Juvenile salmon growth, movement, and survival in Butte Creek and the Sutter Bypass- A look at the past and present tagging studies

Jeremy Notch, Flora Cordoleani, Alex McHuron, Clint Garman, Tracy McReynolds

NOAA FISHERIES | Southwest Fisheries Science Center
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION

UNIVERSITY OF CALIFORNIA
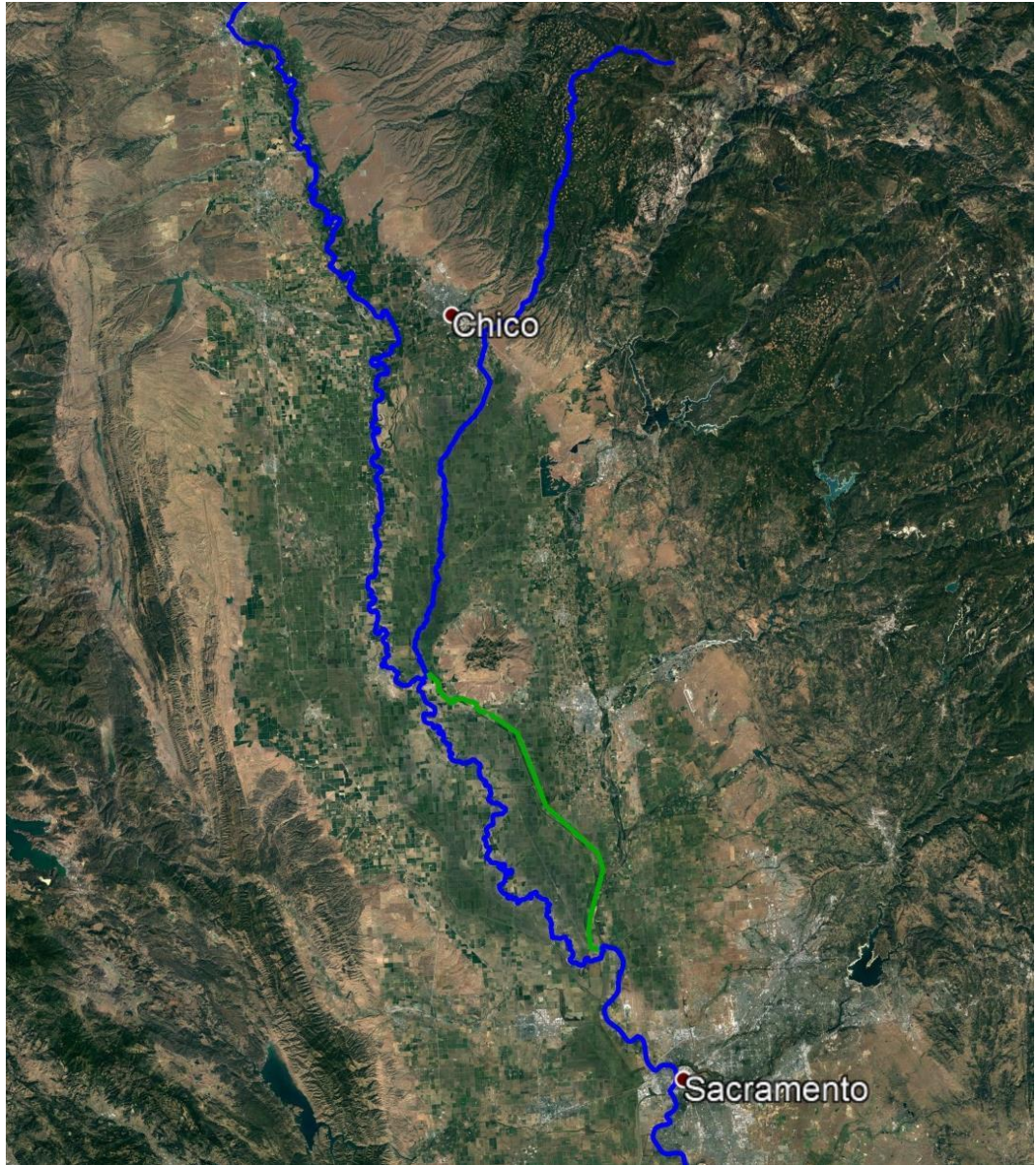SANTA CRUZ

Study Objectives

Part 1:
-What is the growth and residence time of spring-run juveniles rearing in Butte Creek and the Sutter Bypass? (CDFW CWT Study, 1996 - 2004)
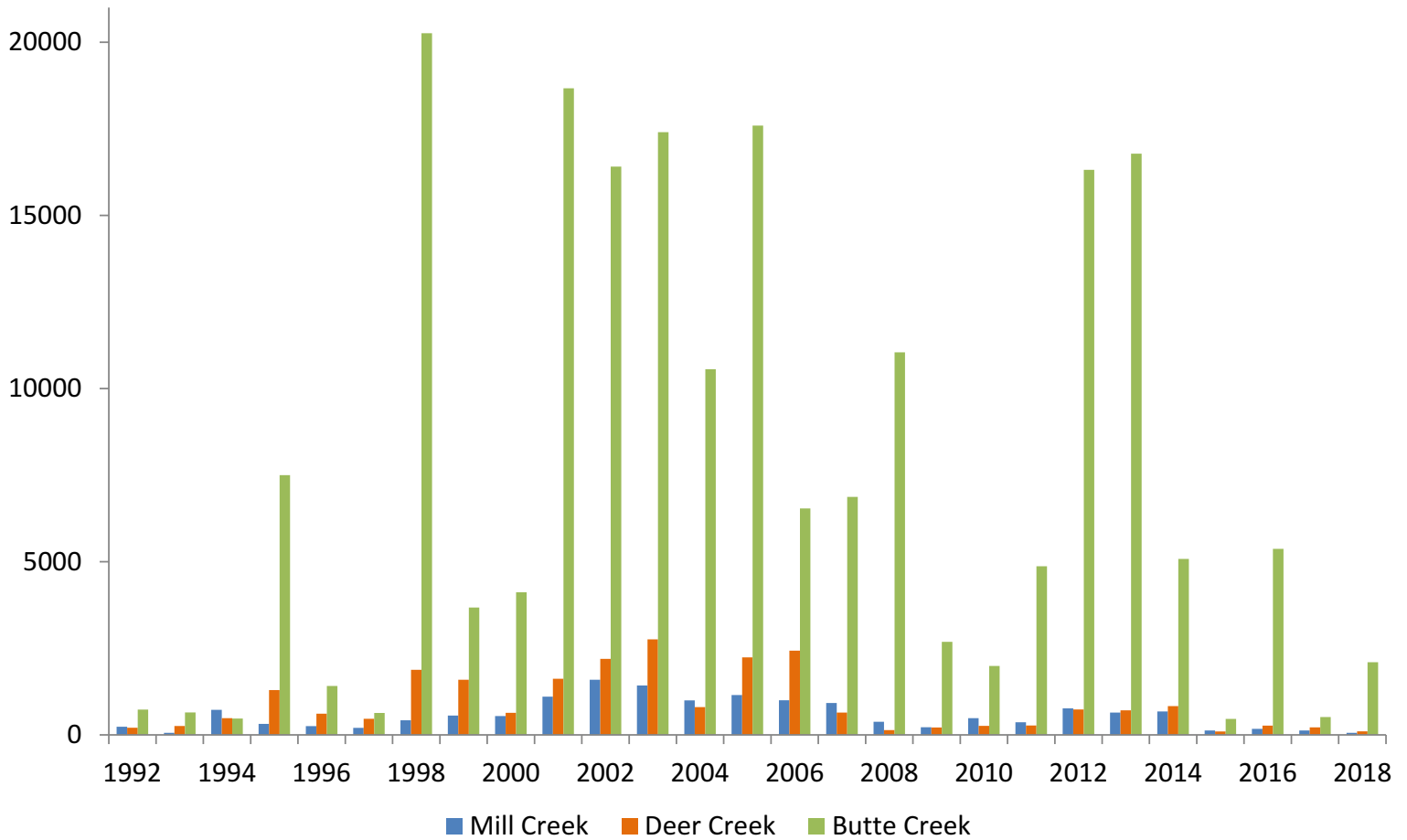
Part 2:
-What are the survival and movement rates of smolts out-migrating from the Sutter Bypass? (NOAA Acoustic Tagging Study, 2015 - 2017)

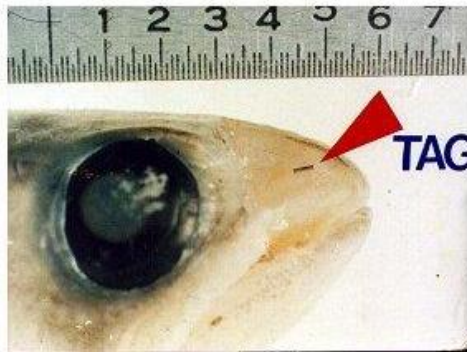Mill, Deer, Butte Creek Spring-Run Escapement 1992 - 2018

Part 1
CDFW Coded Wire Tagging (CWT) Study – 1996-2004

- ~750,000 spring-run juveniles (30-40mm) CWT tagged between 1996 – 2004 near spawning grounds in late January – early February

- 769 recaptured ~70 miles downstream in the Sutter Bypass

- Unique ID on CWT allows for analysis of group movement and growth rates

1996 – 2004 CWT Recaptures in Sutter Bypass
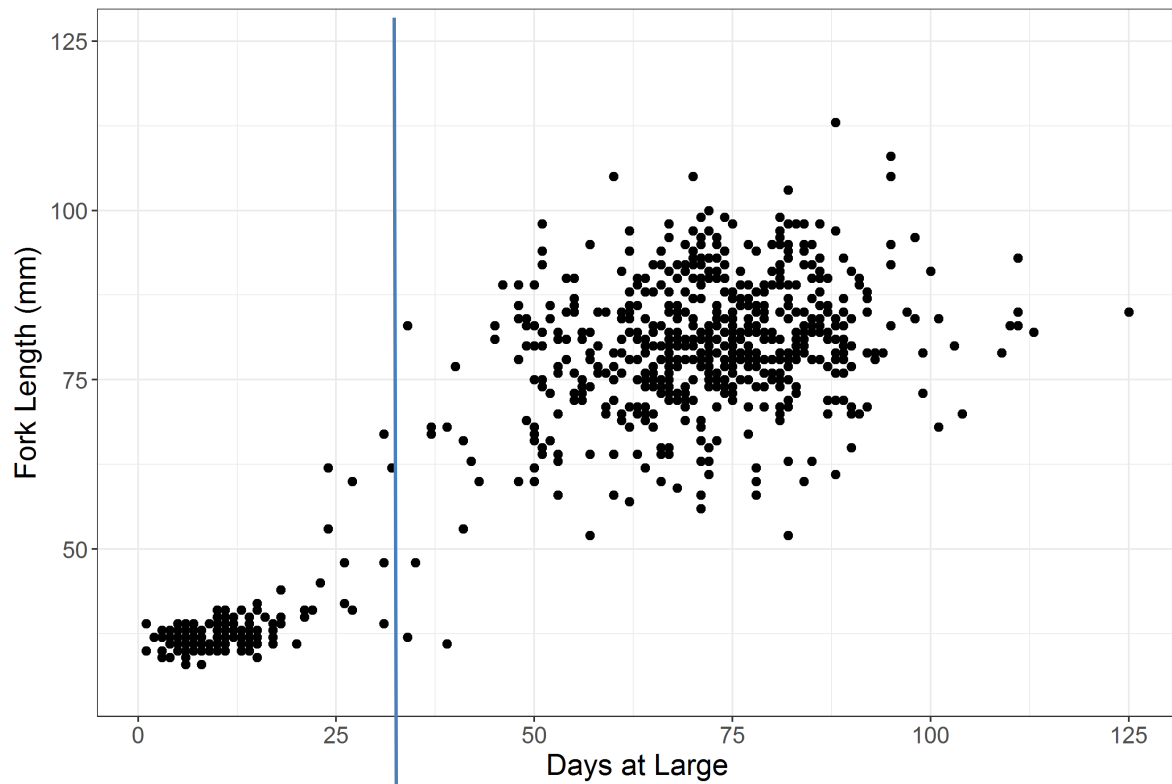
Runners
n = 137 (17%)
Av. residency = 11 days (± 5.6)
Av. growth = 3mm (0.27mm/day)
Av. length = 38mm (± 4mm)

Walkers
n = 628 (83%)
Av. residency = 72 days (± 13.5)
Av. growth = 44mm (0.62mm/day)
Av. length = 80mm (± 10mm)

1996 – 2004 CWT Recaptures in Sutter Bypass
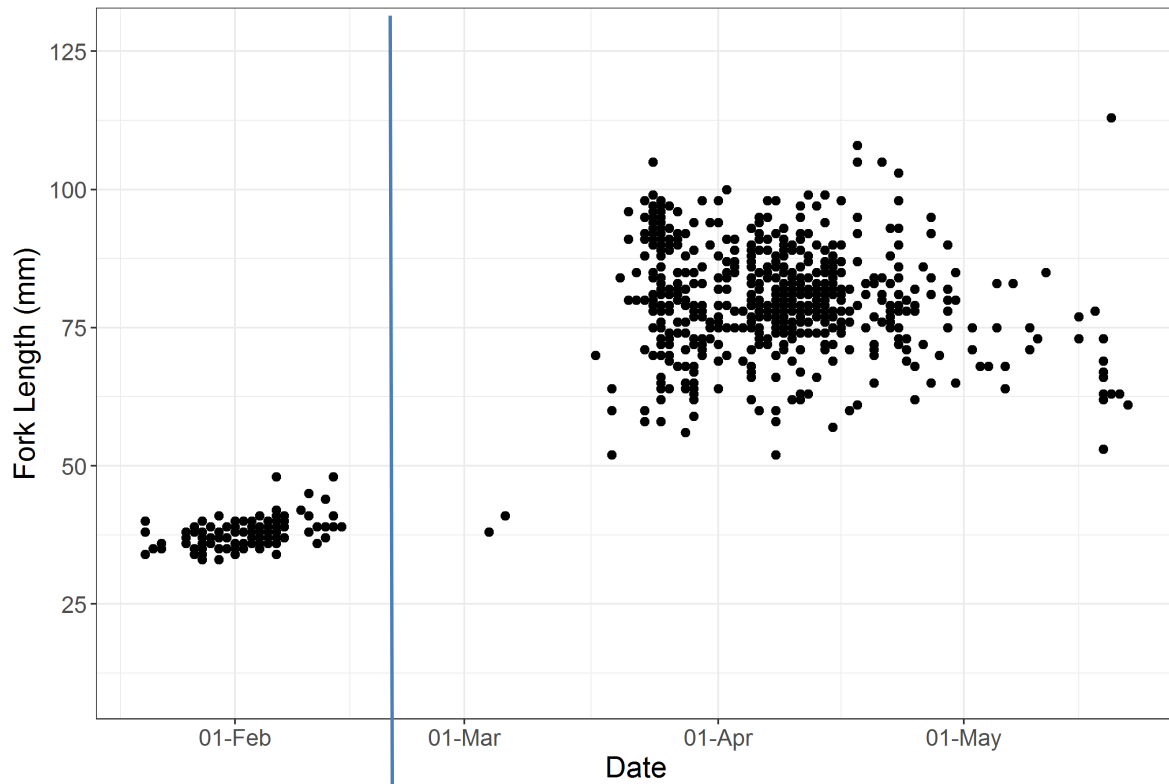
Runners
n = 137 (17%)
Av. residency = 11 days (± 5.6)
Av. growth = 3mm (0.27mm/day)
Av. length = 38mm (± 4mm)

Walkers
n = 628 (83%)
Av. residency = 72 days (± 13.5)
Av. growth = 44mm (0.62mm/day)
Av. length = 80mm (± 10mm)

Walker

Runners
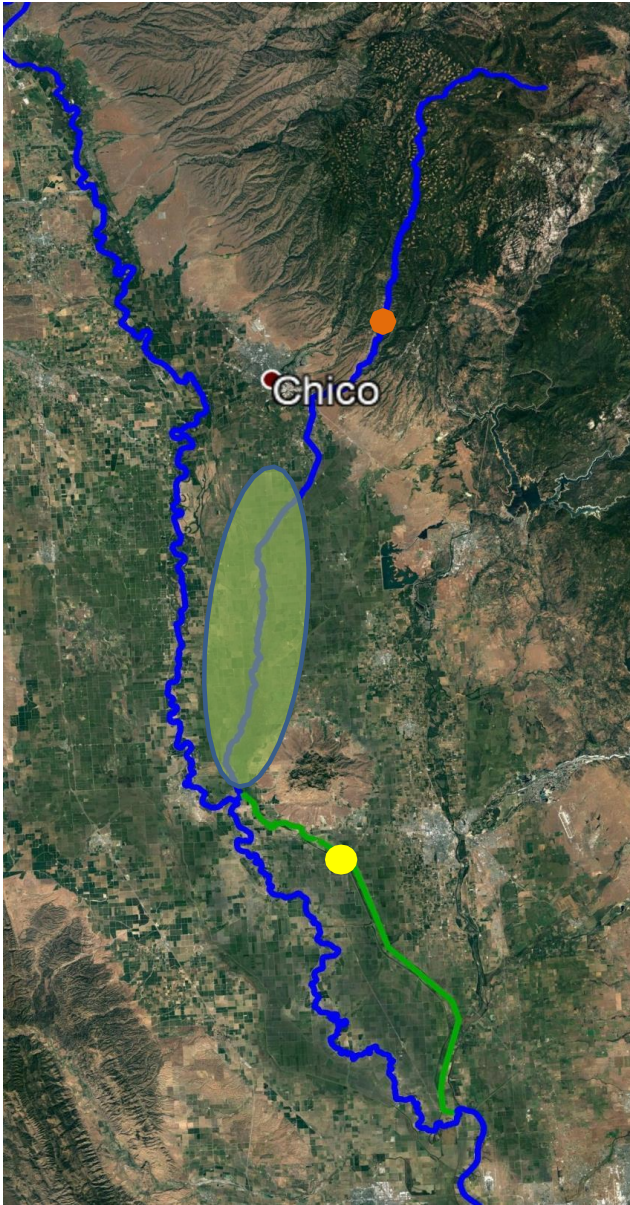
Butte Basin

- Largest contiguous wetland habitat in the Sacramento Valley

- Butte Sink managed by USFWS as a wildlife refuge

- Mostly comprised of private land with 32 conservation easements

Part 2
2015 – 2017 Sutter Bypass Acoustic Tagging Project
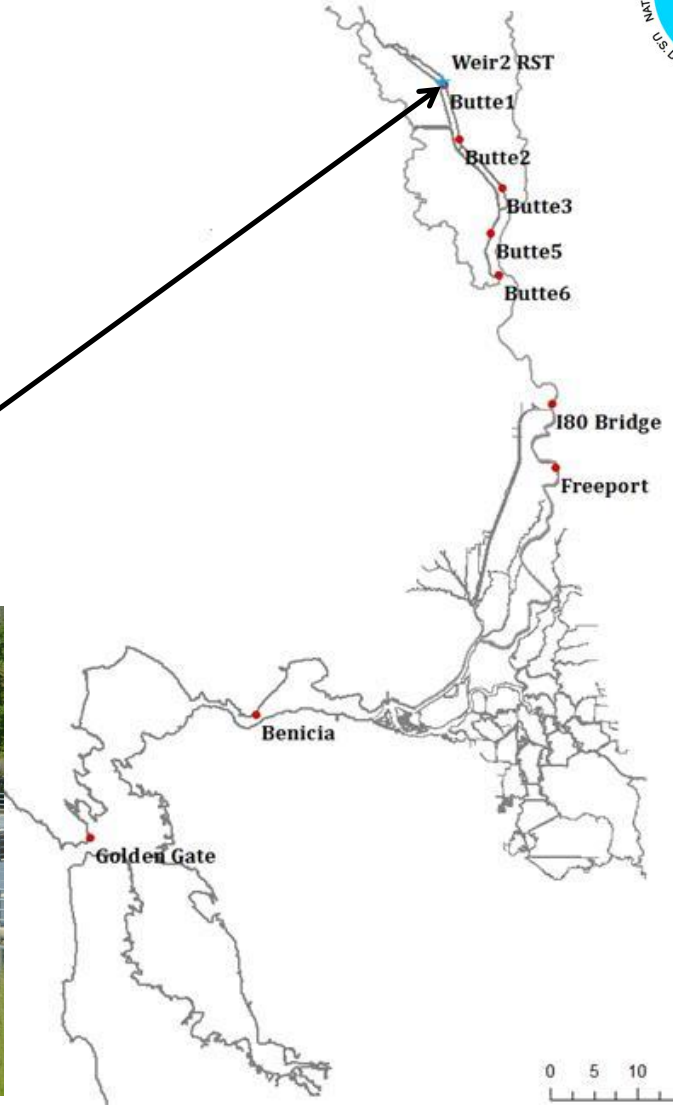
JSATS – Juvenile Salmon Acoustic Telemetry System

- Minimum fish size > 80mm, 6.0 g

- Unique ID for each tag, pings every 5 seconds for 30 days

- Fish released at 9pm to allow for recovery
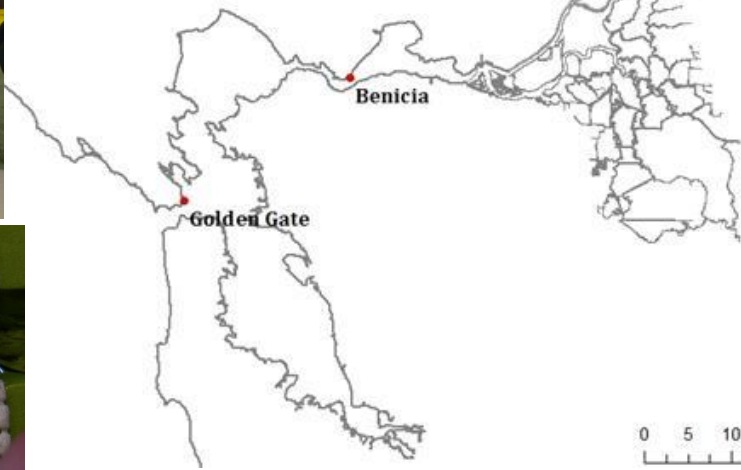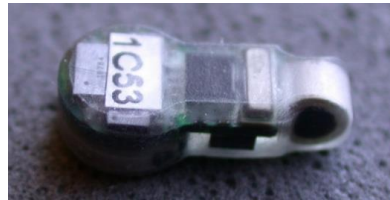
Genetics By Year
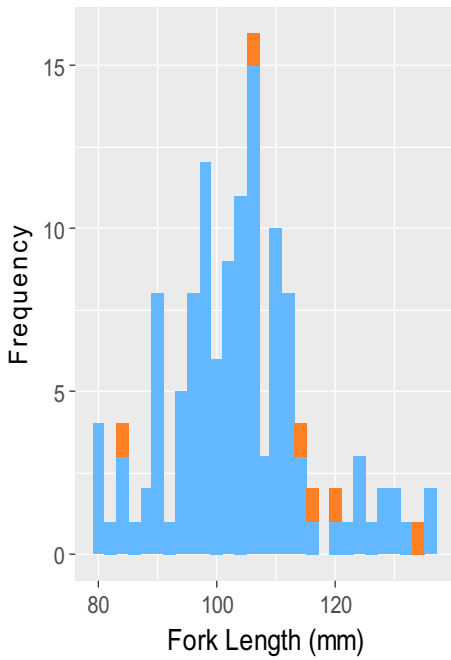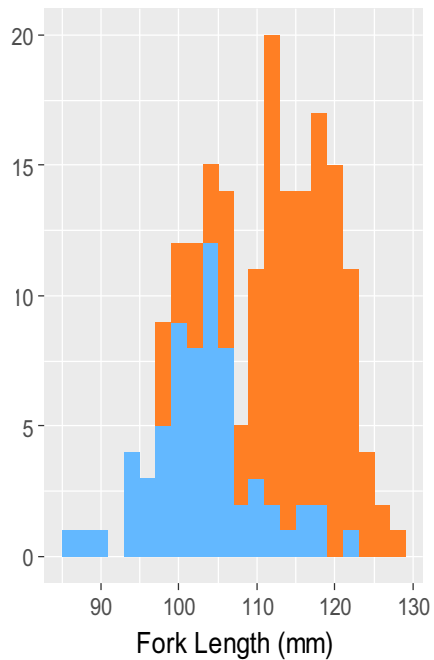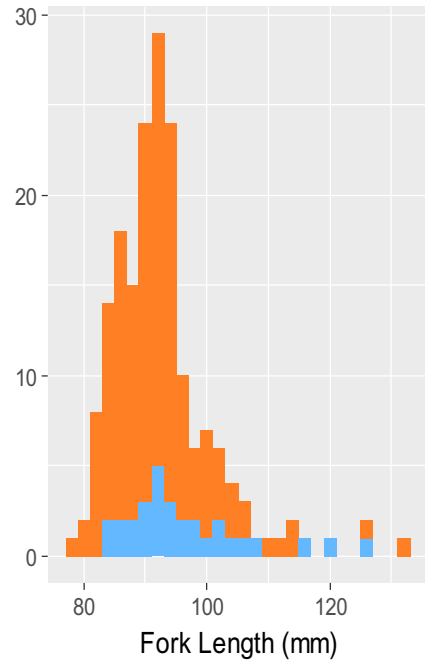
Survival estimation
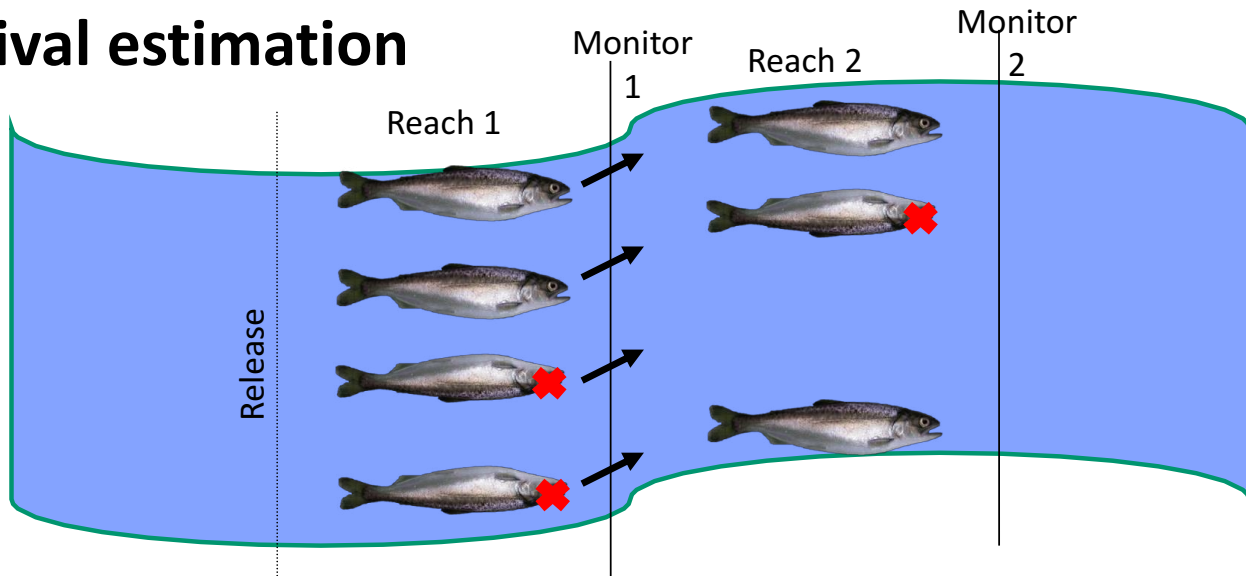
- Covariates: fish length, fish condition factor, temperature at release, flow at release, travel rate

