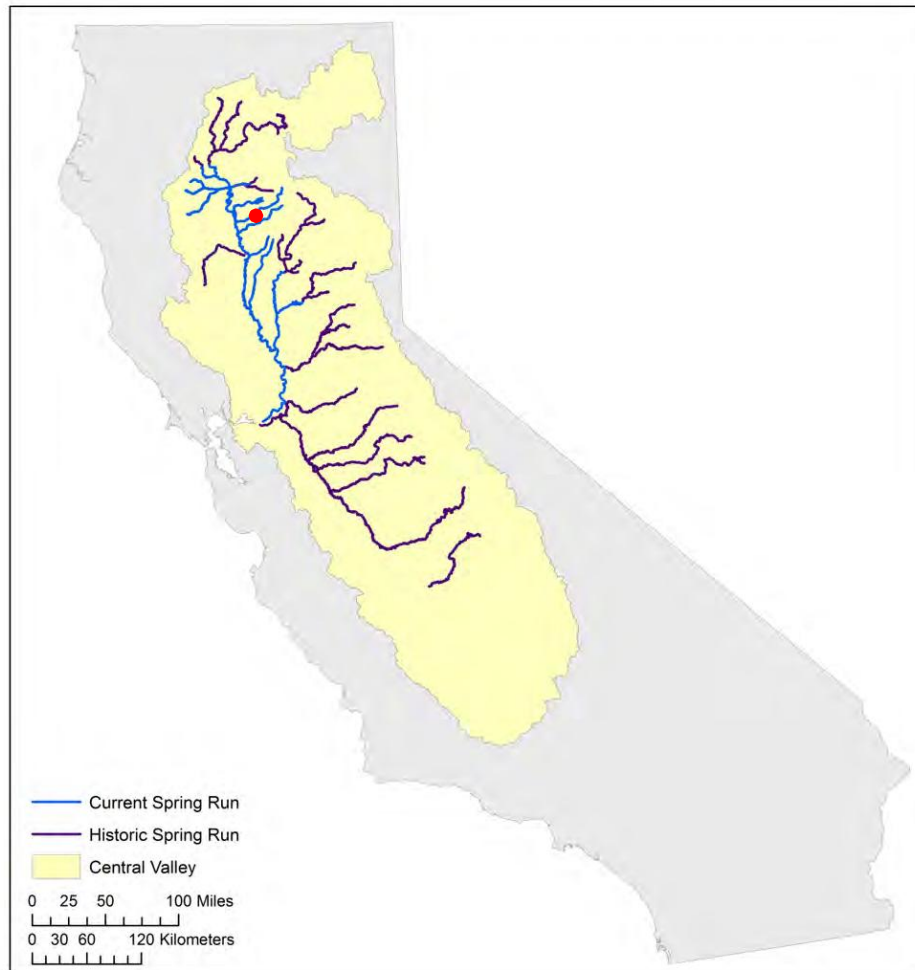


Figure 1. Map of California's Central Valley indicating the historic spring-run Chinook habitat (purple) and current habitat (blue) remaining. The red dot indicates the location of the RST and tag effect study on Mill Creek.

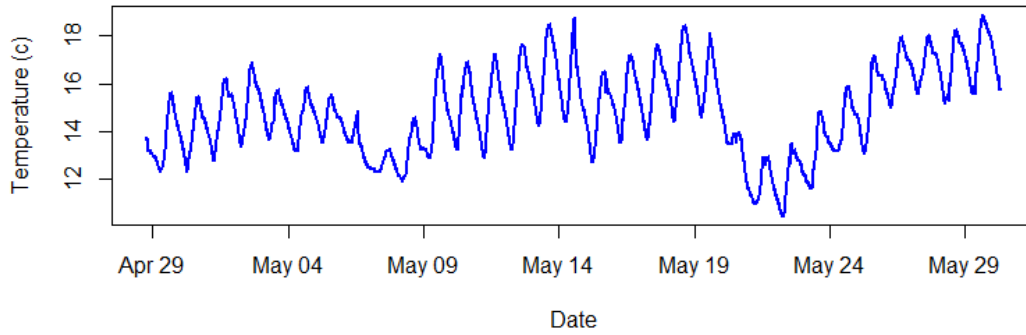


Figure 2. Daily water temperature recordings from holding tanks throughout the study, showing the diel variations the salmon experienced.