Model	# Parameters	Delta AICc
Reach + Year	18	0
Reach + Travel Rate (Sutter, Sac, Delta, Bay)	20	0.7
Reach + Flow at Release	17	8.34
Reach + Temp at Release	17	8.67

Regional Survival Rates
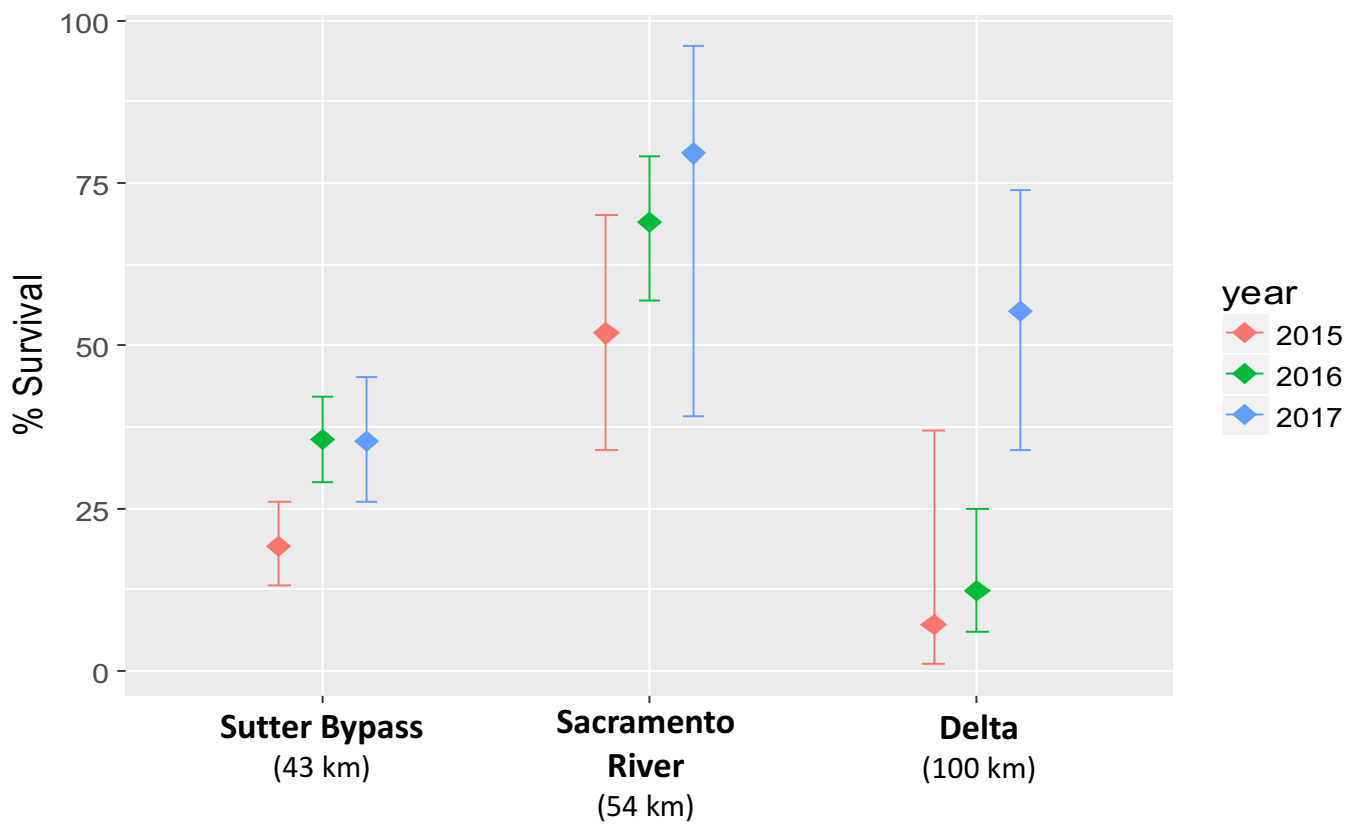
Movement Rates vs. Survival
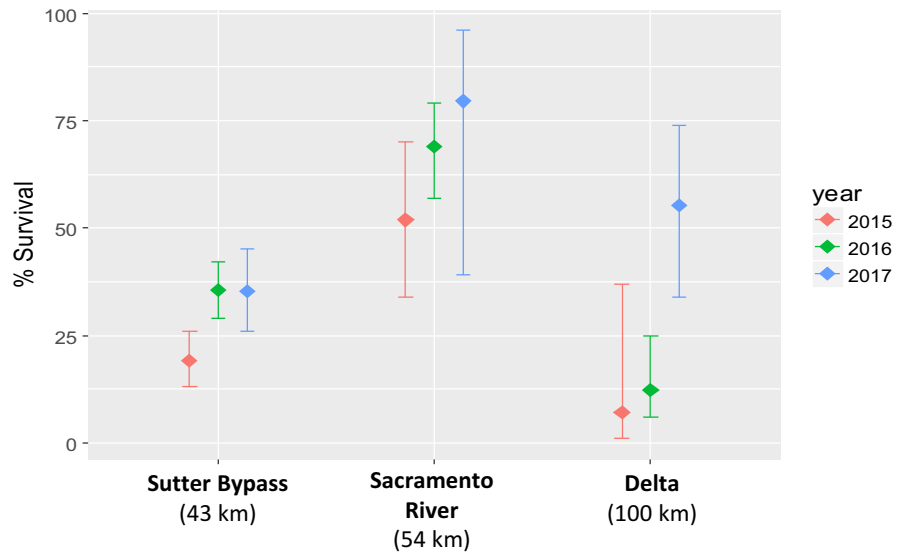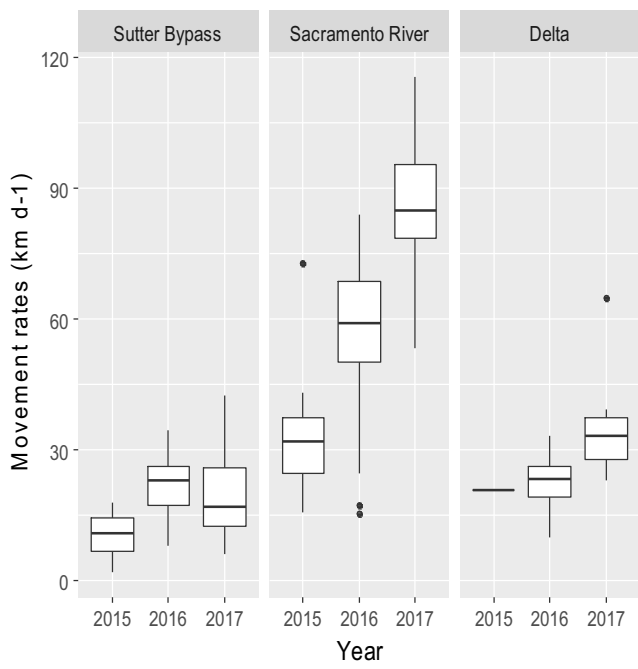
Conclusions

- Juveniles tend to walk (72 days, 83%) vs run (11 days, 17%) through Butte Creek and the Sutter Bypass

- Growth rates averaged 44mm (0.6mm/day) for walkers

- Low smolt survival rates through the Sutter Bypass and Delta in recent years

- Smolt survival appears to be correlated with movement speed: faster movement speeds lead to higher survival rates

Thank you

Alex McHuron

Flora Cordoleani

- Clint Garman
- Tracy McReynolds
- Paul Ward

Questions ?

NOAA Technical Memorandum NMFS

LIFE HISTORY AND CURRENT MONITORING INVENTORY OF SAN FRANCISCO ESTUARY STURGEON

Joseph Heublein, Russ Bellmer, Robert D. Chase, Phaedra Doukakis,
Marty Gingras, Douglas Hampton, Joshua A. Israel, Zachary J. Jackson,
Rachel C. Johnson, Olaf P. Langness, Sean Luis, Ethan Mora, Mary L. Moser,
Larissa Rohrbach, Alicia M. Seesholtz, Ted Sommer, and Jeffrey S. Stuart

NOAA Technical Memorandum NMFS

The National Oceanic and Atmospheric Administration (NOAA), organized in 1970, has evolved into an agency which establishes national policies and manages and conserves our oceanic, coastal, and atmospheric resources. An organizational element within NOAA, the Office of Fisheries is responsible for fisheries policy and the direction of the National Marine Fisheries Service (NMFS).

In addition to its formal publications, the NMFS uses the NOAA Technical Memorandum series to issue informal scientific and technical publications when complete formal review and editorial processing are not appropriate or feasible. Documents within this series, however, reflect sound professional work and may be referenced in the formal scientific and technical literature.

SWFSC Technical Memorandums are accessible online at the SWFSC web site. (http://swfsc.noaa.gov)

Print copies are available from the National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161. (http://www.ntis.gov)

SEPTEMBER 2017

LIFE HISTORY AND CURRENT MONITORING INVENTORY OF SAN FRANCISCO ESTUARY STURGEON

Joseph Heublein, Russ Bellmer, Robert D. Chase, Phaedra Doukakis,
Marty Gingras, Douglas Hampton, Joshua A. Israel, Zachary J. Jackson,
Rachel C. Johnson, Olaf P. Langness, Sean Luis, Ethan Mora, Mary L. Moser,
Larissa Rohrbach, Alicia M. Seesholtz, Ted Sommer, and Jeffrey S. Stuart

U.S. DEPARTMENT OF COMMERCE

National Oceanic and Atmospheric Administration

National Marine Fisheries Service

Southwest Fisheries Science Center

Life History and Current Monitoring Inventory of San Francisco Estuary Sturgeon

Joseph Heublein[1*], Russ Bellmer[2], Robert D. Chase[3], Phaedra Doukakis[1], Marty Gingras[4], Douglas Hampton[1], Joshua A. Israel[5], Zachary J. Jackson[6], Rachel C. Johnson[7], Olaf P. Langness[8], Sean Luis[1], Ethan Mora[9], Mary L. Moser[10], Larissa Rohrbach[11], Alicia M. Seesholtz[12], Ted Sommer[12], and Jeffrey S. Stuart[1]

[1]West Coast Region, California Central Valley Office, NOAA Fisheries, Sacramento, CA 95814 USA (*corresponding author: joe.heublein@noaa.gov)

[2]California Department of Fish and Wildlife, Sacramento, CA 95811 USA

[3]U.S. Army Corps of Engineers, Redding, CA 96002 USA

[4]California Department of Fish and Wildlife, Stockton, CA 95206 USA

[5]U.S. Bureau of Reclamation, Sacramento, CA 95814 USA

[6]U.S. Fish and Wildlife Service, Pinetop, AZ 85935 USA

[7]Fisheries Ecology Division, Southwest Fisheries Science Center, NOAA Fisheries, Santa Cruz, CA 95060 USA and Department of Animal Sciences & Center for Watershed Sciences, University of California Davis, Davis, CA 95618 USA

[8]Washington Department of Fish and Wildlife, Vancouver, WA 98661 USA

[9]Fisheries Ecology Division, Southwest Fisheries Science Center, NOAA Fisheries and Cooperative Institute for Marine Ecosystems and Climate, University of California Santa Cruz, Santa Cruz CA 95060 USA

[10]Northwest Fisheries Science Center, NOAA Fisheries, Seattle, WA 98112 USA

[11]Anchor QEA, LLC, Wenatchee, WA 98801 USA

[12]California Department of Water Resources, West Sacramento, CA 95691 USA

Note: The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

Preface

This document describes life history and current monitoring of the two endemic sturgeon species of the San Francisco Estuary watershed: the southern Distinct Population Segment (sDPS) of North American green sturgeon green sturgeon and the Sacramento-San Joaquin River white sturgeon. It serves as background information used in the development of the conceptual models in Heublein et al. (2017). This document as well as Heublein et al. (2017) are fundamental in identifying existing and expanded monitoring needs necessary to track the status, trend, and viability of sDPS green sturgeon identified in National Marine Fisheries Service recovery planning efforts. Finally, this synthesized information is relevant in the development of future quantitative life cycle models for both sturgeon species. A comparative life history and a monitoring inventory are summarized below to relate areas where management actions and monitoring opportunities overlap for the two species and identify factors that may be unique to each species. More detailed life history descriptions and monitoring inventories follow; these are organized by species life stage.

Table of Contents

List of Figures and Tables

Comparative Life History and Monitoring of SFE Sturgeon

The spawning distribution of southern Distinct Population Segment (sDPS) green sturgeon and Sacramento-San Joaquin River or San Francisco Estuary (SFE) white sturgeon do not typically overlap (geographic regions of the SFE watershed are illustrated in Figure 1 of Heublein et al. [2017]). The majority of spawning for both species occurs in the mainstem Sacramento River; however, the downstream extent of sDPS green sturgeon spawning is approximately 80 kilometers (km) upstream of the typical spawning range of white sturgeon (Schaffter 1997; Poytress et al. 2015). Most sturgeon spawning in the SFE watershed occurs in spring, although white sturgeon can spawn earlier in winter, and green sturgeon spawning extends into early summer with periodic late summer and fall spawning (CDFG 2002; W. Poytress, USFWS, 2017a, unpublished data, see "Notes"). Spawning by both species typically occurs in areas that are deep and turbulent, but white sturgeon eggs occur in lower gradient reaches where channelized river habitat and fine substrate are common. There is no long-term monitoring of sturgeon spawning events (i.e., sampling for sturgeon eggs) on the Sacramento River. Recently, however, sturgeon egg sampling has occurred with some consistency in secondary spawning rivers (Feather and San Joaquin rivers).

With many of California's native fish subject to elevated and unsuitable water temperatures green sturgeon spawning in the upper Sacramento River is somewhat unique. Managed reservoir releases from Shasta Lake typically generate relatively low temperatures in the upper reaches of green sturgeon spawning and incubation habitat on the Sacramento River, and maintain suitable temperatures even in extreme drought conditions. In contrast, water temperatures that are suitable for normal egg development do not persist through the entire spawning and incubation period for white sturgeon in the San Joaquin River. Conditions on the Feather River in late spring and summer are also not appropriate for green sturgeon spawning and incubation in most years. This limitation to spawning habitat may become a more prominent issue if water temperatures continue to increase. Notably, spawning habitat in the upper reaches of the Sacramento River may provide sDPS green sturgeon resilience to climate change under a future scenario where most SFE sturgeon spawning habitats exceed optimal temperature ranges.

Coupling river conditions during sturgeon spawning and incubation with habitat requirements for egg and larval survival is a clear management consideration for both species. In laboratory studies, embryos of northern Distinct Population Segment (nDPS) green sturgeon and SFE white sturgeon have similar temperature optima and tolerances (see Fertilization to Hatch sections in this document for specific temperature ranges by species; Wang et al. 1985; Van Eenennaam et al. 2005). In this regard, management targets for spawning and incubation temperature may be similar for both species. In addition, river flows (which also influence water temperature) are heavily manipulated throughout the spawning ranges of both species. The direct effect of river flow magnitude and timing on spawning and incubation for both species remains uncertain. There is an outstanding management need for a complete understanding of the effects of managed and unmanaged flow and temperature on SFE sturgeon spawning and incubation.

General patterns of larval dispersal and habitat occupancy are different for green and white sturgeon. Although there is temporal overlap in the larval distributions of the two species, green sturgeon larvae in the Sacramento River have been collected from early spring through summer and white sturgeon larvae are typically collected from late winter through spring. In the Sacramento River, green sturgeon larvae are consistently collected near spawning reaches (Poytress et al. 2009, 2010, 2011, 2012, 2013). White sturgeon larvae, however, disperse from hatching areas and are collected throughout the freshwater estuary (CDFW, 2016a, unpublished data, see "Notes"). In the San Joaquin River, white sturgeon larvae appear to disperse less broadly than their Sacramento River counterparts (Z. Jackson, USFWS, 2017, unpublished data, see "Notes").

There is no intentional long-term monitoring of larval sturgeon in the SFE but larvae of both sturgeon species are captured incidentally in studies targeting other fish. Larval green sturgeon are captured annually in salmonid monitoring at Red Bluff Diversion Dam (RBDD) with rotary screw traps, and larval white sturgeon are captured episodically in the California Department of Fish and Wildlife (CDFW) "20mm Survey," which uses a rigid-opening trawl net constructed of 1,600-micrometer mesh to monitor delta smelt in the SFE. Data from these surveys represent an incomplete picture of larval sturgeon distribution, but some general patterns emerge. White sturgeon larvae may move into the freshwater estuary in spring and, as a result, would have access in some years to freshwater estuarine habitat and seasonally inundated wetlands. In contrast, sDPS green sturgeon larvae remain in riverine habitats until juvenile metamorphosis. This difference in larval distributions between species poses unique considerations for management of environmental conditions in their distinct habitats. Larval green sturgeon habitat in the upper Sacramento River is relatively stable due to flow and temperature management through operation of upstream dams and reservoirs. However, larval white sturgeon potentially utilize lower river and estuarine areas where conditions are more variable.

As described above, green sturgeon likely rear in spawning habitat on the Sacramento River for a few months or more before migrating to the estuary as juveniles (W. Poytress, USFWS, 2017a, unpublished data, see "Notes"), whereas white sturgeon may enter the estuary as larvae or early stage juveniles. Juveniles of both sturgeon species have been found throughout the Delta. There is likely significant overlap in distribution at the juvenile life stage, but green sturgeon appear to utilize brackish and seawater portions of the SFE more readily than white sturgeon (Thomas and Klimley 2015; M. Holm 2016, personal communication, see "Notes"). Catch of small juvenile sturgeon of both species in the estuary is episodic with year-class successes likely occurring during wet years with elevated flow (CDFW, unpublished data, 2015, 2016d, see "Notes"; Fish 2010). In laboratory studies using nDPS green sturgeon and SFE white sturgeon, exogenous larvae and juveniles reared with ample food show rapid growth rates in water temperatures at or above 19 degrees Celsius (°C; Cech et al. 1984; Mayfield and Cech 2004; Allen et al. 2006).

Juvenile green and white sturgeon are rarely caught in estuarine monitoring surveys; in many years, juvenile sDPS green sturgeon are absent from all monitoring. Data from juvenile white sturgeon sampling in the estuary is used to generate a coarse recruitment index and forecast of adult cohort abundance (Fish 2010). Although increasing juvenile collection of both species may be challenging, these potential data are critical to understanding environmental factors influencing juvenile sturgeon recruitment and establishing necessary early life stage abundance measures for sDPS green sturgeon.

Adult white sturgeon are found throughout the year in brackish areas of the SFE, and individuals tagged in the SFE are rarely detected or recaptured in marine areas or non-natal estuaries (Kohlhorst et al. 1991). The SFE appears to be exclusively occupied by sDPS green sturgeon with subadult and adult life stages more common in summer and fall compared to other seasons (Israel et al. 2009; National Marine Fisheries Service [NMFS] 2015). A mixture of nDPS and sDPS subadult and adult green sturgeon also occupy estuaries and nearshore marine areas in summer and early fall in Oregon and Washington (Lindley et al. 2011). Green sturgeon in the SFE may comprise a small proportion of the subadult and adult sDPS based on population analysis of non-natal estuarine aggregations of green sturgeon (NMFS 2015; Schreier et al. 2016). As a result, sDPS green sturgeon have been studied extensively through sampling of these mixed distinct population segment aggregations in non-natal estuaries. Additionally, green sturgeon are encountered with some regularity as bycatch in ocean commercial fisheries, allowing opportunities for commercial fishery-dependent monitoring.

White sturgeon are the more common and abundant sturgeon species in the SFE and support a large sport fishery. Thus, directed sturgeon sampling studies and fishery-dependent monitoring in the SFE watershed are focused predominantly on white sturgeon. While disproportionate catch may suggest habitat segregation between species in the SFE, directed sampling of adult green sturgeon in the SFE has almost always involved catch of both species (M. Holm 2016, personal communication, see "Notes"). In this regard, green and white sturgeon most likely occupy similar areas within the SFE. As described above, juvenile SFE sturgeon are rarely encountered, and larval SFE sturgeon are only collected incidentally in studies directed at other species and are typically too small for non-lethal tissue analyses. Ongoing monitoring of adult sturgeon in the SFE and associated studies (e.g., population modeling, tagging, analysis of genetics and contaminants) presents an opportunity to increase understanding of both species.

Spawning sDPS green sturgeon enter the SFE from the ocean from late winter to spring and ascend the Sacramento River with minimal staging and feeding in the estuary (Heublein et al. 2009). Adult white sturgeon spend the majority of their lives in the SFE and can initiate upstream migration in the late fall through spring (Kohlhorst and Cech 2001). Thus, consumption of contaminated food in the SFE may have a greater effect on white sturgeon vitellogenesis and eggs compared to sDPS green sturgeon. Both green and white sturgeon are susceptible to stranding at the Sutter and Yolo Bypass Weirs during the same hydrologic conditions and timing. The observed spawning habitat partitioning on the Sacramento River most likely indicates different preferences for spawning substrate or other habitat attributes between

species (e.g., channel gradient and velocity). Both species show a variety of post-spawn migration and holding behaviors, but it is more common for post-spawn green sturgeon to hold for a few months or more in freshwater habitats and for white sturgeon to return to the SFE immediately after spawning (Heublein et al. 2009; Klimley et al. 2015).

The sDPS green sturgeon spawning run on the Sacramento River has been estimated annually using dual-frequency identification sonar (DIDSON) survey data since 2010 (Mora 2016). There is no directed monitoring of the white sturgeon spawning run on the Sacramento River beyond angler catch reporting in spawning reaches. Recently, directed study of spawning sturgeon has occurred on the San Joaquin River (white sturgeon) and, to lesser extent, the Feather River (primarily green sturgeon). White and green sturgeon migrating to spawning habitat in the Sacramento and Feather rivers are periodically sampled at the Sutter and Yolo Bypass Weirs, and white sturgeon are collected in general fish community monitoring in the Yolo Bypass. Annual spawning measures (e.g., annual run-size, spawning distribution, verification of successful spawning) are fundamental metrics necessary for management of both sturgeon species. Monitoring of spawning sturgeon should be expanded such that these metrics are uniformly available throughout the spawning ranges of both species.

Specific Life History Descriptions and Monitoring by Life Stage

Prior to developing the comparative life history and monitoring of SFE sturgeon (above), the following inventory of monitoring (summarized in Tables 1 and 2) and specific life history descriptions by life stage were established.

Table 1. Green sturgeon monitoring inventory.

Four general categories are used to organize the discussion of monitoring: life stage—surveys; collection or survey of fish; tissue analyses—analysis of fish tissue samples to estimate age, sex, reproductive condition, migratory histories, etc.; telemetry—monitoring of fish movement and behavior through implantation of active or passive tags and subsequent tag detection; and population modeling and synthesis—modeling or synthesis of survey, tissue analysis, and/or telemetry data to estimate demographics, population trends, movement patterns, etc. Study leads are provided in parentheses.

Green Sturgeon	Eggs	Larvae	Juveniles	Subadults/Adults	Spawning Adults
Life stage surveys	• Sacramento River rotary screw trap collections at RBDD (2016, 2017; USFWS) • intermittent egg mat surveys on the Feather River (DWR) • habitat mapping of past egg collection sites and putative spawning areas on the Sacramento River (USFWS; NMFS)	• Sacramento River rotary screw trap collections at RBDD (USFWS) and GCID (GCID) • intermittent larval D-netting on Sacramento River (USFWS) and Feather River (DWR)	• benthic trawl surveys near RBDD (USFWS) • Sturgeon Fishing Report Cards (location and length; CDFW) • intermittent collection in Bay Study (Delta; CDFW) intermittent salvage at the federal and state Delta pumping facilities (DWR; BOR)	• Sturgeon Study (trammel netting in Bay), Sturgeon Fishing Report Cards, boat logs, creel surveys (CDFW) • bycatch in California halibut trawl fishery (NMFS; CDFW) • intermittent sampling in San Pablo Bay, Columbia River, Grays Harbor, and Willapa Bay (UCD; WDFW; NMFS)	• DIDSON surveys in spawning habitat NMFS; CDFW; DWR) • hook and line sampling in Feather River (DWR) • Sturgeon Fishing Report Cards, creel surveys (CDFW) • Yolo Bypass and Knights Landing fyke traps, stranding at Fremont and Tisdale weirs (DWR; CDFW)
Tissue analyses		• analysis of larval development (spawn timing; UCD)	• genetic analysis of benthic trawl samples (NMFS)	• fin ray analysis from Sturgeon Study (age; USFWS) • genetic analysis of California halibut fishery bycatch (NMFS)	• reproductive stage of sturgeon stranded at Fremont and Tisdale weirs (CDFW; UCD)
Telemetry			• lower Sacramento River monitoring (primarily gill-netting) for acoustic tag implantation (CDFW; UCD) • acoustic tagging of juveniles captured in benthic trawls near RBDD (USFWS; UCD)	• satellite tagging of bycatch in California halibut trawl fishery (NMFS; CDFW); • detection of previously tagged fish in existing acoustic arrays (UCD; NMFS)	• detection of previously tagged adults in acoustic array (NMFS; WDFW; UCD; DWR) • acoustic tagging of sturgeon stranded a Fremont and Tisdale weirs (CDFW; UCD) • acoustic tagging of hook and line capture of adults in Feather River (DWR)
Population modeling and synthesis		• comparison of RBDD larval timing and abundance and environmental conditions (USFWS)	• hind-cast of recruitment success through estimated age of collected and reported juveniles (CDFW)		• modeling of run size using DIDSON and acoustic detection data, expansion of run size estimates to adult abundance estimates with spawning periodicity (NMFS)

Notes:
Study leads are provided in parentheses in table (RBDD: Red Bluff Diversion Dam; USFWS: U.S. Fish and Wildlife Service; NMFS: National Marine Fisheries Service; DWR: California Department of Water Resources; GCID: Glenn Colusa Irrigation District; UCD: University of California, Davis; CDFW: California Department of Fish and Wildlife; BOR: Bureau of Reclamation; WDFW: Washington Department of Fish and Wildlife)

Table 2. White sturgeon monitoring inventory.

White Sturgeon	Eggs	Larvae	Juveniles	Adults	Spawning Adults
Life stage surveys	• egg mat surveys, habitat mapping (San Joaquin River; USFWS)	• larval D-netting (San Joaquin River; USFWS) • 20mm Survey (CDFW) • salvage at the federal and state Delta pumping facilities (BOR; DWR)	• Bay Study (Delta; CDFW) • salvage at the federal and state Delta pumping facilities (BOR; DWR)	• Sturgeon Study (trammel netting in Bay), Sturgeon Fishing Report Cards, boat logs, creel surveys (CDFW) • salvage at the federal and state Delta pumping facilities (BOR; DWR)	• Sturgeon Study (post-spawn), Sturgeon Fishing Report Cards, creel surveys (CDFW) • Yolo Bypass and Knights Landing fyke traps (DWR;) • stranding at Fremont and Tisdale weirs (DWR; CDFW) • gill and trammel netting in San Joaquin River spawning areas (USFWS)
Tissue analyses	• development (spawn timing; UCD) • preliminary genetic analysis of eggs (UCD; Cramer Fish Sciences)	• development analysis of larvae (spawn timing; UCD; BOR)	• juvenile age at length (CDFW)	• fin ray analysis from Sturgeon Study (age and growth), tissue analysis from fishing derbies (age and contaminants), preliminary fin microchemistry analysis (USFWS)	• fin ray, reproductive condition, and genetic analysis of sturgeon captured in San Joaquin River spawning habitat (USFWS; UCD)
Telemetry			• lower Sacramento River monitoring (primarily gill-netting) for acoustic tag implantation (CDFW; UCD)	• detection of previously tagged fish in existing array (DWR; UCD)	• tagging of adults from fykes, bypass stranding, and San Joaquin River spawning habitat and detection of current and previously tagged adults in acoustic array (DWR; USFWS; UCD)
Population modeling and synthesis			• ongoing analysis of YCI and hind-cast relative brood year abundance (CDFW)	• ongoing estimates of harvest and adult abundance with Sturgeon Study and Sturgeon Fishing Report Card data (CDFW)	• analyses of recapture rates of externally tagged sturgeon in spawning habitat (CDFW)

Notes:
Monitoring category descriptions provided in Table 1. Study leads are provided in parentheses in table (USFWS: U.S. Fish and Wildlife Service; UCD: University of California, Davis; CDFW: California Department of Fish and Wildlife; BOR: Bureau of Reclamation; DWR: California Department of Water Resources)

Fertilization to Hatch

Green sturgeon eggs. Southern DPS green sturgeon spawn during the spring and summer in the middle and upper mainstem Sacramento River. Spawning has been documented on the Feather River in only two years, 2011 and 2017 (Seesholtz et al. 2015; M. Manuel, PSMFC, 2017, personal communication, see "Notes"). Late summer and fall spawning on the Sacramento River has also been documented in four years by larval collections at RBDD (2016; W. Poytress, USFWS, 2017a, unpublished data, see "Notes") and Glenn-Colusa Irrigation District (GCID) oxbow (1997, 1999, and 2000; CDFG 2002).

A time range for fertilization can be estimated using information on egg and larval development and growth from laboratory studies, observed length or development stage at capture, and river water temperatures (Dettlaff et al. 1993; Poytress et al. 2015). Coarse spatial distribution of fertilized eggs or spawning can be generated by combining estimated time ranges of fertilization with corresponding adult detections in spawning habitat. Poytress et al. (2009, 2010, 2011, 2012, 2013) sampled eggs directly in the upper and middle Sacramento River between 2008 and 2012 (summarized in Poytress et al. 2015). The authors confirmed that spawning occurred at seven locations by egg matt sampling along the Sacramento River between the GCID oxbow (river kilometer [rkm] 332.5 from the confluence of the Sacramento and San Joaquin rivers) and Inks Creek (rkm 426). Eggs were collected at depths from 0.6 to 11.3 meters (m), with water temperatures ranging from 9.8 to 17.1°C. Based on the observed egg development stages and temperatures, spawning had occurred from April through July (Poytress et al. 2015). Notably, green sturgeon eggs were collected in rotary screw traps at RBDD (rkm 391) for the first time in 2016 (W. Poytress, USFWS, unpublished data, see "Notes").

Sturgeon early life history sampling has been conducted in the Feather River since 2011 with egg mats and intermittent D-net sampling (Seesholtz et al. 2015; A. Seesholtz, DWR, 2017, unpublished data, see "Notes"). Sturgeon have never been collected in rotary screw traps in the Feather River. Spawning on the Feather River has been confirmed in only two locations: below Fish Barrier Dam, which is a barrier to anadromous fish passage, and 13 km downstream at the outlet of the Thermalito Afterbay (Thermalito Outlet). Seesholtz et al. (2015) estimated that spawning at the Thermalito Outlet occurred from June 12 through 19, 2011, when water temperatures were 16 to 17°C, whereas spawning occurred in substantially cooler temperatures at FishFish Barrier Dam (approximately 11°C) in late May or early June 2017 (M. Manuel, PSMFC, 2017, personal communication, see "Notes").

Direct observation or DIDSON detection of sturgeon suggests that sDPS green sturgeon may spawn in other areas of the Feather River watershed. Anglers reported catch of numerous green sturgeon about 5-km downstream from Fish Barrier Dam in 2006 (A. Seesholtz, DWR, 2017, unpublished data, see "Notes"). Green sturgeon aggregations have been detected with DIDSON surveys much lower in the Feather River near Shanghai Bend (69-km downstream of Fish Barrier Dam) in habitats that appear suitable for spawning (e.g., suitable depth, water velocity, substrate; A. Seesholtz, DWR, 2017, unpublished data, see "Notes"). Adult green sturgeon have also been observed in spring and summer at Daguerre Point Dam on the Yuba

River (a large tributary to the Feather River) in 2011, 2016, and 2017 (Bergman et al. 2011; M. Beccio, CDFW, 2017, personal communication, see "Notes").

There are no long-term surveys that sample green sturgeon eggs, and locations of egg collection from short-term surveys are unlikely to represent the entire egg distribution. Adult detections in potential spawning habitat during spring and early summer can be used to infer a broader egg distribution. Adults have been detected in spring and summer in approximately 21 areas with suitable spawning habitat in the Sacramento River from above the GCID to the confluence of the Sacramento River and Cow Creek (rkm 451; Heublein et al. 2009; Klimley et al. 2015). Based on these observed adult distributions, contemporary egg distribution on the Sacramento River can range from the GCID oxbow in the middle Sacramento River to Cow Creek in the upper Sacramento River basin.

Nearly all laboratory-based data on green sturgeon physiology (e.g., growth rates, metabolism, swimming performance) involve the nDPS. With the overlap in estuarine and marine habitat between the population segments, and with similarities of adjacent historical natal freshwater habitats (e.g., watersheds of the Sacramento and upper Klamath rivers), it is assumed that physiology of the two distinct population segments is similar. However, the nDPS is an "untested surrogate" for the laboratory-based physiology of the sDPS because laboratory-based data for the sDPS do not exist for comparison. In areas or life stages where field-based information on habitat optima or preference is unavailable for sDPS, laboratory-based nDPS data should be cautiously applied because it is generated in a controlled setting and involves a latitudinally distinct population segment.

The following early life stage physiology information was collected in laboratory study of nDPS green sturgeon. Eggs sampled from a single nDPS Klamath River female hatched after 144 to 192 hours of incubation at 15.7 ± 0.02°C and were an average of 4.44 ± 0.15 millimeter (mm) in diameter (Deng et al. 2002). Van Eenennaam et al. (2005) exposed the fertilized eggs of one nDPS female to six temperature regimes (11, 14, 17, 20, 23, and 26°C). Egg survival to hatch was highest in the 14°C and 17°C treatments (39% and 36%, respectively), with total mortality at temperatures of 23°C and above (Van Eenennaam et al. 2005). Van Eenennaam et al. (2005) also found a decreased hatching rate in the 11°C treatment compared to 14°C, but the lower temperature limit for embryo survival was not determined. Elevated water temperature can cause deformities in embryos. The proportion of hatched embryos with deformities was relatively high at 17°C and 20°C (10.3% and 51.6%, respectively) and low at 11°C and 14°C treatments (3.7% and 1.2%, respectively; Van Eenennaam et al. 2005). Based on this information, Van Eenennaam et al. (2005) concluded temperatures less than 17.5°C are optimal for normal development of embryos (results summarized in Table 3).

Table 3. Green sturgeon temperature tolerances by life stage.

Laboratory studies involving nDPS green sturgeon from Klamath River broodstock (a, b, c, d, dd, f) were used to rate water temperatures for the eggs, larvae, and juveniles. Water temperatures recorded during sDPS green sturgeon egg and larvae collection on the upper Sacramento and Feather rivers (e, g, and h) were used to establish "acceptable temperature" for spawning adults and larvae. Categorization of temperature tolerance is not directly comparable at upper and lower levels in this table because "impaired fitness" may be related to both indirect sources of mortality (e.g., reduced growth rate) and direct sources of mortality (e.g., increased rate of deformities). a = Mayfield and Cech 2004; b = Van Eenennaam et al. 2005; c = Werner et al. 2007; d = Allen et al. 2006; e = Poytress et al. 2012; f = Linares-Casenave et al. 2013; g = Poytress et al. 2015; h = Seesholtz et al. 2015; and dd = Allen et al. 2006b.

temperature °C	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
temperature °F	46.4	48.2	50.0	51.8	53.6	55.4	57.2	59.0	60.8	62.6	64.4	66.2	68.0	69.8	71.6	73.4	75.2	77.0	78.8	80.6	82.4
egg				b	b	b	b	b	b	b	b	b	b	b	b,f	b,f	b,f	b,f	b,f	b	b
larvae							e	e	e	c	f	dd,f	dd,f	dd,f	dd,f	dd,f	dd,f	dd,c,f	f	f	f
juvenile				a	a	a	a	a	a	a	a	a	a	a	a	a	a,d	a	a	a	a
spawning adult			g	g	g	g	g	g	g,h	g,h											

(green)	optimal temperature
(yellow)	acceptable temperature
(orange)	impaired fitness; avoid prolonged exposure; increasing chance of lethal effects
(red)	likely lethal
(black)	lethal
(light blue)	unknown effect upon survival and fitness

The following general discussion of water temperature in sDPS green sturgeon egg habitat involves coarse gauge data reported by the DWR California Data Exchange Center (CDEC; Sacramento River gauges at Keswick Dam – rkm 488, Bend Bridge – rkm 415, RBDD – rkm 391, and Wilkins Slough – rkm 190, see hyperlinks for historical and current CDEC gauge data, DWR, 2017a, in "Notes") and more-specific temperature information from unpublished agency monitoring and modeling efforts. In late spring and summer, flow and temperature on the Sacramento River are manipulated in part for agricultural diversion (GCID - rkm 332.5, and RBDD are the largest diversion facilities on the Sacramento River) and maintenance of a 13.3°C (56° Fahrenheit) water temperature "compliance point" for Sacramento River winter-run Chinook salmon (SRWC; *Oncorhynchus tshawytscha*) spawning and incubation. The compliance point typically ranges from rkm 415 to rkm 444, and water temperatures upstream of rkm 444 are progressively cooler up to Keswick Dam, where Shasta Lake reservoir release temperatures typically range from 10 to 12°C. As a result, optimal temperatures for sturgeon egg incubation (below 17°C) extend downstream to RBDD in spring and summer of most years, but typically remain below laboratory-based optima for egg incubation upstream of existing spawning and egg incubation areas (closer to Keswick Dam). In downstream areas closer to GCID, water temperatures are typically suboptimal for incubation in the late spring and summer (above 17.5°C). During periods of extremely low reservoir storage and outflow, incubation temperatures may be suboptimal in the late spring and summer near RBDD and approach potentially lethal temperatures (above 20°C) in areas closer to GCID.

Fish Barrier Dam on the Feather River creates a small impoundment below Oroville Reservoir called the Thermalito Diversion Pool. Water from the Thermalito Diversion Pool is either released to the river at Fish Barrier Dam or routed through the shallow Thermalito Afterbay, thereby bypassing a short tailwater and warming for crop irrigation. Warmer water is then diverted directly from the Thermalito Afterbay or released back into the Feather River at the Thermalito Outlet. Water management downstream of the Thermalito Outlet may have a variable effect on green sturgeon spawning habitat depending on the time of the year and operations. Peak winter and spring flows on the Feather River are typically captured in upstream reservoirs. Summer base flows can then be augmented by releases from the Thermalito Outlet, and flow augmentation may also decrease summer water temperatures. Water released from the Thermalito Outlet is warmer than the potential cold water pool released into the Feather River at Fish Barrier Dam. Hence, suitable conditions for normal egg incubation (water temperatures below 17.5°C) typically only persist into May downstream of the Thermalito Outlet.

White sturgeon eggs. The SFE white sturgeon spawn primarily in the mainstem Sacramento River and to a lesser extent in the San Joaquin River in late winter and spring. Based on collection of gravid adults, spawning also periodically occurs in other rivers (e.g., the Feather and Bear rivers) in the Sacramento River basin. There is no long-term monitoring of white sturgeon eggs in the Sacramento River, but egg distribution is likely similar to the putative spawning reach, which typically ranges from just upstream of Colusa (rkm 252) to near Verona (rkm 129; Kohlhorst 1976; Schaffter 1997). Adult white sturgeon have been reported by anglers

near the confluence of the Sacramento River and Deer Creek (rkm 354) and have been observed and collected during summer and early fall near the GCID oxbow (rkm 332.5; Bergman 2011; M. Manuel, PSMFC, 2016, personal communication, see "Notes"). Juvenile white sturgeon have been collected in the rotary screw traps at GCID and reported by anglers in the area (M. Manuel, PSMFC, 2016, personal communication, see "Notes"). Given those observations, spawning white sturgeon and eggs presumably occur upstream from the GCID oxbow in some years. Egg distribution upstream of GCID requires verification by egg or larval collections because juveniles collected in the GCID trap may have moved there from downstream.

Sturgeon egg sampling is underway in the San Joaquin and Feather rivers in years when adult sturgeon are detected in spawning habitats. However, no white sturgeon eggs have been identified in samples from the Feather River. As described above, sturgeon egg distribution can also be inferred from ongoing acoustic detections of tagged adults in spawning habitat, reports of adults in spawning habitat gathered from the Sturgeon Fishing Report Cards, and from incidental bycatch of larvae and early stage juveniles in other monitoring or research studies.

In the Sacramento River, white sturgeon typically spawn between February and June. Tagged adult white sturgeon move from the SFE to spawning reaches of the Sacramento River between mid-February and early June (Miller 1972; Schaffter 1997; E. Miller UCD Biotelemetry Laboratory, 2017, unpublished data, see "Notes"). Kohlhorst (1976) used D-nets to collect white sturgeon eggs and larvae as early as mid-February, with the majority (93%) collected in March and April. Schaffter (1997) collected eggs in the Sacramento River on artificial substrates from March through May. Angler reporting of tagged adults in spawning habitat coincident with early season flow events also indicates migration and possibly spawning occur in December and January in some years (CDFW, 2016b, unpublished data, see "Notes"). In the San Joaquin River basin, fertilized eggs were collected downstream of Grayson at rkm 138 (measured from the Sacramento River confluence) in late April 2011 and downstream of Vernalis between rkm 115 and 140 from late March through mid-May in 2012 (Jackson et al. 2016). In March and April 2016, fertilized eggs were collected between rkm 115 and 140, though collection of a single larvae approximately 1 day post-hatch (dph) at rkm 101 indicates that spawning occurs further downstream than previously known (Z. Jackson, USFWS, 2017, unpublished data, see "Notes").

Benthic substrate in white sturgeon spawning habitat is variable. Substrate in the Sacramento River ranges from fine sand to coarse sand near Verona and Wilkins Slough (rkm 189.5), fine gravel to medium gravel farther upstream near Colusa, and gravel and cobble in spawning sites just upstream from Colusa where the river gradient is higher. Schaffter (1997) found eggs in water depths of 1.5 to 4.6 m, with water velocities greater than 1.0 meter per second. Eggs were also collected in San Joaquin River spawning areas at depths of 1.6 to 10.5 m (Jackson et al. 2016). The river bottom in egg-collection areas of the San Joaquin River was dominated by silt and sand substrates, though patches of hardpan clay and fine gravels were present near several sites (Jackson et al. 2016). Fine substrate and lack of interstitial space in spawning habitat can decrease survival of white sturgeon eggs (Hildebrand et al. 2016). Thus,

substrate in SFE white sturgeon spawning habitats, especially on the San Joaquin River, may limit recruitment to the larval or juvenile life stage.

Wang et al. (1985) found that development and survival of white sturgeon embryos were temperature-dependent. Optimal survival to hatching was observed when water temperatures during incubation in the hatchery were between 14°C (88.6% ± 2.2% survival) and 17°C (83.6% ± 1.9% survival). Embryo mortality increased as water temperatures increased to 20°C (49.1% ± 3.2% survival), and water temperatures of more than 20°C were lethal to developing embryos. Water temperatures in spawning habitat on the Sacramento River typically remain below this level, but median daily water temperatures in excess of 20°C were recorded in Sacramento River incubation habitat during drought conditions in April 2015 (CDEC Sacramento River gauges at Wilkins Slough, DWR, 2017a, see "Notes"). Spring water temperatures regularly reach or exceed suitable levels for egg incubation in the San Joaquin River, but viable white sturgeon embryos have been collected in water temperatures above 20°C (Jackson et al. 2016). The time necessary for white sturgeon eggs to hatch is also temperature-dependent (Wang et al. 1985; Deng et al. 2002). Under an optimal incubation water temperature of 15.7 ± 0.2°C, Deng et al. (2002) found that development time to hatching ranged from 152 to 200 hours and averaged 176 hours. Hatch time is an important consideration for managers if there are potentially variable habitat conditions (e.g., inundation levels, temperature) during egg development.

Hatch through Metamorphosis

Larval green sturgeon. Metamorphosis of nDPS green sturgeon (to juveniles) occurs at approximately 45 dph and an approximate length of 75 mm (Deng et al. 2002). Growth begins to increase as larvae transition from endogenous to exogenous feeding, which occurs at approximately 15 dph (Gisbert et al. 2001). Laboratory studies have shown that nDPS larvae possess limited swimming ability and generally seek refuge at 0 to 18 dph, suggesting that complex habitat with interstitial space for refuge (e.g., large cobble substrate) is critical at this life stage (Kynard et al. 2005). Under laboratory conditions, nDPS individuals 18 to 45 dph demonstrated initiation of diel downstream migration, favoring nighttime migratory movements (Kynard et al. 2005). Based on egg mat and rotary screw trap sampling at RBDD, Poytress et al. (2011) found similar results in field study of sDPS larvae compared to the laboratory investigations of nDPS larvae described above; larval dispersal was initiated at 18 dph, it peaked at 23 to 24 dph, and complete dispersion from hatching areas occurred by 35 dph.

Historically, larval sturgeon collected in the Sacramento and San Joaquin river systems were not routinely identified to species. However, green sturgeon larvae were identified in RBDD rotary screw trap samples when the study was initiated in 1995, which confirmed green sturgeon spawning at or above this location (Poytress et al. 2009). Larvae have been consistently collected in rotary screw traps in spring and summer at RBDD and GCID as part of a long-term monitoring program in the Sacramento River focused on juvenile salmonids. Data from rotary screw traps at RBDD have shown a similar temporal distribution data for larvae in the Upper Sacramento River compared to D-net sampling data (W. Poytress, USFWS, 2015a, unpublished data, see "Notes"). Larval catch numbers at GCID rotary screw traps are typically lower than

RBDD rotary screw traps (CDFG 2002), and appear to be less representative of temporal spawning downstream of RBDD.

Brown (2007) discovered larvae in the upper Sacramento River at Bend Bridge (rkm 415), and spawning has been confirmed as far downstream as the GCID facility (Poytress et al. 2015), suggesting that larvae occupy over 100 km of the Sacramento River. Due to the limited number of larval collections, the upstream egg distribution described above (Sacramento River to Cow Creek and Feather River to Fish Barrier Dam) is also applied to larvae. Larval sturgeon distribution may range well downstream from spawning habitat. Larval white sturgeon and unidentified larval sturgeon have been collected more than 100-km downstream from known white or sDPS green sturgeon spawning areas during the 20mm Survey and in salvage at the Tracy Fish Collection Facility and John E. Skinner Fish Protection Facility near federal and state Delta pumping facilities (CDFW, 2016a, unpublished data, see "Notes"). Thus, larval distribution is estimated to extend at least 100-km downstream from spawning habitats on the Sacramento and Feather rivers in high flow years. This estimated downstream distribution corresponds with the Colusa area on the Sacramento River (rkm 252) and the confluence of the Sacramento and Feather rivers near Verona (rkm 129) for larvae originating in the Sacramento River and Feather River, respectively.

Larval abundance and distribution may be influenced by spring and summer outflow. There appears to be a positive relationship between annual outflow and larval abundance in the RBDD rotary screw traps; RBDD rotary screw trap collections of larval green sturgeon were far greater in the three most recent wet years[1] (2011, 2016, and 2017) since the monitoring began in 1995 (W. Poytress, USFWS, 2015a, unpublished data, see "Notes"). Moreover, green sturgeon eggs and larvae were only collected during wet years (2011 and 2017) on the Feather River (Seesholtz et al. 2015; M. Manuel, PSFMC, 2017, personal communication, see "Notes").

In laboratory-based studies with abundant food and oxygen, larval nDPS green sturgeon (35 dph) growth was significantly greater at 24°C than 19°C or cycling 19 to 24°C (Allen et al. 2006b). Furthermore, larval nDPS green sturgeon reared at 11 and 13°C under normal food conditions had significantly reduced growth rates compared to larvae reared at 16 and 19°C, but temperature had no significant effect on size or growth rate when larvae were food-limited (J. Poletto, 2016, unpublished data, see "Notes"). Green sturgeon eggs, larvae, and juveniles co-occur in the middle and upper Sacramento River due to the protracted spawning period of sDPS green sturgeon. Spawning of critically endangered SRWC also occurs closer to Keswick Dam during sDPS spawning. Laboratory-based optima for larval and juvenile green sturgeon growth exceed suitable temperatures for green sturgeon spawning and embryo development (Table 3), and are well above suitable temperatures for Chinook salmon spawning and incubation. Thus,

---

[1] With the exception of 2016, the "wet year" phrase is based on resource agency water-year type or classification (CDEC water year classification, DWR, 2017b, see "Notes"). The 2016 water year for the Sacramento and San Joaquin valleys was classified as below normal and dry, respectively. However, 2016 is qualitatively described in this document as a wet year because above-average precipitation was recorded in most of the SFE watershed and spawning and migratory conditions typically associated with wet years occurred (e.g., elevated winter or spring flows, extended periods of bypass inundation).

water temperature in the middle and upper Sacramento River may have different effects on specific green sturgeon life stages and SRWC. Potentially optimal water temperatures for larval growth near RBDD could correspond to low concurrent spawning production and egg survival. Furthermore, warmer water temperatures near RBDD could be associated with poor survival of early life stages of green sturgeon in lower reaches of Sacramento River spawning habitat and SRWC closer to Keswick Dam.

Larval white sturgeon. In a laboratory study, metamorphosis of larval white sturgeon to juveniles occurred at approximately 45 dph (Deng et al. 2002). Larval white sturgeon are not specifically monitored, except for pilot efforts in 2013, 2015, and 2016 on the lower San Joaquin River (Faukner and Jackson 2014; Jackson et al. 2016) and a more directed effort begun in 2017 (Z. Jackson, USFWS, 2017, unpublished data, see "Notes"). White sturgeon larvae are also periodically collected in various locations throughout the Delta in general larval fish monitoring (e.g., 20mm Survey) in late winter and spring and in salvage at federal and state Delta pumping facilities.

Upstream larval distribution in the Sacramento River can be extrapolated from adult monitoring in spawning habitat (e.g., in-river sportfishing catch data, adult telemetry studies). Periodic aggregations of gravid white sturgeon or telemetry data in the Feather River, Yolo Bypass, and Bear River indicate spawning and larval distribution may also extend to those upstream areas. Based on this information, larval distribution ranges from downriver of spawning habitats (primarily in the Sacramento and San Joaquin rivers) to the approximate downstream extent of the Delta at Chipps Island.

Kynard and Parker (2005) report that Sacramento River white sturgeon larvae use benthic habitat following brief post-hatch dispersal and availability of interstitial benthic space may increase larval survival through multiple mechanisms (i.e., reduction in metabolic demand, stress, and predation; Hildebrand et al. 2016). Laboratory studies indicate exogenous larval white sturgeon are tolerant of salinities up to 16 parts per thousand (ppt) and have relatively high growth rates in 20°C water (Cech et al. 1984; McEnroe and Cech 1985). However, suitable temperatures for white sturgeon larvae outside of controlled laboratory conditions and for early stage larvae may be lower (less than 16°C; Hildebrand et al. 2016). A positive relationship exists between relative larval abundance and wet years based on data from long-term collection of white sturgeon larvae in the 20mm Survey (CDFW, 2016a, unpublished data, see "Notes"). Furthermore, larvae were only collected in San Joaquin River spawning habitats in 2016 (relatively cool conditions) and 2017 (during flooding conditions; Z. Jackson, USFWS, 2017, unpublished data, see "Notes").