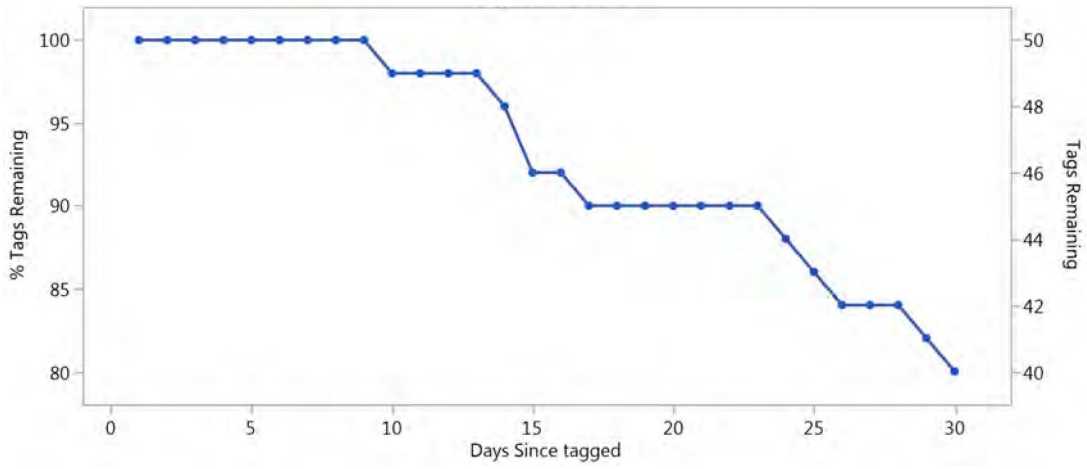


Figure 3. Cumulative number of tags shed and total percent remaining in juvenile Chinook through time over the 30 days study.

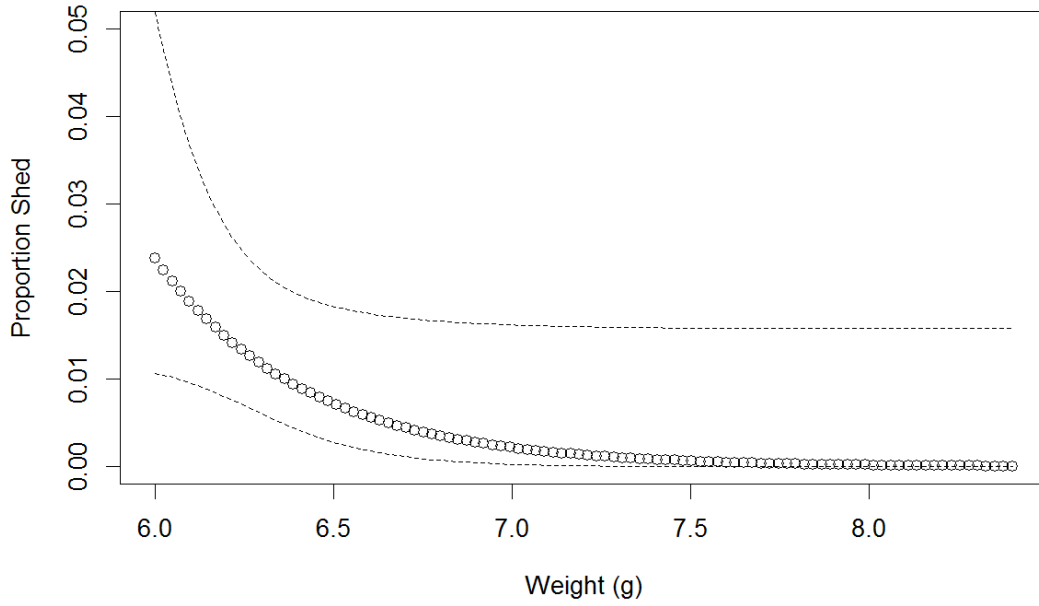


Figure 4. Predicted tag shed rates as a function of weight (grams) before surgery for smolts used during the study. Dashed lines represent the upper and lower 95% confidence intervals.