Complete Metamorphosis to Ocean Migration or 75 Centimeters Fork Length

Juvenile green sturgeon. It is unknown how long juvenile sDPS green sturgeon remain in upriver rearing habitats after metamorphosis. Juveniles captured in the Delta by Radtke (1966) ranged in size from 200 to 580 mm fork length (FL), suggesting that juveniles remain upriver for several months before entering the Delta. The lack of juveniles smaller than 200 mm FL in Delta capture records further supports extended upriver rearing of sDPS juveniles before entering the

estuary (CDFG 2002). The first successful study of juveniles in the Sacramento River occurred in 2015 in the Red Bluff area, where approximately 40 large age-0 green sturgeon (60 to 320 mm total length [TL]) were captured using benthic trawls throughout the summer (W. Poytress, USFWS, 2015b, unpublished data, see "Notes"). Based on those studies, it is likely that juveniles rear near spawning habitat for a few months or more before migrating to the Delta.

Duration of juvenile estuary rearing prior to ocean entry and subadult transition is also unknown. Small juvenile green sturgeon (age-0 and presumably age-1) have been incidentally captured in the following general fish community monitoring efforts and commercial fisheries during all months of the year: the CDFW San Francisco Bay Study trawl survey (hereafter referred to as the Bay Study), which has occurred throughout the SFE since 1980; salvage at the federal and state Delta pumping facilities; the USFWS Delta Juvenile Fish Monitoring Program; the San Francisco Bay herring gillnet fishery (M. Holm, 2016, personal communication, see "Notes"); and the San Francisco Bay shrimp trawl fishery (juvenile Acipenseridae, not identified to species). Larger juveniles are periodically captured in the following sampling studies targeting sturgeon: CDFW Sturgeon Population Study (hereafter referred to as the Sturgeon Study) trammel netting in San Pablo Bay and Suisun Bay (hyperlink to annual CDFW study summary in "Notes"); Sturgeon Fishing Report Card capture records from throughout the SFE (hyperlink to annual CDFW study summary, 2017, in "Notes"); and the historical CDFW juvenile sturgeon set-line study in the SFE (Dubois et al. 2010).

Thomas and Klimley (2015) reported juvenile sDPS green sturgeon movement in the SFE in a study that involved capturing larval green sturgeon at RBDD, rearing the fish in the laboratory for several months, and releasing those fish as tagged juveniles to the Delta. The tagged juveniles showed a broad range of movement patterns, from remaining in the Delta for several months to entering the ocean within a few months of release (Thomas and Klimley 2015). Results from Thomas and Klimley (2015) suggest that some individuals in the sDPS may enter the ocean and transition to the subadult life stage in their first year.

Juvenile growth in the nDPS is rapid as they move downstream, reaching up to 300-mm TL in the first year and more than 600-mm TL in years 2 and 3 (Nakamoto et al. 1995). Juveniles in the sDPS may grow considerably faster, with some having reached approximately 300-mm TL in 6 months or less (W. Poytress, USFWS, 2015b, 2017b, unpublished data, see "Notes"). Northern DPS juveniles tested under laboratory conditions have optimal bioenergetic performance (growth, metabolic rate, temperature preference, and swimming performance) at 15 to 19°C (Mayfield and Cech 2004) and are highly tolerant to changes in salinity during their first 6 months (Allen et al. 2011). Although green sturgeon have the ability to enter seawater well before 1 year of age (Allen et al. 2011), the typical length of fish encountered in the ocean (greater than 600 mm TL) suggests ocean entry occurs at a later age. However, length distributions of green sturgeon captured in the ocean may be biased high because most of those records are from commercial fisheries targeting relatively large fish species.

A pilot effort is underway by the UCD Biotelemetry Laboratory and CDFW to implant acoustic transmitters in juvenile green and white sturgeon captured in the Sacramento River and

Delta. Results from this study are likely to improve understanding of juvenile sturgeon habitat use in the SFE. California fishing regulations since 2007 have required sturgeon anglers to complete a Sturgeon Fishing Report Card, and juvenile green sturgeon capture date and length have been reported by this program. A preliminary recruitment time series by CDFW—using lengths of juvenile sDPS green sturgeon and nDPS age-length data—suggests recruitment was highest in the two most recent wet years[2] (M. Gingras, CDFW, 2016, unpublished data, see "Notes"). The recent implementation of the Sturgeon Fishing Report Card and refinement of age-length keys also provide managers with an early qualitative indicator of recruitment or cohort success using reported lengths of juvenile sDPS green sturgeon and records in the Sturgeon Study.

From scant collections of small sDPS green sturgeon in the Bay Study, nearly all recruitment appears to have occurred in wet years (M. Gingras, CDFW, 2016, unpublished data, see "Notes"). Furthermore, at federal and state Delta pumping facilities the highest juvenile green sturgeon collection on record and the highest estimated salvage since 1985 occurred in a wet year (2006; Gartz 2007). Based on lengths of salvaged green sturgeon reported in Gartz (2007), it is likely that the majority of juveniles salvaged in 2006 hatched in the same year. All of those findings are consistent with white sturgeon and the relationship between recruitment to age-0 and wet years (CDFG 1992; Fish 2010).

Juvenile green sturgeon entrainment in the presence of unscreened water diversions (Mussen et al. 2014) and diversions with fish protection devices (Poletto et al. 2014a, 2014b, 2015) have been studied extensively in the laboratory. These studies suggest juvenile green sturgeon are at high risk of entrainment in unscreened diversions and impingement on screened diversions. Furthermore, Vogel (2013) captured four green sturgeon and one white sturgeon during evaluation of fish entrainment at 12 unscreened diversions in the middle Sacramento River. Verhille et al. (2014) reported larval and juvenile green sturgeon swimming performance and flow velocity recommendations for diversions by life stage; however, fish screen design criteria specifically for larval sturgeon have not been developed.

Juvenile white sturgeon. The typical white sturgeon life history does not involve extensive marine migration, and an obvious limit to the juvenile life stage (e.g., first ocean entry in sDPS green sturgeon) is not known for the species. Chapman et al. (1996) estimated 75- and 95-centimeter (cm) FL as minimum sizes of maturity for male and female white sturgeon, respectively. Based on this estimate, 75-cm FL was selected as the upper size limit of the juvenile life stage.

Juvenile white sturgeon are believed to initiate a secondary dispersal (the primary dispersal occurring at the larval stage) in spring by actively swimming downstream during the night (Kynard and Parker 2005). Dispersal duration is unknown, but observed swimming intensity and duration in laboratory studies indicate dispersal likely lasts several days and over many kilometers (Kynard and Parker 2005).

---

[2]This refers to juveniles from brood years 2006 and 2011. At the time of writing, juvenile samples from brood year 2016 have not been analyzed.

Radtke (1966) indicated that juvenile white sturgeon are found in the Sacramento River and Delta, with the majority of juveniles captured in the Sacramento River. Numerous juvenile and larval white sturgeon have been sampled from the lower San Joaquin River, but those fish are presumed to have entered the system from the Sacramento River through the lower Mokelumne River, Georgiana Slough, or Three Mile Slough (Stevens and Miller 1970). However, spawning has been documented in the San Joaquin River, such that small juvenile white sturgeon collected in San Joaquin River spawning areas (upstream of the Delta) are almost certainly of San Joaquin River origin.

Small juvenile white sturgeon are collected sporadically in various tributaries of the SFE, and the following are some notable examples: one juvenile white sturgeon was captured in a rotary screw trap on the lower Mokelumne River over the past 15 years of monitoring (Workman 2003); one juvenile white sturgeon (possibly two) was detected in the Feather River about 2- to 3-km downstream of Thermalito Afterbay Outlet in May 2000 (Schaffter and Kohlhorst 2001); juvenile white sturgeon have been sampled in the Yolo Bypass during fisheries surveys (B. Schreier, DWR, 2015, personal communication, see "Notes"); and one juvenile white sturgeon was captured in a rotary screw trap located in the American River during February 2015 (C. McKibbin, CDFW, 2015, personal communication, see "Notes"). Juvenile white sturgeon are typically salvaged in low numbers at the federal and state Delta pumping facilities, but a relationship between salvage numbers at the state facility and year-class abundance is lacking (Gingras et al. 2013).

Managers have an early indication of cohort strength and can relate general environmental conditions associated with cohort success. The only index of age-0 production comes from general fish community sampling throughout the SFE in the Bay Study and the index is typically influenced heavily by catch in the lower Sacramento River in the Rio Vista area before May. Indices of recruitment, or year-class index (YCI) have been generated by otter trawl catch of age-0 and age-1 white sturgeon in the Bay Study since 1980. Recruitment trends in the YCI are supported by back-calculation of recruitment with direct or assigned estimates of age (e.g., age analysis of pectoral fin rays or use of age-length keys) from collections of white sturgeon by various monitoring studies. CDFW and USFWS continue to develop those recruitment-modeling techniques by refining estimates of age at length, gear selectivity, and mortality rates.

A positive relationship between high outflow and white sturgeon recruitment in the SFE is supported by juvenile surveys (CDFG 1992; Fish 2010) and hind-cast estimates of relative brood-year abundance from adult monitoring studies (Shirley 1987; M. Gingras, CDFW, 2015a, unpublished data, see "Notes"). Recent investigations show a Delta outflow-recruitment threshold at about 1,416 cubic meters per second (m^3/s; 50,000 cubic feet per second), such that the juvenile YCI is generally strong when flows are above that level (Fish 2010). Cohort abundance information since 1938 shows a boom-and-bust pattern that appears to be related to those high outflow periods (Shirley 1987; CDFG 1992; Fish 2010). Large white sturgeon cohorts have only been detected twice in the last 20 years—in 1998 and 2006—and both years were

classified as wet (CDFW, 2016b, unpublished data, see "Notes"). It should be noted, however, that the primary white sturgeon recruitment survey (Bay Study) was incomplete in 2016 and 2017; indexes have not been generated since 2015.

Small juvenile white sturgeon are likely preyed upon by a variety of native and invasive piscivores (Hildebrand et al. 2016). A mark-recapture study involving small juvenile hatchery white sturgeon (approximately 200 mm FL) was recently conducted to estimate the efficiency of louvers intended to prevent entrainment of fish at the Tracy Fish Collection Facility (Karp and Bridges 2015). Karp and Bridges (2015) found white sturgeon in the stomachs of striped bass collected at the facility during this study. The application of an underwater noise device increased recapture of white sturgeon and louver efficiency estimates from 32.2% to 74.0%, and the increases were attributed to a disruption in predation (Karp and Bridges 2015).

Poor water quality and consumption of contaminated prey species in the SFE watershed may affect juvenile white sturgeon growth and survival. For example, juvenile white sturgeon grew quickly in laboratory studies with ample food at 20 and 25°C but growth was negatively affected by reductions in dissolved oxygen (DO) at all temperature treatments (15, 20, and 25°C; Cech et al. 1984). In laboratory studies, juvenile white sturgeon were able to tolerate abrupt transfer from freshwater (0-ppt salinity) to 15-ppt-salinity water for up to 5 days but experienced high mortality rates in abrupt transfers from freshwater to 25-ppt and 35-ppt-salinity water (McEnroe and Cech 1985; Amiri et al. 2009). Methyl mercury and selenomethionine (two ubiquitous contaminants in the SFE) added to food of juvenile white sturgeon reduced growth and increased mortality (Lee et al. 2011; De Riu et al. 2014). Furthermore, juvenile white sturgeon mortality increased in salinities of 15 to 20 ppt when they were previously exposed to dietary selenium (Tashjian et al. 2007).

Size rather than age appears to provide an osmoregulatory advantage (Amiri et al. 2009), such that larger juvenile white sturgeon are more common in brackish estuarine areas. White sturgeon sampled in CDFW setline surveys in Suisun and San Pablo bays had an average length of 86-cm TL (DuBois et al. 2010). Larger juvenile white sturgeon are also presumed to become more piscivorous, and are known to consume herring (*Clupea harengus pallasi*) and their eggs, American shad (*Alosa sapidissima*), starry flounder (*Platichthys stellatus*), and unidentified gobies (Radtke 1966; McKechnie and Fenner 1971).

Ocean Migration and Maturity

Subadult and adult green sturgeon. The subadult life stage begins at the first entry to the Pacific Ocean and extends to sexual maturation. Adults are mature fish that are not engaged in spawning or spawning migratory behavior. Subadults and adults inhabit marine and estuarine waters along the west coast of North America from Baja California (Rosales-Casian and Almeda-Juaregui 2009) to the Bering Sea (Colway and Stevenson 2007). When not in rivers for spawning, adults and subadults migrate seasonally along the coast and congregate at specific sites in nearshore marine waters (Lindley et al. 2008; Lindley et al. 2011). Subadults and adults enter estuaries and bays during early spring to summer months (presumably for feeding; Dumbauld et al. 2008) and return to the ocean during summer and fall (Moser and Lindley 2007;

Lindley et al. 2011). Southern DPS green sturgeon concurrently occupy several estuaries along the west coast during summer and fall months, primarily San Francisco Bay, Willapa Bay, Grays Harbor, and the Columbia River Estuary. The lack of angler reports or acoustic detection of tagged subadult-sized fish (roughly 60- to 100-cm TL) upstream of the Delta suggest subadults do not use freshwater riverine habitats.

Only a small number (typically, less than 100) of sDPS subadult and adult green sturgeon are collected annually in all monitoring studies in California, and consistent capture occurs only in the long-term (more than 40 years) Sturgeon Study. Data from the Sturgeon Study have been occasionally used to estimate sDPS abundance, but estimates have been imprecise because surveys and associated analyses are primarily designed to study white sturgeon, and because the mark and recapture rates of sDPS green sturgeon has typically been low. Catch of subadult and adult sturgeon is reported by recreational anglers in the SFE and tributaries through the Sturgeon Fishing Report Card program. Some reporting also occurs in the lower Columbia River and bays of Oregon and Washington. Creel surveys of California recreational fisheries and commercial passenger fishing vessels report sturgeon catch; however, prior to 2011, that catch was rarely identified to species. Thus, it is difficult to generate fishery-dependent sDPS green sturgeon harvest and abundance estimates in the SFE from those data beyond applying a rough assumption of the percentage of sDPS green sturgeon in the overall sturgeon population. A major challenge in estimating abundance and overall harvest of sDPS green sturgeon has been mixed aggregations of nDPS and sDPS green sturgeon in Oregon and Washington estuaries and historical harvest in commercial and recreational fisheries in those estuaries.

The Oregon Department of Fish and Wildlife (ODFW) and Washington Department of Fish and Wildlife (WDFW) conducted a large-scale (approximately 1,500 green sturgeon tagged) mark-recapture study to estimate the population size of subadult and adult green sturgeon (described in NMFS 2015). That study generated a wide range of population estimates for adult and subadult green sturgeon (approximately 4,000 to 65,000 fish) in Oregon and Washington estuaries; the authors of that study concluded that an estimate of 40,000 fish was reasonable (NMFS 2015). Genetic analysis by Schreier et al. (2016) revealed 60% of sturgeon tissues collected in this study were from sDPS green sturgeon. Using estimates of annual run-size and spawning periodicity, Mora (2016) estimated the number of sDPS adults to be 1,990 (95% confidence interval [CI] is equivalent to 1,172 to 2,808 adults). Mora (2016) also applied a conceptual demographic structure to that adult population estimate and estimated a sDPS subadult population of 10,450 (95% CI is equivalent to 6,155 to 14,745). The population dynamics inferred in these studies—along with relatively low collection numbers of green sturgeon in SFE surveys—suggest the majority of the sDPS subadult and adult population occupies non-natal estuaries during summer months.

Sport and commercial harvest of green sturgeon has been prohibited since 2006, but past harvest of green sturgeon in California, Washington, and Oregon may have had a significant effect on sDPS green sturgeon abundance (Figure 1). Green sturgeon commercial harvest in the Columbia River Estuary over the last 20 years of record (1983 to 2002) averaged approximately

1,850 individuals per year (ODFW and WDFW 2002). Based on the distinct population segment composition study of green sturgeon in the Columbia River Estuary described in Schreier et al. (2016), the average annual harvest of sDPS green sturgeon in the Columbia River Estuary during this period was more than 1,100 individuals. It is highly plausible that the harvest of subadult and adult sDPS green sturgeon in other commercial and sport fisheries equaled or exceeded harvest in the Columbia River Estuary over this period. The USFWS (1996) estimated the total harvest of adult green sturgeon in Oregon and Washington fisheries at 5,000 to 10,000 individuals per year. The abundance of subadult and adult sDPS green sturgeon prior to Endangered Species Act listing is unknown, but if abundance has remained relatively stable (e.g., 12,440 individuals; Mora 2016), past harvest involved a large portion of the population in some years.
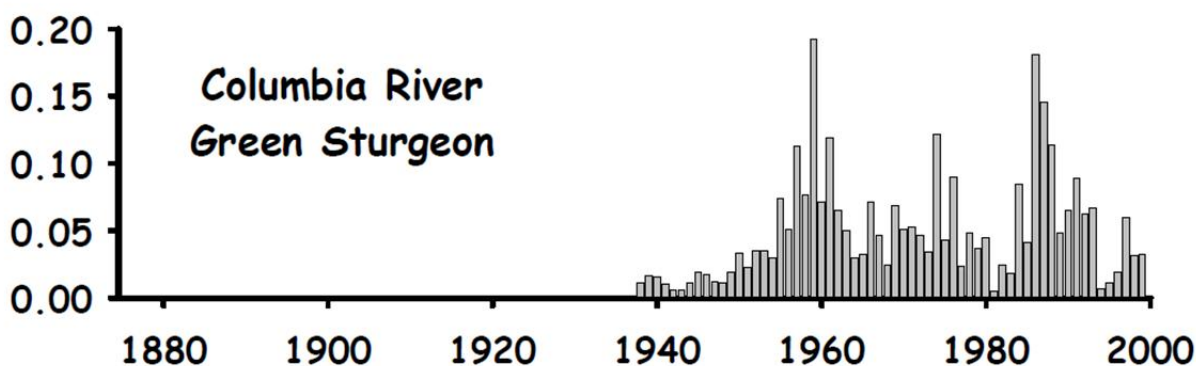
Figure 1. Historical yield of green sturgeon in Columbia River commercial fisheries in millions of pounds from Beamesderfer et al. (2005).

Green sturgeon have been detected in a relatively narrow range of depths and temperatures while in the marine coastal environment. Adults and subadults were typically detected in depths from 20 to 70 m and temperatures from 7.3 to 16.0°C by Erickson and Hightower (2007) and Huff et al. (2011). In the estuarine environment, green sturgeon are exposed to varying water temperature, salinity, and DO. For example, green sturgeon in coastal estuaries have been detected in water temperatures ranging 11.9 to 21.9°C, salinities ranging from 8.8 to 32.1 ppt, and DO ranging from 6.54 to 8.98 milligrams of oxygen per liter (Kelly et al. 2007; Moser and Lindley 2007).

Limited numbers of green sturgeon have been encountered recently in white sturgeon stock assessments in the lower Columbia River, and recapture data from the Oregon and Washington estuary study described above have not been analyzed beyond 2012 due to poor recovery of tagged fish (O. Langness, WDFW, 2015, unpublished data, see "Notes"). Several studies have involved tagging subadult and adult fish with acoustic transmitters, but most tags were implanted before 2012 and will stop transmitting when they exceed the 5- to 10-year battery life. Movement by tagged fish in the SFE and Washington estuaries is monitored with receiver arrays maintained by the UCD Biotelemetry Laboratory and NMFS, respectively, while nearshore marine areas are monitored with compatible receiver arrays associated with other

groups. Subadult and adult nDPS and sDPS green sturgeon are occasionally reported as bycatch in federally managed ground fisheries (Lee et al. 2015; Anderson et al. 2017). The number of sDPS green sturgeon observed in the California halibut fishery (primarily sDPS) exceeded 100 individuals in 2006 and 2015 (Lee et al. 2015; NMFS, 2016, unpublished data, see "Notes") and the only targeted monitoring of subadults and adults in the ocean involves this fishery. Some sDPS green sturgeon caught incidentally by the California halibut fishery operating out of Half Moon Bay and San Francisco since 2015 have been tagged with satellite transponders. This program aims to understand post-release mortality, but also can provide information on movement for up to three weeks after release.

Adult white sturgeon. Tagging studies show that when not migrating, adult white sturgeon are usually found in brackish and estuarine habitat (Kohlhorst et al. 1991; Gleason et al. 2008), including most tidal tributaries to the SFE (Leidy 2007). Several observations of long-distance marine migrations suggest coastal habitats may also be utilized to some degree by those older life stages (Kohlhorst et al. 1991; DeVore et al. 1999; Welch et al. 2006; Ruiz-Campos et al. 2011; E. Miller, UCD Biotelemetry Laboratory, 2017, unpublished data, see "Notes"). For example, white sturgeon tagged in the SFE have been recaptured in the Columbia River, Chehalis River, and Willapa Bay, Washington, as well as the Umpqua River, Yaquina River, and Tillamook Bay, Oregon (Kohlhorst et al. 1991). Furthermore, one adult white sturgeon tagged in the Klamath River entered the ocean and traveled approximately 1,000 km north to be recaptured in the Fraser River (Welch et al. 2006), and an adult white sturgeon was caught by gillnet near Todos Santos Bay in Baja California (Ruiz-Campos et al. 2011).

Daily and seasonal movement of adult white sturgeon may be influenced by salinity and tides. Kohlhorst et al. (1991) found that white sturgeon followed brackish waters upstream in dry years and remained downstream in the SFE in wet years. Foraging movements of white sturgeon in the Columbia River Estuary were also influenced by diel cycles and salinity changes associated with tides (Parsley et al. 2008).

Growth rates of Sacramento-San Joaquin River adult white sturgeon have been estimated by Pycha (1956) and Kohlhorst et al. (1980) by counting annuli in pectoral fin ray sections and fitting von Bertalanffy growth models to the resulting age-length data. The age-length relationship differs between the two studies, with higher apparent growth rates—particularly for older white sturgeon—in the Pycha (1956) study. It is uncertain whether this discrepancy reflects a biological change in growth rate over time or a reflection of the high degree of uncertainty attributable to use of this ageing technique (Rien and Beamesderfer 1994). Growth rates of male and female white sturgeon from the SFE do not appear to be significantly different (Kohlhorst et al. 1980), but a study by Chapman et al. (1996) noted that the smaller individuals they sampled tended to be males while the sex ratio in their sample of larger individuals was skewed towards females.

Sediments in the SFE are heavily contaminated with a variety of toxins. Much of the research on contaminants and fish in the SFE has focused on selenium and mercury, but a suite of other toxins are also present at high levels in sediment throughout the estuary. Some of the

highest levels of toxic trace metals in the coastal United States were recorded in SFE (Cloern et al. 2006). As long-lived, bottom-feeding fish that spend the majority of their lives in the SFE, white sturgeon are highly susceptible to bioaccumulation of those contaminants. Tissues were analyzed from recently sampled adult white sturgeon in the SFE, and selenium and mercury were measured at levels known to impair condition factor (Gundersen et al. 2017). Gundersen et al. (2017) correlated organic contaminant and selenium levels in SFE white sturgeon with altered liver and gonad physiology and plasma hormone levels. Selenium levels in SFE white sturgeon appear to be a longstanding issue. High concentrations of selenium were found in white sturgeon tissue sampled in the SFE from 1970 to 2000 (Greenfield et al. 2003).

Available benthic food items in the SFE have changed in the recent past, and invasive invertebrates have replaced native mollusks and shrimps (Cohen and Carlton 1998). High levels of selenium have been found in common white sturgeon food items (Johns and Luoma 1988; White et al. 1988). Zeug et al. (2014) documented a predominance of invasive overbite clams (*Potamocorbula amurensis*)—a potential vector of bioaccumulation of toxic contaminants—in white sturgeon diets in the SFE. Sturgeon consume, but do not always digest, large quantities of the invasive overbite clam (Kogut 2008; Zeug et al. 2014); consuming indigestible clams may impair digestion of other items and affect sturgeon growth. Furthermore, bivalves have potentially higher levels of contaminants than other prey items in the SFE, and digested overbite clams may be a source of internal exposure to contaminants.

The recreational harvest of white sturgeon in California has remained relatively high in spite of a diminished population, such that monitoring of recreational capture and harvest is a primary management priority. Advances in recreational fishing techniques (e.g., use of shrimp as bait) since 1964 resulted in a rapid reduction in an initially large white sturgeon population (due to harvest prohibitions in the first half of 20th century) and continuous depletion of the few strong subsequent year classes. This is illustrated by commercial passenger fishing vessel log books data summarized by the Sturgeon Study, which shows a severe decline in catch and catch-per-unit effort (CPUE) during the first decade that shrimp were widely used as sturgeon bait (CDFW, 2016e, unpublished data, see "Notes"). This time series also shows a distinct increase in catch and CPUE in the early 1990s attributable to recruitment of the large, early-1980s year classes.

Actual harvest data along with estimates of harvest rate suggest that white sturgeon populations in the SFE may be limited in-part by overfishing. These data are generated by the use of an age-length key, Sturgeon Fishing Report Card data, and mark-recapture data (reward tags) by the Sturgeon Study. Based on ongoing study of age at length, white sturgeon aged 13 to 15 years fall mainly within the current slot limit of 40 to 60 inches FL. Thus, strong mid- to late-1990s year classes were heavily fished over the last 10 years and reduced to a population of fewer than 20,000 fish (Gingras et al. 2014). As part of the Sturgeon Study, reward tags with multiple values are applied to adult white sturgeon. Disproportionately high redemption of $100 tags relative to $20 tags and $50 tags indicates that much of the sturgeon harvest in the SFE goes unreported such that abundance estimates have likely been biased high.

Predation by native species on sub-adult and adult white sturgeon is not well documented. The CDFW has noted an increase in the incidence of California sea lions taking white sturgeon from trammel nets in the annual Sturgeon Study and the occasional presence of damaged or dead white sturgeon from apparent predation by California sea lions. Predation by marine mammals is a significant issue in the Columbia River. The estimated consumption of white sturgeon by pinnipeds in the Bonneville Dam tailrace ranged from approximately 150 to 3,000 individuals annually between 2006 and 2014 (Stansell et al. 2012, 2013, 2014).

Spawning

Spawning green sturgeon. Adults mature at about age 15 and spawn during spring and summer every 2 to 6 years thereafter (NMFS 2015). The putative spawning reach on the Sacramento River extends from above the GCID oxbow to the confluence of the Sacramento River and Cow Creek (Heublein et al. 2009; Klimley et al. 2015). Only two spawning events have been documented outside of the Sacramento River (2011 and 2017) and both occurred in the Feather River (Fish Barrier Dam and the Thermalito Outlet). The Sunset Pumps Weir (33-km downstream of Thermalito Outlet) limits sturgeon passage in certain flows. Modifications of the Sunset Pumps Weir are being designed in hopes that their implementation would improve migration conditions for sturgeon. There are also periodic reports of adult green sturgeon at the base of Daguerre Point Dam on the Yuba River (a tributary to the Feather River), but spawning in the Yuba River has never been documented.

Green sturgeon enter the Sacramento River from late winter through early summer to spawn. Stranding of green sturgeon at migration barriers in the Yolo and Sutter bypasses has only been documented in spring 2011, 2016, and 2017 (wet years). Stranding in 2011 involved at least 24 adults at stilling basins below the Yolo and Sutter Bypass Weirs (Fremont and Tisdale Weirs; Thomas et al. 2013). Entrainment and stranding of adult white sturgeon and salmonids in bypasses is fairly common when bypasses flood, but it is uncertain how bypass channels (e.g., Toe Drain, Tule Canal) affect sturgeon spawning migration during low-flow years. Gravid adult white sturgeon are collected in the Toe Drain in low-flow years when passage barriers prevent access to spawning habitat (DWR 2015). In this regard, route selection may affect inter-annual spawning success as adult sturgeon entrained in bypass channels may not reach spawning habitat within an appropriate time. Records of catch in migratory and spawning habitats are collected through CDFW creel surveys (i.e., Central Valley Angler Survey, California Recreational Fisheries Survey), Sturgeon Fishing Report Cards, and state-mandated commercial passenger fishing vessel log books. A small number of post-spawn fish are periodically collected in San Pablo and Suisun bays during late summer and early fall by the Sturgeon Study.

With the exception of small-scale tagging in the Feather River and at bypass weirs, there is no program tagging adult green sturgeon for acoustic telemetry in the Sacramento River system. An acoustic receiver network is in place throughout the California Central Valley and SFE that is operated and maintained by the UCD Biotelemetry Laboratory along with state and federal agencies. Tagged adults have been detected in spawning habitat in the Sacramento River since 2004, and the majority were tagged outside of California in Pacific Northwest coastal

estuaries. Detections in this array provide information on migration timing and routes, spawning distribution and periodicity, and model inputs for run-size estimates from DIDSON surveys. Efforts are also underway by USFWS, UCD Biotelemetry Laboratory, and NMFS to map habitat in spawning and adult aggregation sites on the Sacramento River. The DWR monitors adult sturgeon in the Feather River, in part through telemetry that began in 2011 and DIDSON surveys that began in 2010. VEMCO VR2 acoustic receivers have been in place throughout the Feather River since 2008 and have detected approximately 15 green sturgeon that were tagged outside the Feather River (primarily in 2017; M. Manuel, PSMFC, 2017, personal communication, see "Notes").

DIDSON survey and telemetry data have been used to estimate green sturgeon run-size in the Sacramento River since 2010 (Mora 2016). Data and modeling from those surveys has greatly improved understanding of adult abundance. However, due to late maturation and variability in maturation age and spawning periodicity, it is challenging to relate trends in green sturgeon run-size to historical conditions that may have affected specific cohorts. Unlike with shorter-lived semelparous species, trends in spawner abundance and historical conditions associated with early life stage success—conditions that may have occurred decades before the observed trend—are intractable without accurate abundance modeling and ageing.

During seasonal RBDD gate closures before 2012, biologists periodically observed aggregations of adult green sturgeon directly below the gates in the spring and early summer. Spawning in this area has been verified several times by the collection of eggs (Poytress et al. 2015). Historical gate operations presumably influenced downstream hydrology, spawning, and holding at RBDD because aggregations have not been observed there since 2012. Although this spawning site was lost when gates were permanently raised in 2012, a new spawning site in an area historically inundated by the impoundment above RBDD was documented with the collection of eggs in RBDD rotary screw traps in 2016 and 2017 (W. Poytress, USFWS, 2017a, unpublished data, see "Notes").

The permanent raising of RBDD gates has the potential to affect multiple life stages of green sturgeon. Historically, adult green sturgeon arriving to RBDD after gate closure were relegated to a warmer reach of the Sacramento River for spawning. In extreme low flows, spawning areas below RBDD may be unsuitable for green sturgeon spawning in early summer. However, temperature above RBDD was suitable for spawning in early summer even in the recent historic drought. Thus, raising the gates at RBDD expanded the accessible spawning range for green sturgeon and—in what may be a key element of green sturgeon life history diversity—facilitated temporal and spatial variation in spawning distribution (A. Steel et al., UCD Biotelemetry Laboratory, 2017, unpublished data, see "Notes"). Furthermore, multiple dead adult green sturgeon have been documented below RBDD after gate closure. Those mortalities were attributed to injuries sustained during attempted downstream migration through a narrow opening below the closed RBDD gates. With gates permanently raised, that source of mortality no longer exists. Finally, the diversion facility at RBDD was recently upgraded. Although sturgeon entrainment at the RBDD facility has not been directly studied, entrainment risk for

larval green sturgeon has presumably been reduced by both raising dam gates and potentially improved hydraulics associated with modern fish screens.

After spawning, green sturgeon hold in-river for varying periods of time but most commonly leave the system the following fall (Benson et al. 2007; Heublein et al. 2009). Early outmigration in late spring or summer may be related to elevated flows (Benson et al. 2007; Heublein et al. 2009). For adults that over-summer in spawning or holding habitats, outmigration occurs in the late fall or (rarely) in winter after spending more than a year in freshwater (R. Chase, USACE, 2015, unpublished data, see "Notes"). Extended occupancy of those spawning and holding habitats may be related to hydrologic cues or food availability, but it is uncertain why occupancy sometimes lasts more than a year. Normal outmigration patterns for adults in the Feather River are unknown because of flow management and the passage barrier at Sunset Pumps Weir. However, the behavior of tagged fish in the Feather River suggests that adult outmigration there is similar to adult outmigration in the Sacramento River (i.e., both spring and summer outmigration and over-summer holding behavior; DWR, 2017b, unpublished data, see "Notes").

Post-spawn outmigration through the SFE is also variable. Adults have been detected migrating to the Pacific Ocean rather quickly (2 to 10 days) and remaining in the SFE for a number of months after leaving upstream holding habitats (R. Chase, USACE, 2015, unpublished data, see "Notes"). Movement between river habitat and the SFE has only been related to spawning, and adults do not appear to migrate upstream from the SFE to forage (R. Chase, USACE, 2015, unpublished data, see "Notes").

Spawning white sturgeon. Chapman et al. (1996) estimated that SFE white sturgeon females reach maturity at 95- to 135-cm FL and white sturgeon males reach maturity at 75- to 105-cm FL. The smallest sexually mature female described in the SFE watershed was 104-cm FL (Chapman et al. 1996) and was estimated to be 9 years old using the von Bertalanffy growth equation from Brennan and Cailliet (1989). Female white sturgeon in the SFE are estimated to first spawn between 10 and 30 years old, and spawn every 2 to 4 years thereafter (Chapman et al. 1996).

White sturgeon in the SFE spawn in freshwater between mid-February and early June (Miller 1972; Kohlhorst 1976; Schaffter 1997; Jackson et al. 2016). Based on recent acoustic detections of tagged adults, white sturgeon may stage in the Delta or begin upstream migration to spawning habitat in fall or early winter (DWR 2015; Klimley et al. 2015). Spawning is known to occur in the San Joaquin River, the Sacramento River, some Sacramento River tributaries, and some watersheds on the northern California coast (Miller 1972; Kohlhorst 1976; Schaffter 1997; Jackson et al. 2016). However, long-term monitoring of adult and juvenile distribution indicates that most SFE white sturgeon originate from the Sacramento River. Spawning locations on the Sacramento River currently appear to be located from Colusa to the Verona area (Kohlhorst 1976; Schaffter 1997), although spawning likely occurs many kilometers upriver in some years (described above in the Fertilization to Hatch section). A relic population of white sturgeon persisted in Shasta Reservoir following construction of Shasta Dam (1940 to 1945), suggesting

historical spawning in upper Sacramento River tributaries such as the Pit River (Schaffter 1997; Moyle 2002). However, historical stocking records for sturgeon are poor, so it is unclear if white sturgeon in Shasta Reservoir were entirely of natural origin. Periodic aggregations of gravid white sturgeon and telemetry data in the Yolo Bypass and Bear River indicate spawning may extend to those areas in some years.

Fishery-independent monitoring of white sturgeon has occurred since the early 1950s and has persisted at low intensity until it became a CDFW emphasis in 2006 with Federal Endangered Species Act listing of sDPS green sturgeon. Adult white sturgeon abundance, relative abundance, harvest rate, and survival rate are estimated annually in the Sturgeon Study, which uses data from commercial passenger fishing vessels, various creel surveys, and mark-recapture data from annual trammel net sampling in San Pablo Bay and Suisun Bay. Based on those data, trends in adult white sturgeon abundance and juvenile recruitment have been developed. However, current life stage monitoring is insufficient to develop mechanisms for episodic recruitment success or to address bias in abundance estimates and harvest rates associated with angler reporting.

Some directed sampling or incidental capture of adult white sturgeon occurs in spawning and migratory habitats. This includes sampling with fyke traps in the Yolo Bypass and Sacramento River, stranding at bypass weirs, and gill and trammel netting in San Joaquin River spawning habitat. Recapture of externally tagged fish (tagged in the Sturgeon Study) by the recreational fishery and data from Sturgeon Fishing Report Cards include information on sturgeon in migratory and spawning habitat. Other information on spawning adult behavior comes primarily from telemetry studies conducted by multiple groups (e.g., UCD, DWR, USFWS) throughout the SFE and spawning tributaries. Tissue from recreational harvest of white sturgeon (40- to 60-inches FL) in SFE fishing derbies was also analyzed in a recent directed study of contaminants (Gundersen et al. 2017).

Migration barriers and stranding have been documented in the Yolo Bypass, Sutter Bypass, and Bear River since the mid-1980s. Those stranding events were associated with poaching and intensive legal harvest that has since been prohibited. The most recent documented events occurred in spring 2011, 2016, and 2017 (wet years) and involved stranding of adult green and white sturgeon in stilling basins below the Fremont and Tisdale Bypass Weirs. It is uncertain how bypass channels affect sturgeon spawning migration and success during low-flow years. For example, adult white sturgeon were captured in relatively high numbers from 2012 to 2014 (dry years) in a fyke trap deployed in the Yolo Bypass Toe Drain (DWR 2015). Delays in upstream sturgeon migration due to the complexity in fish passage at various bypass barriers (e.g., Lisbon and Fremont Weirs) may reduce spawning success. Stranding of adult white sturgeon in the Bear River may occur in normal or dry years. The last documented stranding event on the Bear River was in spring 2012, the first year of the recent drought. Winter and spring flow and water surface elevation on the Bear River can be highly variable even in relatively dry years. These flashy hydrograph conditions are thought to attract spawning white sturgeon to the Bear River, then subject those fish to high stranding risk.

The direct effects of consumption of contaminated prey species are briefly described above, but white sturgeon egg and larval survival may also be impacted through maternal transfer of contaminants. Exposure of gravid female white sturgeon to a diet enriched in selenium resulted in selenium incorporation to plasma vitellogenin and egg yolk proteins (Doroshov et al. 2007). Selenium has been measured in liver and gonad tissues of white sturgeon collected in the SFE at levels known to cause reproductive toxicity (Linares-Casanave et al. 2015) and exceeded concentrations associated with severe deformity and high mortality in the egg yolks of larvae (15 milligrams per gram; Doroshov et al. 2007).

Increasing streamflow is believed to be an important cue for migration and spawning of white sturgeon across their range (Schaffter 1997; Hildebrand et al. 1999; Paragamian and Wakkinen 2011; Jackson et al. 2016). During a drought year, Schaffter (1997) documented white sturgeon spawning in the Sacramento River following 40 m^3/s increases in streamflow, which would correspond to an increase in outflow or runoff of approximately 3,456,000 m^3 or 2,800 acre-feet per day. Similarly, white sturgeon spawning was observed at all four San Joaquin River sampling locations following short-duration streamflow pulses (approximately 18 to 40 m^3/s) during otherwise low streamflow conditions in 2012 (Jackson et al. 2016) and again in 2016 (Z. Jackson, USFWS, 2017, unpublished data, see "Notes").

There is little quantitative information on spawning site habitat requirements. In the Sacramento and San Joaquin watersheds, white sturgeon spawning habitat has substrate ranging from silt-and-sand to gravel-and-cobble and water velocities ranging from low to high (Kohlhorst 1976; Schaffter 1997; Jackson et al. 2016). As indicated by the presence of eggs or larvae, white sturgeon have been observed to spawn at water temperatures of 8 to 23°C, with peak spawning occurring around 14°C (8 to 19°C, peak 14°C, Moyle 2002; 7.8 to 17.8°C, peak 14.4°C, Kohlhorst 1976; and 12 to 16°C, Schaffter 1997). Spawning in the San Joaquin River has occurred at higher temperatures (14.2 to 26.7°C, Jackson et al. 2016), although viability of larvae at the upper end of this range is unlikely. White sturgeon in the SFE typically return promptly to the estuary after spawning. However, adult holding through summer in freshwater spawning habitat has been documented on the Sacramento and San Joaquin rivers (Klimley et al. 2015; M. Manuel, PSMFC, 2016, personal communication unreferenced, see "Notes").

References

Allen, P. J., B. Hodge, I. Werner, and J. J. Cech. 2006. Effects of ontogeny, season, and temperature on the swimming performance of juvenile green sturgeon (*Acipenser medirostris*). Canadian Journal of Fisheries and Aquatic Sciences 63(6):1360-1369.

Allen, P. J., M. Nicholl, S. Cole, A. Vlazny, and J. J. Cech. 2006b. Growth of larval to juvenile green sturgeon in elevated temperature regimes. Trans Am Fish Soc 135:89-96.

Allen, P. J., M. McEnroe, T. Forostyan, S. Cole, M. M. Nicholl, B. Hodge, and J. J. Cech. 2011. Ontogeny of salinity tolerance and evidence for seawater-entry preparation in juvenile green sturgeon, *Acipenser medirostris*. J Comp Physiol B 181(8):1045-1062.

Amiri, M., D. W. Baker, D. Morgan, and C. J. Brauner. 2009. Size dependent early salinity tolerance in two sizes of juvenile White Sturgeon, *Acipenser transmontanus*. Aquaculture 286:121-126.

Anderson, E. C., T. C. Ng, E. D. Crandall, and J. C. Carlos. 2017. Genetic and individual assignment of tetraploid green sturgeon with SNP assay data. Conserv Genet DOI 10.1007/s10592-017-0963-5.

Beamesderfer, R. C. P., G. Kopp, D. Demko. 2005. Review of the distribution, life history and population dynamics of green sturgeon with reference to California's Central Valley. Gresham (OR): S.P. Cramer and Associates, Inc. General technical review. 39 p. Available from: http://www.fishsciences.net/reports/2005/Beamesderfer_2005_Review_of_the_distributio n.pdf.

Benson, R. L., S. Turo, and B. W. J. McCovey. 2007. Migration and movement patterns of green sturgeon (*Acipenser medirostris*) in the Klamath and Trinity rivers, California, USA. Environ Biol Fishes 79:269-279.

Bergman, P. 2011. Videography monitoring of adult sturgeon in the Feather River basin, CA. Report to Anadromous Fish Restoration Program. Gresham, (OR): Cramer Fish Sciences. 22 p. Available from: https://www.fws.gov/lodi/anadromous_fish_restoration/documents/Feather_Sturgeon_Re port_022811.pdf

Bergman, P.S., J. Merz, and B. Rook. 2011. Memo: Green Sturgeon Observations at Daguerre Point Dam, Yuba River, CA. Memo to Anadromous Fish Restoration Program. Gresham, (OR): Cramer Fish Sciences. 6 p. Available from: https://www.fws.gov/lodi/anadromous_fish_restoration/documents/Yuba_River_Sturgeo n_Memo.pdf

Brennan, J. S., and G. M. Cailliet. 1989. Comparative age determination techniques for White Sturgeon in California. Trans Am Fish Soc 118:296-310.

Brown, K. 2007. Evidence of spawning by green sturgeon, *Acipenser medirostris*, in the upper Sacramento River, California. Environ Biol Fishes 79(3-4):297-303.

CDFG (California Department of Fish and Game). 1992. Sturgeon in relation to water development in the Sacramento-San Joaquin estuary; Entered by the California Department of Fish and Game for the State Water Resources Control Board 1992 water rights phase of the Bay-Delta Estuary proceedings. WRINT-DFG-Exhibit 28

CDFG. 2002. California Department of Fish and Game comments to NMFS regarding green sturgeon listing. Available from: http://www.swrcb.ca.gov/waterrights/water_issues/programs/bay_delta/deltaflow/docs/ex hibits/nmfs/spprt_docs/nmfs_exh4_dfg_2002.pdf

Cech, J. J., S. J. Mitchell, and T. E. Wragg. 1984. Comparative growth of juvenile White Sturgeon and Striped Bass: effects of temperature and hypoxia. Estuaries 7:12-18.

Chapman, F. A., J. P. Van Eenennaam, and S. I. Doroshov. 1996. The reproductive conditions of White Sturgeon, *Acipenser transmontanus*, in San Francisco Bay, California. Fish Bull 94:628-634.

Cloern, J. E., S. N. Luoma, and F. H. Nichols. 2006. Managing Coastal Resources of the US. USGS. Available from:
http://sfbay.wr.usgs.gov/general_factsheets/coastal_resources.html

Cohen, A. N., and J. T. Carlton. 1998. Accelerating Invasion Rate in a Highly Invaded Estuary. Science. 279:555-558.

Colway, C., and D. E. Stevenson. 2007. Confirmed records of two green sturgeon from the Bering Sea and Gulf of Alaska. Northwest Nat 88(3):188-192.

De Riu, N., J. W. Lee, S. S. Y. Huang, G. Moniello, and S. S. O. Hung. 2014. Effect of dietary selenomethionine on growth performance, tissue burden, and histopathology in Green and White Sturgeon. Aquat Toxicol 148:65-73.

Deng, X., J. P. Van Eenennaam, and S. I. Doroshov. 2002. Comparison of early life stages and growth of green and white sturgeon. In: Van Winkle W et al., editors. 2002. Biology, management, and protection of North American sturgeon. AFS Symposium 28:237-248.

Dettlaff, T.A., A. S. Ginsburg, and O. I. Schmalhausen. 1993. Sturgeon fishes: developmental biology and aquaculture. Springer-Verlag, New York.

DeVore, J., B. James, and R. Beamesderfer. 1999. Lower Columbia River White Sturgeon current stock status and management implications. Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife, Olympia, Washington.

Doroshov, S. I., J. P. Van Eenennaam, J. Linares, and R. G. Linville. 2007. Potential environmental impacts on reproduction of green and white sturgeons. Oral presentation at Calfed 2007.

DuBois, J., E. Gleason, and M. Gingras. 2010. Review of juvenile sturgeon setline survey. IEP Newsletter 23(3):25-33.

Dumbauld, B. R., D. L. Holden, and O. P. Langness. 2008. Do sturgeon limit burrowing shrimp populations in Pacific Northwest estuaries? Environ Biol Fishes 83:283-296.

DWR (California Department of Water Resources). 2015. Fisheries evaluation of floodplain rearing and migration in the Yolo Bypass floodplain. Prepared by DWR Division of Environmental Services, Aquatic Ecology Section for California Department of Fish and Wildlife Ecosystem Restoration Program. January 2015. 102 p.

Erickson, D. L., and J. E. Hightower. 2007. 2007. Oceanic distribution and behavior of green sturgeon (*Acipenser medirostris*). In: Munro, J, et al., editors. 2007. Anadromous sturgeons: habitats, threats, and management. AFS Symposium 56:197-211.

Faukner, J. R., and Z. J. Jackson. 2014. 2013 San Joaquin River sturgeon spawning survey. Stockton Fish and Wildlife Office, Anadromous Fish Restoration Program, U.S. Fish and Wildlife Service, Lodi, California.

Fabrizio, M. C., and R. A. Richards. 1996. Commercial Fisheries Surveys. In: Murphy, B.R., and D. W. Willis, editors. 1996. Fisheries Techniques, Second Edition. American Fisheries Society, Maryland, U.S.A. p. 625-650.

Fish, M. A. 2010. A white sturgeon year-class index for the San Francisco estuary and its relation to delta outflow. IEP Newsletter 23(2):80-84.

Gartz, R. G. 2007. 2006 Fish Salvage at the Tracy Fish Collection Facility. March 21, 2007. California Department of Fish and Game Bay-Delta Region Fish Facilities Research and Operations Monitoring Unit 4001 North Wilson Way Stockton, CA 95205. Available from: ftp://ftp.dfg.ca.gov/salvage/Annual%20Salvage%20Reports/2006%20TFCF%20Annual %20Salvage%20Report.pdf

Gadomski, D., and M. Parsley. 2005. Effects of turbidity, light level, and cover on predation of white sturgeon larvae by prickly sculpins. Trans Am Fish Soc 134:369-374.

Gingras, M., and J. DuBois. 2013. Monitoring progress toward a CVPIA recovery objective: estimating white sturgeon abundance by age. Interagency Ecological Program for the San Francisco Estuary Newsletter 26(4):6-9.

Gingras, M., J. DuBois, and M. Fish. 2013. Further Investigations into San Francisco Estuary White Sturgeon (*Acipenser transmontanus*) Year-Class Strength. Interagency Ecological Program for the San Francisco Estuary Newsletter 26(4):10-12.

Gingras, M., J. DuBois, and M. Fish. 2014. Presentation: Impact of Water Operations and Overfishing on White Sturgeon, Interagency Ecological Program Annual Conference. 2014. California Department of Fish and Wildlife

Gisbert, E., J. J. Cech, and S. I. Doroshov. 2001. Routine metabolism of larval green sturgeon (*Acipenser medirostris*). Fish Physiology and Biochemistry 25:195-200

Gleason, E., M. Gingras, and J. DuBois. 2008. 2007 sturgeon fishing: preliminary data report. California Department of Fish and Game, Stockton, California.

Greenfield, B. K., J. A. Davis, R. Fairey, C. Roberts, D. B. Crane, G. Ichikawa, and M. Petreas. 2003. Contaminant Concentrations in Fish from San Francisco Bay, 2000. RMP Technical Report: SFEI Contribution 77. San Francisco Estuary Institute, Oakland, California.

Gundersen, D. T., J. Zachary, R. B. Bringolf, J. Merz, S. C. Zeug, and M. A. H. Web. 2017. Tissue contaminant burdens in San Francisco Estuary white sturgeon (*Acipenser transmontanus*) and dietary items: implications for population recovery. Arch Environ Contam Toxicol. DOI 10.1007/s00244-017-0378-9

Heublein, J. C., J. T. Kelly, C. E. Crocker, A. P. Klimley, and S. T. Lindley. 2009. Migration of green sturgeon, *Acipenser medirostris*, in the Sacramento River. Environ Biol Fishes 84:245-258.

Heublein, J., R. Bellmer, R. D. Chase, P. Doukakis, M. Gingras, D. Hampton, J. A. Israel, Z. J. Jackson, R. C. Johnson, O. P. Langness, S. Luis, E. Mora, M. L. Moser, L. Rohrbach, A. M. Seesholtz, and T. Sommer. 2017. Improved Fisheries Management Through Life

Stage Monitoring: the Case for the Southern Distinct Population Segment of North American Green Sturgeon and the Sacramento-San Joaquin River White Sturgeon. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-588.

Hildebrand, L., C. McLeod, and S. McKenzie. 1999. Status and management of white sturgeon in the Columbia River in British Columbia, Canada: an overview. J Applied Ichthyol 15:164-172.

Hildebrand, L. R., A. Drauch Schreier, K. Lepla, S. O. McAdam, J. McLellan, M. J. Parsley, V. L. Paragamian, and S. P. Young. 2016. Status of White Sturgeon (*Acipenser transmontanus*, Richardson, 1863) throughout the species range, threats to survival, and prognosis for the future. J Appl Ichthyol 32(Suppl. 1):261‑312

Huff, D. D., S. T. Lindley, P. S. Rankin, and E. A. Mora. 2011. Green sturgeon physical habitat use in the coastal Pacific Ocean. PLoS ONE 6(9):e25156. doi:10.1371/journal.pone.0025156.

Israel, J.A., K. J. Bando, E. C. Anderson, and B. May. 2009. Polyploid microsatellite data reveal stock complexity among estuarine north American green sturgeon (*Acipenser medirostris*). Can J Fish Aquat Sci 66:1491–1504. doi:10.1139/F09-091

Jackson, Z. J., J. J. Gruber, and J. P. Van Eenennaam. 2016. White sturgeon spawning in the San Joaquin River, California and effects of water management. Journal of Fish and Wildlife Management 7(1):171-180.

Johns C., and S. N. Luoma. 1988. Selenium accumulation in benthic bivalves and fine sediments of San Francisco Bay, the Sacramento-San Joaquin delta, and selected tributaries. Estuar Coast Shelf Sci 27:381-396.

Karp, C., and B. Bridges. 2015. White Sturgeon salvage efficiency at the Tracy Fish Collection Facility. Tracy Technical Bulletin 2015-3. U.S. Department of the Interior, Bureau of Reclamation, Mid-Pacific Region and the Technical Service Center.

Kelly, J. T., A. P. Klimley, and C. E. Crocker. 2007. Movements of green sturgeon, *Acipenser medirostris*, in the San Francisco Bay Estuary, California. Environ Biol Fishes 79:281-295.

Klimley, A. P., E. D. Chapman, J. J. Cech, D. E. Cocherell, N. A. Fangue, M. Gingras, Z. Jackson, E. A. Miller, E. Mora, and J. B. Poletto. 2015. Sturgeon in the Sacramento-San Joaquin Watershed: new insights to support conservation and management. 2015. San Francisco Estuary and Watershed Science 13(4).

Kogut, N. J. 2008. Overbite clams, *Corbula amurensis*, defecated alive by white sturgeon, *Acipenser transmontanus*. Calif Fish Game 94(3):143−149

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

Kohlhorst, D. W., L. W. Miller, and J. J. Orsi. 1980. Age and growth of White Sturgeon collected in the Sacramento - San Joaquin estuary, California: 1965-1970 and 1973-1976. Calif Fish Game 66:83-95.

Kohlhorst, D. W., L. W. Botsford, J. S. Brennan, and G. M. Caillet. 1991. Aspects of the structure and dynamics of an exploited central California population of White Sturgeon (*Acipenser transmontanus*). In: Williott, P., editor. 1991. Acipenser. Cemagref Publishers, Bordeaux, France. p. 277-293.

Kohlhorst, D. W., and J. Cech. 2001. White Sturgeon. In: California's Living Marine Resources: A Status Report. California Department of Fish and Game. p. 467-469.