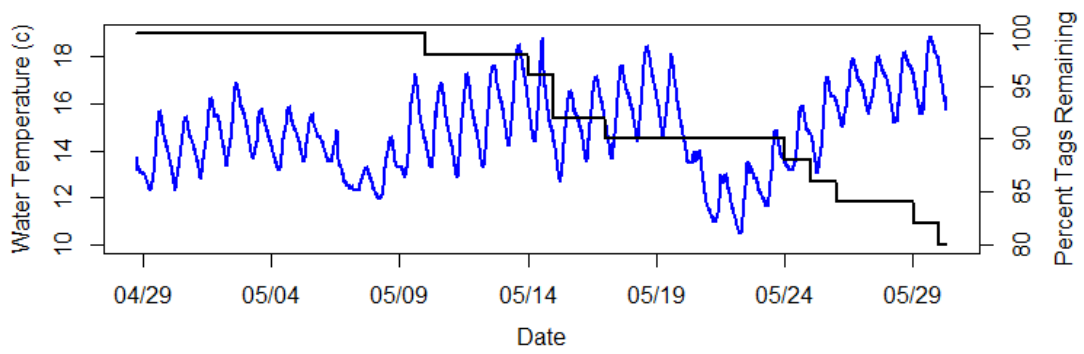


Figure 5. Water temperatures throughout the study in relation to the percent of tags remaining in tagged fish (black line).

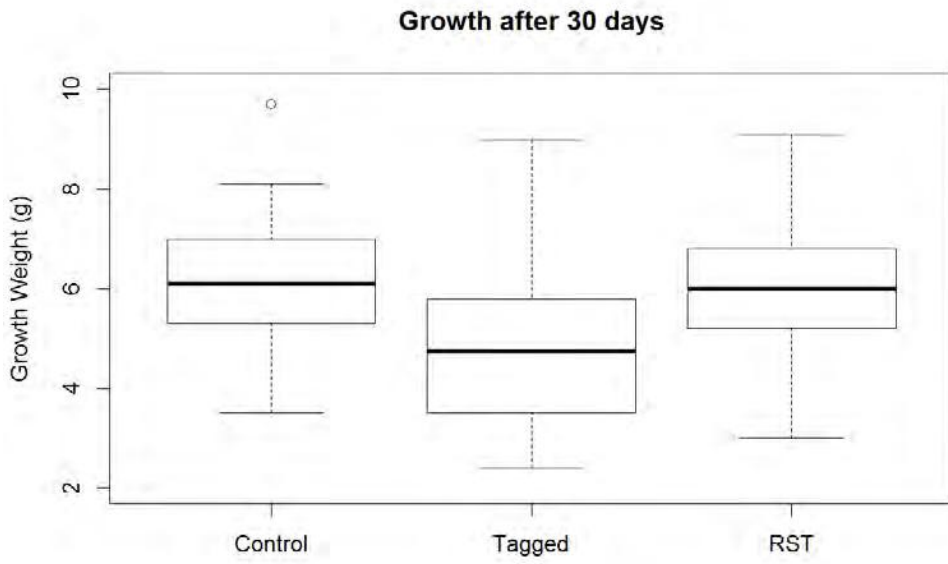


Figure 6. Growth weight in grams for each treatment group, showing the median, 25th and 75th quartiles.

Chapter 4

Conclusion

Central Valley Chinook salmon have endured many modifications to their freshwater habitat over the last 150 years, with the biggest being the inability to access most of their historic spawning and rearing habitat behind large dams. As a result the populations of these fish have been greatly reduced, and in some cases are on the verge of extirpation. Yet on occasion, when high river flows coincide with nutrient and food-rich conditions in the ocean, populations of Central Valley Chinook salmon can rebound greatly. This happened most recently in the late 90's and early 2000's during a series of wet years that were timed perfectly with productive ocean conditions, and resulted in some of the largest salmon runs seen in decades. While these events require both the freshwater and marine environment to correspond with successful out-migration conditions as well as ocean productivity, it is the freshwater side where humans have more control over the system.