Kynard, B., and E. Parker. 2005. Ontogenetic behavior and dispersal of Sacramento River White Sturgeon, *Acipenser transmontanus*, with a note on body color. Environ Biol Fish 74:19-30.

Kynard, B., E. Parker, and T. Parker. 2005. Behavior of early life intervals of Klamath River green sturgeon, *Acipenser medirostris*, with a note on body color. Environ Biol Fishes 72(1):85-97.

Lee, J-W, N. De Riu, S. Lee, S. C. Bai, G. Moniello, and S. S. O. Hung. 2011. Effects of dietary methylmercury on growth performance and tissue burden in juvenile Green (*Acipenser medirostris*) and White Sturgeon (*A. transmontanus*). Aqua Toxicol 105:227-234.

Lee, Y-W, R. Gustafson, J. Jannot, J. McVeigh, N. Riley, K. Somers, V. Tuttle, S. Wang, and E. Ward. 2015. Observed and estimated bycatch of green sturgeon in 2002-2013 U.S. West Coast groundfish fisheries. West Coast Groundfish Observer Program. National Marine Fisheries Service. Available from: http://www.pcouncil.org/wp-content/uploads/2015/06/D4_Sup_Att4_GreenSturgeonBiOpBycatchRpt_E-ONLY_JUN2015BB.pdf

Leidy, R. A. 2007. Ecology, Assemblage Structure, Distribution, and Status of Fishes in Streams Tributary to the San Francisco Estuary, California. San Francisco Estuary Institute. April 2007. Contribution No. 530.

Linares-Casenave, J., I. Werner, J. P. Van Eenennaam, and S. I. Doroshov. 2013. Temperature stress induces notochord abnormalities and heat shock proteins expression in larval green sturgeon (*Acipenser medirostris*, Ayres, 1854). J Appl Ichthyol 29: 958–967.

Linares-Casanave, J., R. Linville, J. P. Van Eenennaam, J. B. Muguet, and S. I. Doroshov. 2015. Selenium tissue burden compartmentalization in resident White Sturgeon (*Acipenser transmontanus*) of the San Francisco SFE Estuary. Environ Toxicol Chem 34(1):152-160.

Lindley, S. T., M. L. Moser, D. L. Erickson, M. Belchik, D. W. Welch, E. Rechisky, J. T. Kelly, J. C. Heublein, and A. P. Klimley. 2008. Marine migration of North American green sturgeon. Trans Am Fish Soc 137:182-194.

Lindley, S. T., D. L. Erickson, M. L. Moser, G. Williams, O. P. Langness, B. W. McCovey, M. Belchik, D. Vogel, W. Pinnix, J. T. Kelly, J. C. Heublein, and A. P. Klimley. 2011. Electronic tagging of green sturgeon reveals population structure and movement among estuaries. Trans Am Fish Soc 140:108-122.

Mayfield, R. B., and J. J. Cech. 2004. Temperature effects on green sturgeon bioenergetics. Trans Am Fish Soc 133(4):961-970.

McEnroe, M., and J. J. Cech Jr. 1985. Osmoregulation in juvenile and adult White Sturgeon, *Acipenser transmontanus*. Environ Biol Fishes 14:2330.

McKechnie, R. J., and R. B. Fenner. 1971. Food habits of white sturgeon, *Acipenser transmontanus*, in San Pablo and Suisun Bays, California. Calif Fish Game, 57:209-212.

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

Mora, E. A. 2016. A Confluence of Sturgeon Migration: Adult Abundance and Juvenile Survival. PhD Dissertation, Univ. Calif., Davis.

Moser, M. L., and S. T. Lindley. 2007. Use of Washington estuaries by subadult and adult green sturgeon. Environ Biol Fishes 79:243-253.

Moyle, P. B. 2002. Inland fishes of California. Berkeley: University of California Press. p. 109-113.

Mussen, T. D., D. E. Cocherell, J. B. Poletto, J. S. Reardon, Z. Hockett, A. Ercan, H. Bandeh, M. L. Kavvas, J. J. Cech Jr., and N. A. Fangue. 2014. Unscreened water-diversion pipes pose an entrainment risk to the threatened green sturgeon, *Acipenser medirostris*. PLoS ONE 9, e86321 doi: http://dx.doi.org/10.1371/journal. pone.0086321

Nakamoto, R. J., T. T. Kisanuki, and G. H. Goldsmith. 1995. Age and growth of Klamath River green sturgeon (*Acipenser Medirostris*). USFWS Project # 93-FP-13. January 31, 1995. 27 p.

NMFS (National Marine Fisheries Service). 2015. Southern Distinct Population Segment of the North American Green Sturgeon (*Acipenser medirostris*); 5-Year Review. West Coast Region, Long Beach, CA. Available from: http://www.nmfs.noaa.gov/pr/listing/southern_dps_green_sturgeon_5-year_review_2015__2_.pdf

ODFW and WDFW (Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife). 2002. Status report Columbia River fish runs and fisheries 1938-2002, Tables only. 180p. Available from: http://www.dfw.state.or.us/fish/OSCRP/CRM/reports/status_report/2002_status_tables.pdf

ODFW and WDFW. 2014. Study of green sturgeon on the West coast of the United States. Project Completion Report. Prepared for the National Oceanic and Atmospheric Association for NOAA Fisheries Protected Species Conservation and Recovery Grant No.: NA10NMF4720037. 191 p.

Paragamian, V. L., and V. D. Wakkinen. 2011. White sturgeon spawning and discharge augmentation. Fish Manag Ecol 18:314-321.

Parsley, M. J., S. D. Duke, T. J. Underwood, and L. G. Beckman. 1989. Report C in A.A. Nigro, editor. Status and habitat requirements of White Sturgeon populations in the Columbia River downstream from McNary Dam. Annual Progress Report. Bonneville Power Authority, Contract DE-AI79-86BP63584. Portland, Oregon.

Parsley, M. J., N. D. Popoff, C. D. Wright, and B. K. van der Leeuw. 2008. Seasonal and Diel Movements of White Sturgeon in the Lower Columbia River. Transactions of the American Fisheries Society. 137(4):1007-1017.

Poletto, J. B., D. E. Cocherell, N. Ho, J. J. Cech Jr, A. P. Klimley, and N. A. Fangue. 2014a. Juvenile green sturgeon (*Acipenser medirostris*) and white sturgeon (*Acipenser transmontanus*) behavior near water diversion fish screens: experiments in a laboratory swimming flume. Can J Fish Aquat Sci 71:1030- 1038. doi: http://dx.doi.org/10.1139/cjfas-2013-0556

Poletto, J. B., D. E. Cocherell, T. D. Mussen, A. Ercan, H. Bandeh, M. Kavvas, J. J. Cech Jr., and N. A. Fangue. 2014b. Efficacy of a sensory deterrent and pipe modifications in decreasing unscreened water diversions. Conserv Physiol 2(1):cou056. doi: http://dx.doi.org/10.1093/ conphys/cou056

Poletto, J. B., D. E. Cocherell, T. D. Mussen, A. Ercan, H. Bandeh, M. Kavvas, J. J. Cech Jr., and N. A. Fangue. 2015. Fish protection devices at unscreened water diversions can reduce entrainment: evidence from behavioral laboratory investigations. Conserv Physiol 3(1):cov040. doi: http://dx.doi.org/10.1093/conphys/ cov040.

Poytress, W. R., J. J. Gruber, D. Trachtenbarg, and J. P. Van Eenennaam. 2009. 2008 Upper Sacramento River green sturgeon spawning habitat and larval migration surveys. Annual Report of U.S. Fish and Wildlife Service to U.S. Bureau of Reclamation, Red Bluff, CA.

Poytress, W. R., J. J. Gruber, and J. P. Van Eenennaam. 2010. 2009 Upper Sacramento River green sturgeon spawning habitat and larval migration surveys. Annual Report of U.S. Fish and Wildlife Service to U.S. Bureau of Reclamation, Red Bluff, CA.

Poytress, W. R., J. J. Gruber, and J. P. Van Eenennaam. 2011. 2010 Upper Sacramento River green sturgeon spawning habitat and larval migration surveys. Annual Report of U.S. Fish and Wildlife Service to U.S. Bureau of Reclamation, Red Bluff, CA.

Poytress, W. R., J. J. Gruber, and J. P. Van Eenennaam. 2012. 2011 Upper Sacramento River green sturgeon spawning habitat and larval migration surveys. Annual Report of U.S. Fish and Wildlife Service to U.S. Bureau of Reclamation, Red Bluff, CA.

Poytress, W. R., J. J. Gruber, C. Praetorius, and J. P. Van Eenennaam. 2013. 2012 Upper Sacramento River green sturgeon spawning habitat and young-of-the-year migration surveys. Annual Report of U.S. Fish and Wildlife Service to U.S. Bureau of Reclamation, Red Bluff, CA.

Poytress, W. R., J. J. Gruber, J. P. Van Eenennaam, and M. Gard. 2015. Spatial and temporal distribution of spawning events and habitat characteristics of Sacramento River green sturgeon. Trans Am Fish Soc 144(6):1129-1142.

Pycha, R.L. 1956. Progress report on White Sturgeon studies. Calif Fish Game 42:23-35.

Quist MC, Pegg MA, DeVries DR. 2012. Age and Growth, pp. 677–731. In: Fisheries Techniques (Zale, A., D. Parrish, and T. Sutton, Eds.), 3rd Edn. Bethesda, MD: American Fisheries Society.

Radtke, L. D. 1966. Distribution of smelt, juvenile sturgeon, and starry flounder in the Sacramento-San Joaquin Delta with observations on food of sturgeon. In J.L. Turner and D.W. Kelly (Comp.) Ecological Studies of the Sacramento-San Joaquin Delta. Part 2 Fishes of the Delta. California Department of Fish and Game Fish Bulletin 136:115-129.

Rien, T. A., and R. C. Beamesderfer. 1994. Accuracy and precision of White Sturgeon age estimates from pectoral fin rays. Trans Am Fish Soc 123:255-265.

Rosales-Casian, J. R., and C. Almeda-Juaregui. 2009. Unusual occurrence of a green sturgeon (*Acipenser medirostris*) at El Socorro Bay, Baja California, Mexico. CalCoFI Rep 50:169-171.

Ruiz-Campos, G., J. L. Castro-Aguirre, and F. J. Garcia-De Leon. 2011. First specimen of the white sturgeon (*Acipenser transmontanus* Richardson, 1836) in coastal waters of Mexico with data on its genetic identity. California Fish and Game 97(1):36-42.

Schaffter, R. G. 1997. White Sturgeon spawning migrations and location of spawning habitat in the Sacramento River, California. Calif Fish Game 83(1):1-20.

Schaffter, R. G, and D. W. Kohlhorst. 2001. Final report for phase 2, Task 5: determination of Green Sturgeon spawning habitats and their environmental conditions. Final report submitted to CALFED, Sacramento, California.

Schreier, A., B. Mahardja, and B. May. 2013. Patterns of population structure vary across the range of the White Sturgeon. Trans Am Fish Soc 142:1273-1286.

Schreier, A., O. P. Langness, J. A. Israel, and E. Van Dyke. 2016. Further investigation of green sturgeon (*Acipenser medirostris*) distinct population segment composition in non-natal estuaries and preliminary evidence of Columbia River spawning. Environ Biol Fish 99:1021 10.1007/s10641-016-0538-1.

Seesholtz, A. M., M. J. Manuel, and J. P. Van Eenennaam. 2015. First documented spawning and associated habitat conditions for green sturgeon in the Feather River, California. Environ Biol Fishes 98(3):905-912.

Shirley, D. E. 1987. Age distribution of white sturgeon (*Acipenser transmontanus*) in the Sacramento-San Joaquin Bay-Delta. M.S. Thesis, Univ. Calif., Davis.

Stansell, R. J., K. M. Gibbons, W. T. Nagy, and B. K. van der Leeuw. 2012. Evaluation of pinniped predation on adult salmonids and other fish in the Bonneville Dam tailrace, 2012. USACE. October 4, 2012.

Stansell, R. J., B. K. van der Leeuw, K. M. Gibbons, and W. T. Nagy. 2013. Evaluation of pinniped predation on adult salmonids and other fish in the Bonneville Dam tailrace, 2013. USACE. October 30, 2013.

Stansell, R. J., B. K. van der Leeuw, K. M. Gibbons, and W. T. Nagy. 2014. Evaluation of pinniped predation on adult salmonids and other fish in the Bonneville Dam tailrace, 2104. USACE. September 16, 2014.

Stevens, D. E., and L. W. Miller. 1970. Distribution of sturgeon larvae in the Sacramento-San Joaquin river system. Calif Fish Game 56(2):80-86.

Tashjian, D., J. Cech Jr., and S. S. O. Hung. 2007. Influence of dietary l-selenomethionine exposure on the survival and osmoregulatory capacity of white sturgeon in fresh and brackish water. Fish Physiol Biochem 33: 109–119.

Thomas, M. J., M. L. Peterson, N. Friedenberg, J. P. Van Eenennaam, J. R. Johnson, J. J. Hoover, and A. P. Klimley. 2013. Stranding of Spawning Run Green Sturgeon in the Sacramento River: Post-Rescue Movements and Potential Population-Level Effects. North American Journal of Fisheries Management 33(2):287-297.

Thomas, M. J., and A. P. Klimley. 2015. Juvenile green sturgeon movements and identification of critical rearing habitat. In: Klimley AP, Doroshov SI, Fangue NA, May BP. 2015. Sacramento river green sturgeon migration and population assessment. Sacramento (CA): U.S. Bureau of Reclamation.

USFWS (United States Fish and Wildlife Service). 1996. Recovery plan for the Sacramento-San Joaquin Delta native fishes. U. S. Department of the Interior Fish and Wildlife Service Region 1, Portland, Oregon. p. 83-94.

Van Eenennaam, J. P., J. Linares-Casenave, X. Deng, and S. I. Doroshov. 2005. Effect of incubation temperature on green sturgeon embryos, *Acipenser medirostris*. Environ Biol Fishes 72:145-154.

Verhille, C. E., J. B. Poletto, D. E. Cocherell, B. DeCourten, S. Baird, J. J. Cech Jr., and N. A. Fangue. 2014. Larval green and white sturgeon swimming performance in relation to water-diversion flows. Conserv Physiol 2: doi:10.1093/conphys/cou031.

Vogel, D. 2013. Evaluation of fish entrainment in 12 unscreened Sacramento River diversions. Final Report July 2013. Prepared for: CVPIA Anadromous Fish Screen Program (USFWS and BOR) and Ecosystem Restoration Program (CDFW, USFWS, and NMFS). Natural Resource Scientists, Inc. P.O. Box 1210 Red Bluff, CA 96080. 153 p.

Wang, Y. L., F. P. Binkowski, and S. I. Doroshov. 1985. Effect of temperature on early development of White and Lake sturgeon, *Acipenser transmontanus* and *A. fulvescens*. Environ Biol Fishes 14:43-50.

Welch, D. W., S. Turo, and S. D. Batten. 2006. Large-scale marine and freshwater movements of white sturgeon. Trans Am Fish Soc 135: 386-389.

Werner, I., J. Linares-Casenave, J. P. Van Eenennaam, and S. I. Doroshov. 2007. The effect if temperature stress on development and heat-shock protein expression in larval green sturgeon (*Acipenser medirostris*). Environ Biol Fishes 79:191-200.

White, J. R., P. S. Hoffman, D. Hammond, and S. Baumgartner. 1988. Selenium Verification Study: 1986-1987. Water Resources Control Report. State Water Resources Control Board, Sacramento, California.

Workman, M. L. 2003. Downstream migration monitoring at Woodbridge Dam on the Lower Mokelumne River, CA, December 2002 through July 2003. Report to the East Bay Municipal Utility District, Lodi, California.

Zeug, S. C., A. Brodsky, N. Kogut, A. R. Stewart, and J. E. Merz. 2014. Ancient fish and recent invaders: white sturgeon *Acipenser transmontanus* diet response to invasive-species-mediated changes in a benthic prey assemblage. Mar Ecol Prog Ser 514:163-174.

Notes

Beccio M. CDFW (California Department of Fish and Wildlife). 2017. In-person conversation between M. Beccio and J. Heublein regarding observations of green sturgeon below Daguerre Point Dam on the Yuba River.

CDFW. 2015. Unpublished data. [Historical catch of green sturgeon in Sturgeon Population Study]. Accessed. http://www.dfg.ca.gov/delta/data/sturgeon/bibliography.asp

CDFW. 2016a. Unpublished data. [Larval sturgeon records in the 20mm Survey]. Accessed. https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentId=133706

CDFW. 2016b. Unpublished data. [White sturgeon tag returns in relation to river flow]. Accessed 5-4-2016. https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentId=75740

CDFW 2016c. Unpublished data. [Distribution of adult sturgeon in the San Francisco Bay].

CDFW 2016d. Unpublished data. [Index of Annual Age-0 White Sturgeon Abundance, 1980-2015]. Accessed 4-19-2016. https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentId=69133

CDFW 2016e. Unpublished data. [Harvest and CPUE for Sturgeon by CPFVs in SF Bay and Delta, 1964-2015]. Accessed 7-30-2016. https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentId=34816

CDFW 2017. [Annual CDFW Sturgeon Fishing Report Card and Adult Sturgeon Population Study summaries]. Accessed. http://www.dfg.ca.gov/delta/data/sturgeon/bibliography.asp

Chase, R. USACE (U.S. Army Corps of Engineers). 2015. Unpublished data. [Movement of green sturgeon tagged in the Sacramento River].

DWR (California Department of Water Resources). California Data Exchange Center (CDEC). 2017a. [Sacramento River water temperature gauge data.] Accessed. http://cdec.water.ca.gov/index.html.

DWR 2017b. [Chronological reconstructed Sacramento and San Joaquin Valley water year hydrologic classification indices.] Accessed. http://cdec.water.ca.gov/cgi-progs/iodir/WSIHIST.

Gingras, M. CDFW. 2015a. Unpublished data. [Age distribution of white sturgeon catch in CDFW monitoring and back-calculated recruitment estimates].

Gingras, M. CDFW. 2015b. Unpublished data. [CDFW Bay Study catch of juvenile green sturgeon].

Gingras, M. CDFW. 2016. Unpublished data. [Compilation of green sturgeon catch data and back-calculated recruitment estimates (2000 to 2016)].

Holm, M. 2016. Telephone conversation with J. Heublein regarding bycatch of green sturgeon in commercial herring fishery and composition of sturgeon species in directed gill-net sampling in San Pablo Bay.

Jackson, Z. USFWS. 2017. Unpublished data. [White sturgeon egg and larval collections on the San Joaquin River].

Langness, O. WDFW (Washington Department of Fish and Wildlife). 2015. Unpublished data. [Recovery of tagged green sturgeon in Pacific Northwest estuaries and lower Columbia River white sturgeon monitoring].

Langness, O. WDFW. 2016. Unpublished data. [Preliminary contaminant analysis of nDPS and sDPS green sturgeon tissue collected in the lower Columbia River].

Manuel, M. PSMFC (Pacific States Marine Fisheries Commission). 2016. In-person and telephone conversation with J. Heublein regarding catch of white sturgeon in rotary screw traps and with hook at line at GCID.

Manuel, M. PSMFC. 2017. Telephone conversation with J. Heublein regarding catch of egg and larval green sturgeon below Fish Barrier Dam on Feather River in June 2017.

McKibbin, C. CDFW. 2015. In-person conversation between C. McKibbin and A. Seesholtz regarding catch of juvenile sturgeon in American River rotary screw trap.

Miller, E. UCD (University of California, Davis) Biotelemetry Laboratory. 2017. Manuscript in preparation. [White sturgeon estuarine and coastal movements using telemetric monitoring data].

NMFS (National Marine Fisheries Service). 2016. Unpublished data. [Green sturgeon observations in the California halibut trawl Fishery].

Poletto, J. UCD. 2016. Unpublished data. [Northern DPS larval green sturgeon growth at 11, 13, 16, and 19°C and under multiple ration treatments]

Poytress, W. USFWS. 2015a. Unpublished data. [Relationship between annual Sacramento River outflow and larval green sturgeon catch numbers at RBDD rotary screw traps].

Poytress, W. USFWS. 2015b. Unpublished data. [Juvenile green sturgeon catch number and size in benthic trawl surveys].

Poytress, W. USFWS. 2017a. Unpublished data. [Egg, larval, and small juvenile green sturgeon catch in RBDD rotary screw traps in 2016 and 2017].

Poytress, W. USFWS. 2017b. Unpublished data. [Juvenile green sturgeon catch and JSATS tag implantation in benthic trawl surveys in Fall 2016].

Seesholtz, A. DWR. 2017. Unpublished data. [DIDSON surveys, acoustic detection of tagged adults, and early life stage sampling of green sturgeon on the Feather River].

Steel A, et al. UCD Biotelemetry Laboratory. 2017. Manuscript in preparation. [Telemetric data show a greater proportion of adult green sturgeon moving upstream of RBDD after gates were permanently raised]

Thomas, M., M. Pagel, A. P. Klimley, and R. Bellmer. UCD Biotelemetry Laboratory and CDFW. 2017. Report in preparation. [Telemetric monitoring data show movements of juvenile white and green sturgeon in the SFE].

1 **Estimating spatial-temporal differences in Chinook salmon outmigration**
2 **survival with habitat and predation related covariates**

3

4   Mark J. Henderson[1*], Ilysa S. Iglesias[2], Cyril J. Michel[2], Arnold J. Ammann[3], David D. Huff[4]

5

6 [1] U.S. Geological Survey, California Cooperative Fish and Wildlife Research Unit, Department

7 of Fisheries Biology, Humboldt State University, Arcata, California, USA

8 [2] Institute of Marine Sciences, University of California, Santa Cruz, California, USA

9 [3] Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries

10 Service, National Oceanic and Atmospheric Administration, Santa Cruz, California, USA

11 [4] Estuary and Ocean Ecology Program, Fish Ecology Division, Northwest Fisheries Science Center,

12 National Oceanic and Atmospheric Administration, Hammond, Oregon, USA

13

14 *Corresponding author:

15 U.S. Geological Survey, California Cooperative Fish and Wildlife Research Unit, Department of

16 Fisheries Biology, Humboldt State University, 1 Harpst Street, Arcata, California, USA 95521

17 Email: mark.henderson@humboldt.edu; Tel: 707-826-5644

<A>Abstract

Low survival rates of Chinook salmon smolts in California's Central Valley have been attributed

to multiple biological and physical factors, but it is not clear which factors have the largest

impact. We used five-years of acoustic telemetry data for 1709 late-fall Chinook salmon smolts

to evaluate the effect of habitat and predation related covariates on outmigration survival through

the Sacramento River. Using a Cormack-Jolly-Seber mark-recapture model, we estimated

survival rates both as a function of covariates (covariate model) and as a function of river

location and release year (spatial-temporal model). Our covariate model was overwhelmingly

supported as the preferred model based on model selection criteria, suggesting the covariates

adequately replicated spatial and temporal patterns in smolt survival. The covariates in the

selected model included individual fish covariates, habitat specific covariates, and temporally

variable physical conditions. The most important covariate affecting salmon survival was flow.

We describe the importance of these parameters in the context of juvenile salmon predation risk

and suggest that additional research on predator distribution and density could improve model

estimates.

Introduction

33

34   Salmon smoltification and outmigration from freshwater rearing habitats is a time of

35 increased mortality as fish undergo physiological changes and encounter new stressors (Connor

36 et al. 2003; Welch et al. 2008; Nislow and Armstrong 2012). Much of the research on

37 outmigration mortality has examined the effect of dam passage on survival (Skalski et al. 2001;

38 Williams et al. 2001; Welch et al. 2008; Elder et al. 2016), with relatively few studies focusing

39 on how other environmental conditions affect survival. Environmental conditions that have been

40 linked to outmigration mortality include flow (Connor et al. 2003; Smith et al. 2003; Michel et

41 al. 2015; Courter et al. 2016), temperature (Connor et al. 2003; Smith et al. 2003), turbidity

42 (Gregory and Levings, 1998; Smith et al. 2003), and predation (Beamesderfer et al. 1996;

43 Friesen and Ward 1999; Schreck et al. 2006). Some of these factors, such as water temperature

44 and flow, are expected to increasingly affect juvenile salmon survival and population production

45 as the climate changes (Jonsson and Jonsson 2009; Mantua et al. 2010; Katz et al. 2013; Russell

46 et al. 2012). Many of the published correlations between outmigration survival and

47 environmental characteristics have examined survival over relatively large temporal and spatial

48 scales, whereas individual fish experience mortality at a particular time and place. To better

49 understand how habitat and predation related covariates influence salmon smolt mortality it is

50 necessary to look at the conditions experienced by fish as they are migrating through a habitat.

51   Most Chinook salmon spawned in the Sacramento River have long outmigrations (~500

52 kilometers) through multiple habitats, and it is believed that the precipitous decline of multiple

53 salmon populations in this system is partially due to anthropogenic habitat modifications and

54 poor out-migration survival (Yoshiyama et al. 1998; Katz et al. 2013; Michel *in press*).

55 Currently, survival of Chinook salmon smolts from the Sacramento River to the ocean is

56   markedly lower than smolt out-migration survival from the Columbia and Fraser rivers in the

57   Pacific Northwest region of the United States and Canada (Welch et al. 2008; Michel et al. 2015;

58   Buchanan et al. 2018), but it is unclear what factors cause this increased mortality. Previous

59   research has found that interannual variability in smolt survival is much greater in the

60   Sacramento River than in the Sacramento-San Joaquin delta or the San Francisco Bay,

61   suggesting that the river has a large influence on outmigration success (Michel et al. 2015).

62   Within the river, outmigration survival rates vary both spatially and interannually (Singer et al.

63   2013; Michel et al. 2013). This spatial and temporal variability is likely driven by changes in the

64   underlying environmental and habitat features comprising the river landscape.

65   Identifying the main factors that affect smolt mortality is important to establish

66   restoration priorities and give managers quantitative data on how to optimize survival of

67   threatened salmonids. This is especially important given recent findings that suggest

68   outmigration survival has a larger effect on smolt-to-adult ratios than marine survival (Michel *in*

69   *press*). To identify which factors had the largest influence on outmigration survival, we

70   developed a series of mark-recapture models using five years of acoustic telemetry data for late-

71   fall Chinook Salmon. We then used model selection to identify which covariates had the largest

72   influence on survival. Our analysis builds upon the research conducted by Singer et al. (2013)

73   and Michel et al. (2015), whose primary objective was to identify temporal and spatial

74   differences in the mortality of outmigrating juveniles. In contrast, our objective was to model

75   survival solely as a function of covariates that were hypothesized to affect salmon survival

76   through habitat modification and increased predation risk.

77

78   **Methods**

79 *Study Area.*—The northernmost extent of our study was the release location for late-fall run

80 smolts at the Coleman National Fish Hatchery (Figure 1). We included all detections of

81 acoustically tagged fish from the release location to the ocean, but we only included covariates

82 for reaches between the release location and the I-80 Bridge in Sacramento. This was for two

83 reasons: 1) hydrodynamic model estimates for temperature and flow below the city of

84 Sacramento were not as reliable as the upstream estimates, and 2) survival variability was much

85 larger in the reaches upstream of Sacramento than in the Sacramento-San Joaquin delta or San

86 Francisco Bay (Michel et al. 2015). Riverine habitat varied spatially across the ~300 kilometers

87 of Sacramento River that defined our study area. There was a general upriver to downriver

88 gradient in habitat features associated with human influence. For example, diversion density,

89 amount of armored bank, and agriculture/developed land use increased from the upper to lower

90 reaches.

91

92 *Acoustic tagging.*— Late-fall run Chinook salmon were obtained from the United States Fish and

93 Wildlife Service (USFWS) Coleman National Fish Hatchery, implanted with acoustic tags, and

94 released annually during the winter months (December and January) from 2007 through 2011.

95 Details regarding the surgical procedures and initial acoustic tag study design are documented in

96 Michel et al. 2013 and Ammann et al. 2013. Briefly, small acoustic tags (Vemco 69 kHz, 7 mm

97 dia. X 20.5 mm long, weighing 1.8 g in air and 1.0 g in water) were surgically implanted into the

98 peritoneal cavity of anesthetized fish through a 12 mm incision. The incision was then closed

99 with two simple interrupted stitches with nonabsorbable nylon cable-type suture. All fish were

100 allowed to recover for a minimum of 24 hours before release. During the first year of this study

101 (2007), smolts were tagged and released directly into Battle Creek, a tributary of the Sacramento

102 River where the Coleman Hatchery is located (Figure 1). From 2008-2010 tagged smolts were

103 released concurrently from three locations along the mainstem Sacramento River: Jelly's Ferry,

104 Irvine Finch and Butte City to increase sample size of fish detected throughout the river and to

105 estimate differences in survival between newly released fish and those released upstream (Figure

106 1). In 2011, all fish were released at Jelly's Ferry due to a slightly reduced sample size. In

107 addition to the acoustic tag data (n=1350) utilized in Michel et al. (2013) and Michel et al.

108 (2015), we used acoustic tag data provided by the USFWS (n=359). These fish were tagged in

109 accordance with the procedures described above, but released directly into Battle Creek in 2010

110 and 2011, simultaneous to the release of the remaining hatchery stock (batch released). The mean

111 hatchery release during these dates was approximately 600,000 fish (range: 155k – 889k).

112 Acoustic receivers were located from the fish release sites in the upper Sacramento River

113 to the Golden Gate Bridge at the entrance to the Pacific Ocean. We divided the Sacramento

114 mainstem study region into 19 reaches demarcated by 20 acoustic receiver locations along the

115 mainstem Sacramento River (Figure 1). These reach locations were selected based on inter-

116 annual consistency in receiver location throughout the 5-year study period; however, detections

117 from inconsistently deployed receivers were retained to improve precision of survival and

118 detection probabilities (see 'mark-recapture analysis' section).

119

120 *Acoustic telemetry data processing.* —We used a series of algorithms to ensure our acoustic

121 telemetry data did not include any false detections. The acoustic receivers automatically

122 processed detection data by dropping incomplete codes from the detection file. To ensure that we

123 removed any false detections due to acoustic pulse train collisions, we performed several

124 additional quality control procedures. First, we removed all detections that occurred prior to the

125   release date and time. We then removed all detections from fish that had only a single detection

126   throughout the study. We required three or more detections within 10 days at a single receiver

127   location to verify those detections were not the result of pulse train collisions. We also examined

128   the encounter history of each individual fish and removed any detections that indicated upstream

129   movements. Furthermore, we calculated the transit time between receivers (number of river

130   kilometers between receivers divided by the difference in seconds between the last upstream

131   detection and first downstream detection) and removed any detections resulting from a fish

132   traveling at speeds greater than 10 km hour^{-1} (2.78 m s^{-1}). We also assumed that any tag

133   consistently detected at a single receiver location for more than 4 weeks, and not subsequently

134   detected downstream, was a mortality. We selected the 4 weeks cutoff after a preliminary

135   examination of the data indicated fish detected at a single location for more than 4 weeks were

136   never detected at another receiver. These fish (n=58) were considered known mortalities (i.e.,

137   treated the same way as a harvested fish in a standard mark-recapture model) and did not have

138   any impact on the estimated survival or detection probabilities downstream from where the

139   presumed mortality occurred.

140

141   *Mark-recapture analysis.*—To estimate survival of out-migrating late-fall run Chinook salmon,

142   we fit a Cormack-Jolly-Seber (CJS) survival model (Cormack 1964; Jolly 1965; Seber 1965)

143   using the marked (Laake et al. 2013) and RMark package (Laake and Rexstad 2008, Collier and

144   Laake 2013) within the R programming language (version 3.3.1, R Core Team 2017). We used

145   the marked package for the initial model selection due to its computational efficiency and RMark

146   for parameter estimation due to better analytical functionality (see appendix). The CJS model

147   was originally conceived to calculate survival of tagged animals over time by recapturing

148 individuals and estimating survival and recapture probabilities using maximum likelihood. A

149 spatial form of the CJS model can be used for species that migrate unidirectionally, and are

150 recaptured, throughout a migratory corridor (Burnham 1987). Using this space for time

151 substitution, we used individual fish encounter histories to estimate the likelihood that a fish

152 would survive and be detected at each receiver (Lebreton et al. 1992). In the standard

153 formulation of the CJS model, detection probabilities are estimated for a single resampling

154 occasion (i) in time or space. However, our encounter histories included detections both from

155 receivers at the reach boundaries as well as receivers within the reach. Thus, our estimated

156 detection parameter represents the probability of detection from receiver (i) to receiver (i+1).

157

158 *Spatial-temporal model.—* Prior to fitting a covariate model, we fit a model that estimated a

159 different survival for every reach in every year. This spatial-temporal model provided a means to

160 evaluate how well our covariate model replicated outmigration survival. We assumed that

161 differences between the spatial-temporal model and the covariate model were the result of

162 unaccounted variance due to missing covariates. Due to the inherent complexity of the

163 Sacramento River ecosystem, it was not feasible to measure or estimate all potential covariates

164 that influence salmon survival. For example, there is no hydrodynamic model currently capable

165 of estimating turbidity levels throughout the river.

166   The spatial-temporal smolt survival estimates were converted to survival per 10km values

167 to allow for comparisons between reaches via:

168
$$\Phi_{10} = \sqrt[l]{\Phi_R}$$

169 where Φ_{10} is the survival estimate per 10km, Φ_R is survival per reach, and l is reach length

170 divided by ten.

171

172   *Covariate model.*—We included multiple individual, release group, reach specific, and time-

173   varying covariates in our analysis to identify the factors contributing to the mortality of out-

174   migrating smolts. Each of the covariates included in the analysis had an *a priori* hypothesized

175   relationship with smolt survival (Table 1).

176   The individual covariates we included were length, condition, and transit speed. Fish size

177   has been known to influence juvenile salmon survival (Zabel and Achord 2004), thus we

178   included both length and condition factor (Fulton's $k = \frac{W}{L^3} * 100$) as individual covariates.

179   Length was hypothesized to affect survival through predator gape limitation whereas condition

180   factor is an indicator of fish health and stamina. We also included individual fish transit speed

181   within each reach, which we estimated with a mixed effects model (see details below), because

182   faster moving fish would have less exposure to predators.

183   Release group effects included release group size, a release reach effect, and the mean

184   annual flow at Bend Bridge (see Figure 1 for location) in the release year. We included a binary

185   group covariate for release group size to distinguish fish released in synchrony with thousands of

186   other hatchery fish from those released in small (e.g. 50-100 fish) batches based on the

187   hypothesis that large releases would result in increased survival due to predator swamping (Fritts

188   and Pearsons 2008; Furey et al. 2016). To test the hypothesis that the potential survival

189   advantage of large releases would diminish as fish diffused downstream, we also included an

190   interaction between release group size and distance from release site. We included a release

191   reach effect to test if survival in the first reach after release differed from fish released upstream

192   of the release site. We hypothesized survival rate in the release reach would be lower because

193   newly released hatchery fish are naïve and more susceptible to predation (Alvarez and Nicieza

194   2003; Huntingford 2004; Jackson and Brown 2011). The final release group specific covariate

195   was the mean annual flow measured at the Bend Bridge gauge during the months of smolt

196   outmigration (December-March). This covariate was included to test if survival decreased in low

197   flow (e.g., drought) conditions. Bend Bridge was selected to represent mean annual flow because

198   it was upstream of the major tributaries and diversions and was collinear with the flow

199   measurements throughout the river.

200   The reach specific covariates included in the model were sinuosity, diversion density,

201   adjacent cover density, and off-channel habitat density. We selected these features because we

202   hypothesized they would influence survival by affecting predation risk. More natural habitats

203   with increased sinuosity, adjacent cover density, and off-channel habitat density are

204   hypothesized to provide more predator refuge (reviewed by Roni et al. 2014). Furthermore,

205   agricultural and municipal water diversions along the Sacramento River pose a risk to out-

206   migrating salmon through direct entrainment (Hanson 2001; Kimmerer 2008; Mussen et al.

207   2014), as well as indirectly by providing structure for salmonid predators (Sabal et al. 2016). We

208   hypothesize that the latter has more of an effect on Chinook smolt survival since the diversions

209   are typically not in operation during the months of outmigration. These reach specific data were

210   derived from GIS layers available from multiple sources (Table 1) and plotted in a Geographic

211   Information System (using ESRI ArcGIS 10.3). Because we were using static GIS layers, we

212   were unable to determine if the available off-channel habitats were connected to the mainstem

213   under different flow regimes. We were also unable to measure inter-annual differences in

214   adjacent cover density.

215   The time-varying covariates we included in the model were flow and temperature, which

216   we obtained from the River Assessment for Forecasting Temperature (RAFT) model. The RAFT

217   model is a 1-dimensional physical model that estimates temperature and flow every 15-minutes

218   at a 2 km spatial resolution (Pike et al. 2013). We included temperature as a covariate because

219   predator metabolisms, and predation rates, increase at higher temperatures (Petersen and Kitchell

220   2001). We included multiple aspects of flow (see below) derived from the RAFT model because

221   flow is important to smolt survival (Kjelson and Brandes 1989; Cavallo et al. 2013; Zeug et al.

222   2014; Michel et al. 2015; Courter et al. 2016). We associated values for each of these variables

223   with each tagged fish in space and time at the 2-km spatial resolution, and then calculated the

224   reach-level means for each fish for each variable. We assumed that RAFT model predictions

225   were accurate (i.e. we did not propagate RAFT model uncertainty into the mark-recapture

226   model) based on results from model validations (Pike et al. 2013; Daniels et al. 2018).

227   Due to the importance of flow to outmigrating salmon survival, we fit a variety of models

228   with different flow standardizations to test which aspects of flow had the largest influence on

229   survival. We scaled (subtracted the mean and divided by the standard deviation) the time-varying

230   estimates of flow in two ways: 1) by reach, and 2) by year and reach. We scaled by reach to

231   detect within reach patterns of survival relative to *inter*-annual flow conditions. In other words, is

232   reach-specific survival dependent on whether flows are above or below average compared to

233   other years? Since this parameter could distinguish between annual differences in flow (i.e., low

234   flow versus high flow year), we did not include the annual flow at Bend Bridge in any models

235   that included flow scaled only by reach. Thus, we could test if the spatially explicit estimates of

236   flow added any additional information beyond a single measure of mean annual flow. The year

237   and reach scaling tested whether *intra*-annual changes in flow within a reach were important to

238   salmon survival. In other words, we wanted to determine if periods of higher flows within a

239   reach, such as those after large precipitation events, would increase survival relative to periods of

240   lower flows within the same year. This hypothesis was based on previous studies that have

241   observed large increases in survival due to controlled changes in flow rate (Cavallo et al. 2013;

242   Courter et al. 2016). Scaling by both year and reach removes the effect of annual differences in

243   flow such that it is impossible to distinguish high flow years from low flow years with this

244   parameter. Thus, models in which flow was scaled by year and reach could also include the mean

245   annual flow at Bend Bridge. We also fit models that included an interaction between the mean

246   annual flow and the time-varying flow standardized by year and reach to test the hypothesis that

247   precipitation events would have a larger impact on survival in years with lower flows. We tested

248   this hypothesis based on work by Courter et al. (2016) that suggested flow has a large impact on

249   survival in reaches with relatively low flow but has a negligible impact in reaches with high

250   flow.

251   To estimate the effect of a covariate (e.g. flow) on fish survival throughout a reach, it is

252   necessary to have a covariate value for every fish in every reach. When we did not detect an

253   individual fish at a receiver there was uncertainty as to when that fish might be within that reach

254   and, thus, what covariate value should be used. To impute covariate data in locations where fish

255   were not detected, we fit a mixed-effects model where the response was transit speed of

256   individual fish detected at both upstream and downstream acoustic receivers of a single reach.

257   Our independent covariates were release year, release week, reach, and fish condition. We also

258   included a random intercept for each individual fish to account for individual behavioral

259   variability. We fit the model using the 'lme4' package (Bates et al. 2015) and selected the model

260   with the lowest Akaike's Information criterion (AIC; Burnham and Anderson 2002). To verify

261   that the mixed-effects model did not unduly violate any assumptions, we examined model

262   diagnostics (QQplot and residuals) using the DHARMa package (Hartig 2018). We then used the

263   results from the mixed-effects model based on detected fish to estimate the dates and times

264   undetected fish were present within each reach.

265   Prior to fitting the CJS models, all continuous covariates were standardized by

266   subtracting the mean and dividing by the standard deviation. Standardized coefficients could

267   then be interpreted as the estimated change in survival predicted from one standard deviation

268   increase in the covariate value. We also conducted pairwise comparisons of all continuous

269   individual, habitat, and physical covariates to determine if any covariates were collinear

270   (Supplemental figure S1). From pairs that had correlation coefficients greater than 0.7 (Dormann

271   et al. 2012), we selected a single covariate that we hypothesized would have the largest influence

272   on survival based on results from previous studies.

273

274   *Model selection.—*We fit a series of CJS models to determine which covariates (individual,

275   release group, reach specific, or time varying) had the greatest impact on out-migrating smolt

276   survival. With the exceptions of collinear variables and the restrictions noted above, we fit

277   models with all possible combinations of covariates and selected the most appropriate models

278   with adequate support using Quasi-Akaike's information criterion (QAICc) (Burnham and

279   Anderson 2002). QAIC adjusts the AIC value based on an overdispersion parameter ($\hat{c}$), which

280   we estimated using the median $\hat{c}$ method for the spatial temporal model within program MARK

281   (White and Burnham 1999). If the observed data has no overdispersion, $\hat{c}$ will be approximately

282   equal to 1. Values of $\hat{c}$ greater than 4 indicates the model structure is inadequate and does not

283   account for a sufficient amount of variation in the data (Burnham and Anderson 2002). Our

284   median $\hat{c}$ was 1.45, indicating the model was satisfactory but slightly overdispersed. We selected

285   the most appropriate model by examining the difference in QAIC values between each model

286   and the model with the lowest QAIC (ΔQAIC). We assumed models with ΔQAIC < 2 had equal

287   support (Burnham and Anderson 2002); thus, if multiple models had a ΔQAIC < 2, we selected

288   the one with the fewest parameters.

289

290   *Covariate plots.*—To determine which covariates had the largest influence on survival, we

291   plotted the ΔQAIC between the selected covariate model and the same model without a single

292   covariate. In the case of covariates that were included as main effects and in an interaction, we

293   also removed the interaction. We will refer to these models as our covariate importance analysis.

294   We used marginal model plots to evaluate the effect of individual covariates on

295   outmigrating smolt survival. To produce these plots, the β parameter coefficients from the

296   selected covariate model were used to simulate what survival would be for the 95% observed

297   range of a single covariate. With the exception of reach length, covariates not included in the

298   individual response plots were set to zero for binomial covariates or to their mean for continuous

299   covariates. Reach length was set to 10 km for all plots except the one that explicitly focused on

300   the effect of reach length.

301

<A> Results

303   <B> *Spatial-temporal model*

304   Based on the model that included a reach by year interaction, we observed that survival

305   was not consistent spatially or temporally. We saw a general trend of lower per-reach survival in

306   the upper and middle reaches, compared to the more downstream reaches, but the location and

307   severity of mortality varied inter-annually (Figure 2). The high flows in 2011 negatively

308   impacted our detection efficiencies, rendering 12 receivers without reliable detection data;

309   however, the detection efficiencies in the lower river and the estuary remained high and provided

310   sufficient data to estimate out-migration survival through the river. The receiver locations with

311   low detection efficiencies often resulted in survival estimates of 1 due to numerical boundary

312   issues.

313

314   <B> *Covariate model*

315   The selected covariate model had 15 survival parameters and fit the data nearly as well as

316   the spatial-temporal model that had 110 survival parameters. As a result, the covariate model had

317   a much lower QAICc value (ΔQAICc = 55.90), implying it was more parsimonious. Although

318   the covariate model showed some deviation from the spatial-temporal model, especially in the

319   most upstream reaches, these tended to be relatively small and not significantly different from

320   zero (Figure 3).

321   The top covariate model included a combination of an individual covariate (transit

322   speed), group covariates (batch release, interaction between batch release and distance from

323   release site, release reach, and the mean annual flow recorded at Bend Bridge), reach specific

324   covariates (reach length, sinuosity, and diversion density), and time-varying covariates that were

325   estimated for when a fish passed through a specific reach (reach flow, interaction between reach

326   flow and annual flow, and water temperature). Based on the standardized beta coefficients for the

327   covariates (Table 2) and the results from the covariate importance analysis (Figure 4), annual

328   flow and reach length had the largest influence on survival. Flow was the most important

329   covariate in predicting outmigration success, with increased levels of annual flow correlating to

330   increased smolt survival (Figure 5a). Above average reach flows within a year (e.g., large

331   precipitation events) helped improve survival much more in low flow years than in high flow

332   years. As would be expected, longer reaches had lower survival rates (Figure 5b). Based on the

333   covariate importance analysis, the next most important variables affecting survival were

334   diversion density, release reach, and the interaction between release group size and distance from

335   release location. Survival increased relative to diversion density (Figure 5c), was lower in the

336   first reach after release (Figure 5d), and increased for approximately the first 200 km from the

337   release site when fish were released concurrently with thousands of hatchery fish (Figure 5e).

338   Finally, the covariates that had the least effect on survival were sinuosity (increase), transit speed

339   (increase), and water temperature (decrease) (Figure 5 f-h).

340

341   <A>**DISCUSSION**

342   Conservation of salmonid populations depends on understanding what physical and

343   biological factors have the largest impact on mortality during different life history stages. Recent

344   research has shown that the outmigration period may have the largest influence on smolt to adult

345   survival rates and cohort strength (Michel *in press*). Therefore, identifying the primary factors

346   that affect survival of outmigrating smolts can help prioritize management actions that will be

347   most beneficial to the conservation of imperiled populations. While we could not include all

348   possible sources of mortality in our analysis, we conclude that flow remains the single most

349   influential factor for determining survival of late-fall Chinook salmon smolts outmigrating from

350   California's Central Valley.

351

352   <B>*Spatial and temporal survival heterogeneity*

353   The spatial-temporal model indicated that survival through different reaches varied

354   interannually, which is likely a result of the dynamic nature of the Sacramento River system.

355   Overall, we can conclude from our reach-specific survival estimates that increased mortality

356   rates occurred most frequently in the upper and middle regions of the Sacramento River, and

357   decreased rates occurred through the lower reaches. We compared the observed values for the

358   covariates included in the selected model to determine if fish had different behaviors in the upper

359   reaches and if any aspects of the physical habitat differed. The most striking difference between

360   the upper reaches and the lower reaches was the diversion density. This implies that increased

361   diversion desity, and the coincident anthropogenic habitat modifications of the lower river,

362   reduced mortality of outmigrating smolts. Much of the previous work that has examined the

363   effects of habitat modification and restoration on salmonid populations has focused on egg

364   incubation, freshwater/estuarine rearing, and available spawning habitat (reviewed in Roni et al.

365   2014) or the effects of fish passage on outmigration mortality (Skalski et al. 2001; Williams et al.

366   2001; Welch et al. 2008; Elder et al. 2016). We do not know of any studies that have explicitly

367   looked at the effect of channel alteration on salmon outmigration survival. A valuable future

368   study would be to examine if channelized habitats have lower predator densities or if the deeper

369   waters make it easier for salmon to avoid predators.

370   In addition to the higher mortality rates in the upper reaches, the biggest discrepancies

371   between the spatial-temporal model and the covariate model also occurred in the upper reaches.

372   This suggests our covariate model would benefit from including additional covariates that

373   contributed to smolt mortality in the upper reaches. Based on previous research, we believe that

374   including covariates such as turbidity and predator density would likely improve our explanatory

375   power. Turbidity likely improves salmon survival by decreasing predation risk (Gregory and

376 Levings 1998). Likewise, high predator densities in the upper and middle reaches may partially

377 explain the increased mortality rates in these locations. Naïve, hatchery raised fish, are more

378 susceptible to predation after release (Alvarez and Nicieza 2003; Huntingford 2004; Jackson and

379 Brown 2011). This was reflected in our covariate model where newly released fish had a lower

380 survival rate than fish released upstream. Including turbidity and predator density in a mark

381 recapture model could improve model fit and provide important information necessary to

382 develop a purely mechanistic model to estimate outmigration mortality.

383

384 <B>*Time-varying covariates*

385 Model selection for the covariate model provided insight into which time-varying

386 physical covariates had the largest influence on survival of out-migrating late-fall Chinook

387 Salmon. Flow exerted the greatest overall effect on outmigration success, with increased annual

388 flow positively related to increased smolt survival. Studies have repeatedly demonstrated that

389 flow is the most important factor affecting survival of Chinook salmon (Conner et al. 2003,

390 Smith et al. 2003; Zeug et al. 2014; Michel et al. 2015). In addition to the effect of annual flow,

391 we also found that variability in flow within a reach affected survival rates, particularly in low

392 flow years. If flow within a reach was well above the annual average, as it would be after a

393 precipitation event, there was relatively little (1.6% per 10 km) difference between survival in a

394 low and high flow years. In contrast, below average flows within a reach resulted in large (5%

395 per 10 km) differences in survival between low and high flow years. This provides a potential

396 explanation for results observed by Courter et al. (2016), where survival was highly dependent

397 on flow within a low flow (< 125 cms) reach, but had no effect in a reach with higher flows

398 (100-300 cms).

399   Our study also builds on previous work by including measurements of both spatially

400   explicit flow and transit speed as covariates in our model. This allowed us to separate the effect

401   of flow from transit speed, suggesting that there are features inherent to flow itself, not just its

402   effect on travel time, which affects survival. Flow has been significantly reduced and

403   homogenized in the Sacramento River system from historic levels (Buer et al. 1989), in

404   particular during the winter months when runoff from storm events is captured behind dams.

405   Flow magnitude affects the amount of off-channel and floodplain habitat available for juvenile

406   salmon rearing (Nislow and Armstrong, 2012; Merenlender and Matella 2013). Fish residing in

407   these habitats have accelerated growth rates that may aid individuals in predator avoidance and

408   survival (Sommer et al. 2001; Limm and Marchetti 2009). Furthermore, the highest sediment

409   loads for the Sacramento River were observed with the highest peak flows (Stern et al. 2016),

410   which can increase turbidity rates and decrease predation rates (Gregory and Levings 1998).

411   Whatever the specific mechanism, flow was clearly the most important factor influencing the

412   outmigration success of late-fall run Chinook smolts in 2007-2011. Perhaps more importantly,

413   the effect of flow propagates throughout a cohort's life history and can be used to estimate smolt-

414   to-adult ratios (Michel *in press*). Threshold flow values could be determined through combined

415   controlled-release and tagged-release studies in the Central Valley.

416   We also found survival was higher at lower water temperatures. We hypothesize that this

417   effect was the result of increased predator metabolism, and thus consumption, at increased

418   temperatures (Petersen and Kitchell 2001). This effect was relatively minor (1.3% per 10 km)

419   over the small range of temperatures we observed during the fall-run winter outmigration

420   months. However, we expect this effect will be more pronounced for fall and winter run fish that

421   are outmigrating during warmer months and may exhibit adverse responses to warmer

422   temperatures (Baker et al. 1995; Lehman et al 2017).

423

424   <B> *Release group covariates*

425   Acoustically tagged fish had higher survival rates when they were released concurrently

426   with thousands of hatchery fish. Based on the interaction between release size and distance from

427   release location, this effect persisted for approximately 200 km from the release location. One

428   explanation for this improved overall survival is the theory of "predator swamping;" whereby

429   predators, inundated by prey, pose less of a threat to individual smolts. This effect has been

430   demonstrated for Chinook salmon in the Yakima River (Fritts and Pearsons 2008) and juvenile

431   sockeye salmon in British Columbia (Furey et al. 2016). We examined the difference in arrival

432   times at the acoustic receiver locations for each of the release groups, and found that fish from

433   the same release group arrived at the same location within approximately 24 hours for the first

434   100 km (Supplemental fig S2). After the first 100 km the river has more channel alterations and

435   fish arrival times were more dispersed. However, fish survival rates in these lower sections of the

436   river were generally higher than in the upstream reaches, most likely due to decreased predation

437   rates in the channelized portions of the river.

438

439   <B> *Individual covariates*

440   Predicted transit speeds were also an important factor, with increasing transit speeds

441   corresponding to increased survival. For out-migrating yearling smolts, it is likely that transit

442   speed in the context of our study is a proxy for duration of exposure to mortality factors.

443   Previous studies have found that survival rates decline over longer migration distances (Bickford

444   and Skalski 2000; Muir et al 2001; Smith et al. 2002). However, these studies have primarily

445   found that survival was related to distance traveled but not to travel time. Anderson et al. (2005)

446   explained this apparent discrepancy by suggesting that survival was a function of both migration

447   distance and predation risk. This provides further motivation to study the factors that influence

448   the spatial distribution, and density, of salmon predators throughout the Sacramento River.