In today's era of flood control and water management, the flow regimes of dammed rivers are highly regulated and tend to have the opposite seasonal dynamics of a natural system. Flows are typically high during the summer to deliver water for agricultural uses, and low in the winter/spring when water is conserved to fill reservoirs during the rainy season. This way of managing streamflow for human interests has negatively impacted anadromous fish populations, as these fish have evolved with high winter/spring flows which increase juvenile rearing capacity and help them successfully out-migrate to the ocean as smolts. In many ways the current

water management system of the Sacramento and San Joaquin Rivers leave them in a perpetual state of drought, even during wet years when there is plentiful water stored upstream of reservoirs. In addition, small irrigation dams on tributaries such as Mill Creek are having the same effect on flow regimes during the out-migration of salmon smolts but on a smaller scale. These irrigation dams can divert much of the water for out-of-stream uses during the spring, especially during drought conditions when natural runoff is already impaired, leaving low flows for salmon smolts to out-migrate through.

These altered flow regimes present many challenges for salmon smolts out-migrating from Mill Creek during the late spring, which encounter rapidly changing water conditions within a relatively short amount of time. This study shows that with increased flows in both Mill Creek and the Sacramento River, out-migration survival increases. In Mill Creek this finding was extremely evident, with low survival rates observed during periods of low flow, and high survival rates observed during wet years and high stream flow. With these survival estimates throughout a range of flow values, it is possible to implement a minimum flow criteria in Mill Creek to support desired smolt survival rates through the diverted stream reaches. This information will be particularly helpful during drought conditions when the amount of natural runoff may not be enough to satisfy the needs of both water diversions and the aquatic ecosystem in Mill Creek. In addition, water conservation actions may be implemented to help conserve the water diverted from Mill Creek to supply small scale farms and ranches. Using drip rather than flood irrigation, or watering at night

rather than mid-day to reduce evaporation rates can help reduce the amount of water needed to accomplish the goals of local farmers while keeping more water in the stream for salmon.

In the Sacramento River, implementing a more natural spring flow regime would most likely increase smolt survival rates through the river and into the Delta. Using the data collected during this study it is possible to develop baseline estimates for smolt survival rates through the upper and lower Sacramento River as a function of flow. While this management strategy may be difficult to execute as a result of the many stakeholders who have interest in the water behind Shasta Dam, if the current trend of declining salmon populations continues this action may gain more support. One way to implement this strategy is to construct off-site storage reservoirs in neighboring valleys to the Sacramento River which are filled during periods of winter runoff, and then drained in the spring to increase the flow in the Sacramento River when water is being conserved behind Shasta Dam. This action would allow the conservation of water for agriculture during the summer yet still provide higher flows for the aquatic ecosystem during the spring, which has in recent years experienced chronically low spring stream flow as a result of the altered flow regime.

In addition to the information gathered on salmon smolt survival rates, this study shows that survival estimates in acoustic telemetry studies may be biased low as a result of tag shedding. When conducting acoustic telemetry experiments it is critical to tag groups of fish that are representative of the population in question. However, when tagging smolts weighing close to 6 grams it becomes increasingly

possible that these fish will expel their tag at some point. As a result, correction factors can be implemented into the survival analysis for fish which are close to this weight threshold, and survival estimates can generally be increased for smolts being tracked for longer than 9 days. However, as technology continues to advance, the type and style of acoustic tags will become smaller and allow the tracking of fish much smaller than 6 grams. This will likely change the tag shedding rates associated with salmon of the same size used in this study, and further studies should continue to be conducted into how tag shedding rates respond to different types of acoustic tags.

With the populations of many Central Valley salmon currently in dire straits, the information presented in this thesis will hopefully shed light into the mechanisms impacting salmon smolt survival rates. Understanding how environmental factors such as flow and temperature influence salmon smolt survival, especially during drought conditions, is critical in managing these fish for recovery. The positive correlation between increasing flow and increasing survival makes the simple point that survival improves with higher flows during critical spring-time migration windows. During drought conditions supplying enough water for salmon smolts and agricultural uses will be challenging, but the flow criteria presented in this thesis can be used to determine a minimum flow value that will still promote a desired survival rate.