449

450   <B>*Reach specific characteristics*

451   Model selection results provided evidence that reach length, diversion density, and

452   sinuosity were associated with outmigrating smolt survival. After accounting for all other

453   covariates, survival was higher with increasing sinuosity, suggesting that more natural river

454   conditions were better for smolt survival than the deeper and more armored portions of the river.

455   This result is in contrast to our other finding that the highest survival rates were in the lower,

456   more channelized sections of the river. We suspect that the larger covariate effect of diversion

457   density accounts for the variation associated with increased survival in the lower reaches.

458   Because the diversions are typically not operational during the period when late-fall Chinook are

459   outmigrating, we suspect this effect is more a function of the habitat conditions in locations

460   where diversions are more abundant. Diversions were highly correlated to other habitat variables

461   typical of agricultural zones; namely depth, armored banks and agricultural and developed land

462   use (Supplemental figure S1). Because we did not wish to obfuscate the results of our analysis,

463   we withdrew these collinear factors from our modeling efforts, but the role of "diversions" on

464   survival could be equally viewed as the role of depth, agriculture and developed land, and

465   armored banks. These modified habitats may result in reduced predator densities and predation

466   mortality.

467

468   *<B> Conclusions*

469   Flow, diversion density, and release strategy had the strongest influence on survival of

470   out-migrating, hatchery origin, late-fall run Chinook salmon during the 2007-2011 water years.

471   For years with high flow, gains in in-river survival can lead to a three-fold increase in total

472   outmigration survival, while survival in the delta and estuary remain the same (Michel et al.

473   2015). There is limited natural habitat remaining for Chinook salmon in the Central Valley as a

474   result of human activities, and increasingly managers are turning to habitat restoration efforts to

475   restore salmon populations. When we compare physical covariates, metrics for habitat features

476   and individual covariates, flow remains the most important factor affecting out-migration

477   survival of late-fall run hatchery raised smolts. Although our study used hatchery fish, which

478   have limitations as wild fish surrogates, these results suggest that maintaining flow during

479   periods of salmon outmigration is an important step towards conserving Chinook salmon in the

480   Central Valley.

481

482   <A> **Acknowledgements**

490 assistance and support of the tagging efforts for this project, Sara John of the SWFSC for

491 extracting the requisite RAFT data, and Dr. Nyssa Silbiger and our internal NOAA reviewers for

492 feedback on the manuscript. Sean Hayes was instrumental in obtaining funding and initial study

493 design. We would especially like thank Dan Meier of the USFWS for funding and support. Fish

494 handling was conducted under University of California - Santa Cruz IACUC #KIERJ1604. Any

495 use of trade, firm, or product names is for descriptive purposes only and does not imply

496 endorsement by the U.S. Government.

497

498 <A>**References**

499 Alvarez, D. and Nicieza, A.G. 2003. Predator avoidance behavior in wild and hatchery-reared

500   brown trout: the role of experience and domestication. Journal of Fish Biology 63: 1565-

501   1577.

502 Ammann, A. J., Michel, C.J. and MacFarlane, R.B. 2013. The effects of surgically implanted

503   acoustic transmitters on laboratory growth, survival and tag retention in hatchery yearling

504   Chinook salmon. Environmental Biology of Fishes **96**:135-143.

505 Anderson, J.J. Gurarie, E., and Zabel, R.W. 2005. Mean free-path length theory of predator-prey

506   interactions: Application to juvenile salmon migration. Ecological Modelling 186: 196-

507   211.

508 Baker, P.F., Ligon, F.K., and Speed, T.P. 1995. Estimating the influence of temperature on the

509   survival of chinook salmon smolts (Oncorhynchus tshawytscha) migrating through the

510   Sacramento-San Joaquin River Delta of California. Canadian Journal of Fisheries and

511   Aquatic Sciences, 52: 855-863.

512   Bates, D., Maechler, M., Bolker, B., and Walker, S. 2015. Fitting Linear Mixed-Effects Models

513   using lme4. Journal of Statistical Software, 67(1): 1-48. doi:10.18637/jss.v067.i01.

514   Beamesderfer, R.C.P., Ward, D.L, and Nigro, A.A. 1996. Evaluation of the biological basis for a

515   predator control program on northern squawfish (Ptychocheilus oregonensis) in the

516   Columbia and Snake rivers. Canadian Journal of Fisheries and Aquatic Sciences, 53:

517   2898-2908.

518   Bickford, S.A. and Skalski, J.R. 2000. Reanalysis and interpretation of 25 years of Snake-

519   Columbia River juvenile salmon survival studies. North American Journal of Fisheries

520   Management 20: 53-68.

521   Buchanan, R.A., Brandes, P.L., and Skalski, J.R. 2018. Survival of juvenile fall-run Chinook

522   salmon through the San Joaquin River Delta, California, 2010-2015. North American

523   Journal of Fisheries Management, 38: 663-679.

524   Burnham, K.P. 1987. Design and analysis methods for fish survival experiments based on

525   release-recapture. American Fisheries Society, Bethesda, MD. (USA).

526   Burnham, K.P. and Anderson, D.R. 2002. Model selection and multimodel inference: A practical

527   information – Theorectic Approach. 2nd edition. New York: Springer-Verlag.

528   Cavallo, B., Merz, J., and Setka, J. 2013. Effects of predator and flow manipulation on Chinook

529   salmon (Oncorhynchus tshawytscha) survival in an imperiled estuary. Environmental

530   Biology of Fishes:1-11.

531   Collier, B.A., and Laake, J.L. 2013. RMark: An R interface to capture-recapture analysis with

532   MARK. Mark Workshop Notes, Ft. Collins, CO,.

533   Connor, W.P., Burge, H.L., Yearsley, J.R., and Bjornn, T.C. 2003. Influence of flow and

534   temperature on survival of wild subyearling fall Chinook salmon in the Snake River. 23:

535   362-375.

536   Cormack, R.M. 1964. Estimates of Survival from the Sighting of Marked Animals. Biometrika

537   51:429-438.

538   Courter, I.I., Garrison, T.M., Kock, T.J., Perry, R.W., Child, D.B. and Hubble, J.D. 2016.

539   Benefits of prescribed flows for salmon smolt survival enhancement vary longitudinally

540   in a highly managed river system. River Research and Applications 32: 1999-2008.

541   Daniels, M.E., Sridharan, V.K., John, S.N., and Danner, E.M. 2018. Calibration and validation of

542   linked water temperature models for the Shasta Reservoir and the Sacramento River from

543   2000 to 2015. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-

544   SWFSC-597. https://doi.org/10.7289/V5/TM-SWFSC-597

545   Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G.,

546   Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E.,

547   Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., and Lautenbach, S. 2012.

548   Collinearity: a review of methods to deal with it and a simulation study evaluating their

549   performance. Ecography:001–020.

550   Elder, T., Woodley, C.M., Weiland, M.A., and Strecker, A.L. 2016. Factors influencing the

551   survival of outmigrating juvenile salmonids through multiple dam passages: an

552   individual-based approach. Ecology and Evolution, 6: 5881-5892.

553   Friesen, T.A. and Ward, D.L. 1999. Management of Northern Pikeminnow and implications for

554   juvenile salmonid survival in the lower Columbia and Snake Rivers. North American

555   Journal of Fisheries Management, 19: 406-420

556   Fritts, A.L., and Pearsons, T.N. 2008. Can non-native smallmouth bass, Micropterus dolomieu,

557   be swamped by hatchery fish releases to increase juvenile Chinook salmon,

558   Oncorhynchus tshawytscha, survival? Environmental Biology of Fishes 83:485-494.

559   Furey, N.B., Hinch, S.G., Bass, A.L., Middleton, C.T., Minke-Martin, V., and Lotto, A.G. 2016.

560   Predator swamping reduces predation risk during nocturnal migration of juvenile salmon

561   in a high-mortality landscape. Journal of Animal Ecology 85: 948-959.

562   Gregory, R.S., and Levings, C.D. 1998. Turbidity reduces predation on migrating juvenile

563   Pacific Salmon. Transactions of the American Fisheries Society 127:275-285.

564   Hanson, C. H. 2001. Are juvenile chinook salmon entrained at unscreened diversions in direct

565   proportion to the volume of water diverted? Contributions to the Biology of Central

566   Valley Salmonids 2:331-342.

567   Hartig, F. 2018. DHARMa: Residual diagnostics for hierarchical (multi-level / mixed)

568   Regression Models. R package version 0.1.6. https://CRAN.R-

569   project.org/package=DHARMa

570   Huntingford, F.A. 2004. Implications of domestication and rearing conditions for the behavior of

571   cultivated fishes. Journal of Fish Biology. 65: 122-144

572   Jackson, C.D. and Brown, G.E. 2011. Differences in antipredator behavior between wild and

573   hatchery-reared juvenile Atlantic salmon (Salmo salar) under seminatural condtions.

574   Canadian Journal of Fisheries and Aquatic Sciences 68: 2157-2165.

575   Jolly, G.M. 1965. Explicit Estimates from Capture-Recapture Data with Both Death and

576   Immigration-Stochastic Model. Biometrika 52:225-247.

577   Jonsson, B. and Jonsson, N. 2009. A review of the likely effects of climate change on

578   anadromous Atlantic salmon salmo salar and brown trout Salmo trutta, with particular

579   reference to water temperature and flow. Journal of Fish Biology, 75: 2381-2447.

580   Katz, J., Moyle, P., Quiñones, R., Israel, J., and Purdy, S. 2013. Impending extinction of salmon,

581   steelhead, and trout (Salmonidae) in California. Environmental Biology of Fishes

582   96:1169-1186.

583   Kimmerer, W. J. 2008. Losses of Sacramento River chinook salmon and Delta Smelt to

584   entrainment in water diversions in the Sacramento-San Joaquin Delta. San Francisco

585   Estuary and Watershed Science 6. Retrieved from:

586   https://escholarship.org/uc/item/7v92h6fs

587   Kjelson, M. A., and Brandes, P.L. 1989. The use of smolt survival estimates to quantify the

588   effects of habitat changes on salmonid stocks in the Sacramento-San Joaquin River,

589   California. Pages 100-115 in C. D. Levings, L. B. Holtby, and M. A. Henderson, editors.

590   Proceedings of the National Workshop on the effects of habitat alteration on salmonid

591   stocks. Canadian Special Publication of Fisheries and Aquatic Sciences.

592   Laake, J., and Rexstad, E. 2008. RMark- an alternative approach to building linear models in

593   MARK.

594   Laake, J.L., Johnson, D.S., Conn, P.B. and Isaac, N. 2013. marked: an Rpackage for maximum

595   likelihood and Markov Chain Monte Carlo analysis of capture-recapture data. Methods in

596   Ecology and Evolution 4:885-890.

597   Lebreton, J.-D., Burnham, K.P., Clobert, J., and Anderson, D. 1992. Modeling survival and

598   testing biological hypotheses using marked animals: a unified approach with case studies.

599   Ecological Monographs 62:67-118.

600   Lehman B., Huff, D.D., Hayes, S.A., and Lindley, S.T. 2017. Relationships between Chinook

601   salmon swimming performance and water quality in the San Joaquin River, California.

602   Transactions of the American Fisheries Society, 146: 349-358.

603   Limm, M.P. and Marchetti, M.P. 2009. Juvenile Chinook salmon (Oncorhynchus tshawytscha)

604   growth in off-channel and main-channel habitats on the Sacramento River, CA using

605   otolith increment widths. Environmental Biology of Fishes, 85: 141-151.

606   Mantua, N., Tohver, I., and Hamlet, A. 2010. Climate change impacts on streamflow extremes

607   and summertime stream temperature and their possible consequences for freshwater

608   salmon habitat in Washington State. Climate Change 102: 187-223.

609   Merenlender, A.M. and Matella, M.K. 2013. Maintaining and restoring hydrologic habitat

610   connectivity in Mediterranean streams: an integrated modeling framework.

611   Hydrobiologia, 719: 509-525.

612   Michel, C.J., Ammann, A.J., Chapman, E.D., Sandstrom, P.T., Fish, H.E., Thomas, M.J., Singer,

613   G.P., Lindley, S.T., Klimley, A.P., and MacFarlane, R.B. 2013. The effects of

614   environmental factors on the migratory movement patterns of Sacramento River yearling

615   late-fall run Chinook salmon (Oncorhynchus tshawytscha). Environmental Biology of

616   Fishes 96:257-271.

617   Michel, C.J., Ammann, A.J., Lindley, S.T., Sandstrom, P.T., Chapman, E.D., Thomas, M.J.,

618   Singer, G.P., Klimley, A.P., and MacFarlane, R.B.. 2015. Chinook salmon outmigration

619   survival in wet and dry years in California's Sacramento River. Canadian Journal of

620   Fisheries and Aquatic Sciences 72:1749-1759.

621 Michel, C.J. *in press* Decoupling outmigration from marine survival indicates outsized influence

622   of streamflow on cohort success for California's Chinook salmon populations. Canadian

623   Journal of Fisheries and Aquatic Sciences.

624 Muir, W.D., Smith, S.G., Williams, J.G., Hockersmith, E.E., Skalski, J.R. 2001. Survival

625   estimates for migrating yearling chinook salmon and steelhead tagged with passive

626   integrated transponders in the Lower Snake and Lower Columbia Rivers, 1993-1998.

627   North American Journal of Fisheries Management 21: 269-282.

628 Mussen, T.D., Patton, O., Cocherell, D., Ercan, A., Bandeh, H., Levent Kavvas, M., Cech Jr.,

629   J.J., Fangue, N.A. 2014. Can behavioral fish-guidance devices protect juvenile Chinook

630   salmon (Oncorhynchus tshawytscha) from entrainment into unscreend water diversion

631   pipes. Canadian Journal of Fisheries and Aquatic Sciences, 71: 1209-1219.

632 Nislow, K.H. and Armstrong, J.D. 2012. Towards a life-history-based management framework

633   for the effects of flow on juvenile salmonids in streams and rivers. Fisheries Management

634   and Ecology, 19: 451-463.

635 Petersen, J.H. and Kitchell, J.F. 2001. Climate regimes and water temperature changes in the

636   Columbia River: bioenergetics implications for predators of juvenile salmon. Canadian

637   Journal of Fisheries and Aquatic Sciences 58: 1831-1841.

638 Pike, A., Danner, E., Boughton, D., Melton, F., Nemani, R., Rajagopalan, B., and Lindley, S.

639   2013. Forecasting river temperatures in real time using a stochastic dynamics approach.

640   Water Resources Research 49:5168-5182.

641 R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for

642   Statistical Computing, Vienna, Austria. URL: https://www.R-project.org.

643 Roni, P., Pess, G.R., Beechie, T.J., and Hanson, K.M. 2014. Fish-habitat relationships and the

644   effectiveness of habitat restoration. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-

645   NWFSC-127.

646 Russell, I.C., Aprahamian, M.W., Barry, J., Davidson, I.C., Fiske, P., Ibbotson, A.T., Kennedy,

647   R.J., Maclean, J.C., Moore, A., Otero, J., Potter, T.E.C.E., and Todd, C.D. 2012. The

648   influence of the freshwater environment and the biological characteristics of Atlnatic

649   salmon smolts on their subsequent marine survival. ICES Journal of Marine Science, 69:

650   1563-1573.

651 Sabal, M., Hayes, S., Merz, J., and Setka, J. 2016. Habitat Alterations and a Nonnative Predator,

652   the Striped Bass, Increase Native Chinook Salmon Mortality in the Central Valley,

653   California. North American Journal of Fisheries Management 36:309-320.

654 Schreck, C.B., Stahl, T.P., Davis, L.E., Roby, D.D., and Clemens, B.J. 2006. Mortality estimates

655   of juvenile spring-summer Chinook salmon in the lower Columbia River and Estuary,

656   1992-1998: Evidence for Delayed Mortality? Transactions of the American Fisheries

657   Society, 135: 457-475.

658 Seber, G. A. F. 1965. A Note on the Multiple-Recapture Census. Biometrika 52:249-259.

659 Singer, G. P., Hearn, A.R., Chapman, E.D., Peterson, M.L., LaCivita, P.E., Brostoff, W.N.,

660   Bremner, A., and Klimley, A.P. 2013. Interannual variation of reach specific migratory

661   success for Sacramento River hatchery yearling late-fall run Chinook salmon

662   (Oncorhynchus tshawytscha) and steelhead trout (Oncorhynchus mykiss). Environmental

663   Biology of Fishes 96:363-379.

664 Skalski, J.R., Lady, J., Townsend, R., Giorgi, A.E., Stevenson, J.R., Peven, C.M., and

665   McDonald, R.D. 2001. Estimating in-river survival of migrating salmonid smolts using

666   radiotelemetry. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1987-1997.

667 Smith, S.G., Muir, W.D., Williams, J.G., Skalski, J.R. 2002. Factors associated with travel time

668   and survival of migrant yearling chinook salmon and steelhead in the lower Snake River.

669   North American Journal of Fisheries Management 22: 385-405.

670 Smith, S.G., Muir, W.D., Hockersmith, E.E., Zabel, R.W., Graves, R.J., Ros, C.V., Connor,

671   W.P., and Arnsberg, B.D. 2003. Influence of River Conditions on Survival and Travel

672   time of Snake River subyearling fall Chinook salmon. North American Journal of

673   Fisheries Management 23: 939-961.

674 Sommer, T.R., Nobriga, M.L., Harrell, W.C. Batham, W., and Kimmerer, W.J. 2001. Floodplain

675   rearing of juvenile chinook salmon: evidence of enhanced growth and survival. Canadian

676   Journal of Fisheries and Aquatic Sciences, 58: 325-333.

677 Stern, M., Flint, L., Minear, J., Flint, A., and Wright, S. 2016. Characterizing changes in

678   streamflow and sediment supply in the Sacramento River Basin, California, Using

679   Hydrological Simulation Program – FORTRAN (HSPF). Water 8 (10): 432.

680   https://doi.org/10.3390/w8100432

681 Welch, D.W., Rechisky, E.L, Melnychuck, M.C., Porter, A.D., Walters, C.J., Clements, S.,

682   Clemens, B.J., McKinley, R.S., and Schreck, C. 2008. Survival of migrating salmon

683   smolts in large rivers with and without dams. PLoS Biology, 6(10): e265.

684   doi:10.1371/journal.pbio.0060265

685 White, G.C. and Burnham, K.P. 1999. Program MARK: survival estimation from populations of

686   marked animals. Bird Study, 46:sup1, S120-S139, DOI: 10.1080/00063659909477239

687 Williams, J.G., Smith, S.G., and Muir, W.D. 2001. Survival estimates for downstream migrant

688   yearling juvenile salmonids through the Snake and Columbia Rivers hydropower system,

689   1966-1980 and 1993-1999. North American Journal of Fisheries Management, 21: 310-

690   317.

691 Yoshiyama, R.M., Fisher, F.W., and Moyle, P.B. 1998. Historical Abundance and Decline of

692   Chinook Salmon in the Central Valley Region of California. North American Journal of

693   Fisheries Management 18:487-521.

694 Zabel, R.W., and Achord, S. 2004. Relating size of juveniles to survival within and among

695   populations of Chinook Salmon. Ecology 85:795-806.

696 Zeug, S.C., Sellheim, K., Watry, C., Wikert, J.D., and Merz, J. 2014. Response of juvenile

697   Chinook salmon to managed flow: lessons learned from a population at the southern

698   extent of their range in North America. Fisheries Management and Ecology 21:155-168

699 **Figure Captions**

700 **Figure 1:** Map of the mainstem Sacramento River. Our study area extended from above

701 Red Bluff in the north to the city of Sacramento in the south. Late-fall run Chinook

702 salmon yearling smolts were released at Battle Creek, Jelly's Ferry, Irvine Finch or Butte

703 City during the winter (Dec-Jan) of each of our study years. The locations of the 20

704 acoustic receivers that delineated our 19 river reaches are shown as red stars.

705 **Figure 2**: Map depicting reach-specific survival estimates (per 10km) for 2008-2010.

706 Colors represent per reach survival risk and standard error is represented as the grey

707 buffer surrounding each reach. The values adjacent to each reach represent the survival

708 estimate for a given reach (per 10 km) from our full survival model.

709 **Figure 3.** Difference between survival estimates in the spatial-temporal model and the

710 covariate model for each reach (labeled as the distance (River km) between the upstream

711 boundary and the Golden Gate Bridge). Negative values represent occasions when the

712 covariate model had a larger estimate of survival and was presumably missing covariates

713 that increased smolt mortality. Error bars represent the 95% confidence interval estimated

714 with the delta method.

715 **Figure 4**: A barplot depicting the results of covariate removal analysis to determine the

716 importance of each variable to the final model. Delta QAIC values represent the change

717 in QAIC when specific variables are removed from the full model.

718 **Figure 5:** Covariate response plots showing the effect of the individual covariates on the

719 apparent survival rate through a 10 km reach. The grey shaded region represent the 95%

720 confidence interval.
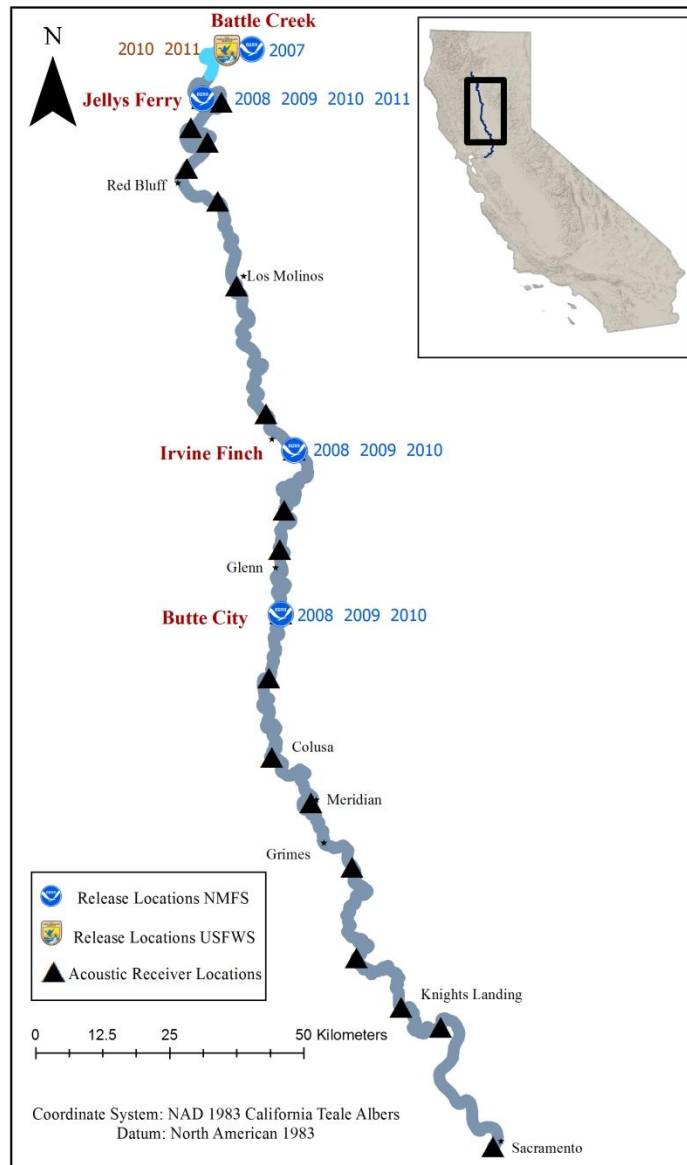
Fig 1: Map of the mainstem Sacramento River. Our study area extended from above Red Bluff in the north to the city of Sacramento in the south. Late-fall run Chinook salmon yearling smolts were released at Battle Creek, Jelly's Ferry, Irvine Finch or Butte City during the winter (Dec-Jan) of each of our study years. The locations of the 20 acoustic receivers that delineated our 19 river reaches are shown as black triangles.

215x279mm (300 x 300 DPI)
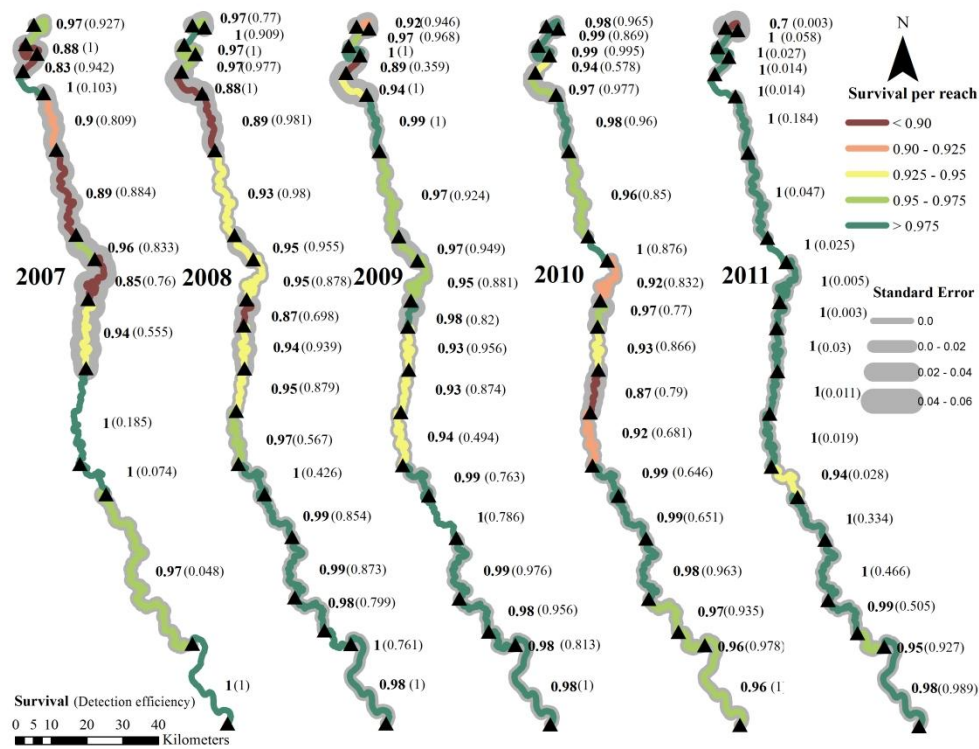
Figure 2: Map depicting reach-specific survival estimates (per 10km) for 2007-2011. Colors represent survival per 10 km for each reach and standard error is represented as the grey buffer surrounding each reach. The values adjacent to each reach are the survival estimates and detection probabilities.

279x215mm (300 x 300 DPI)
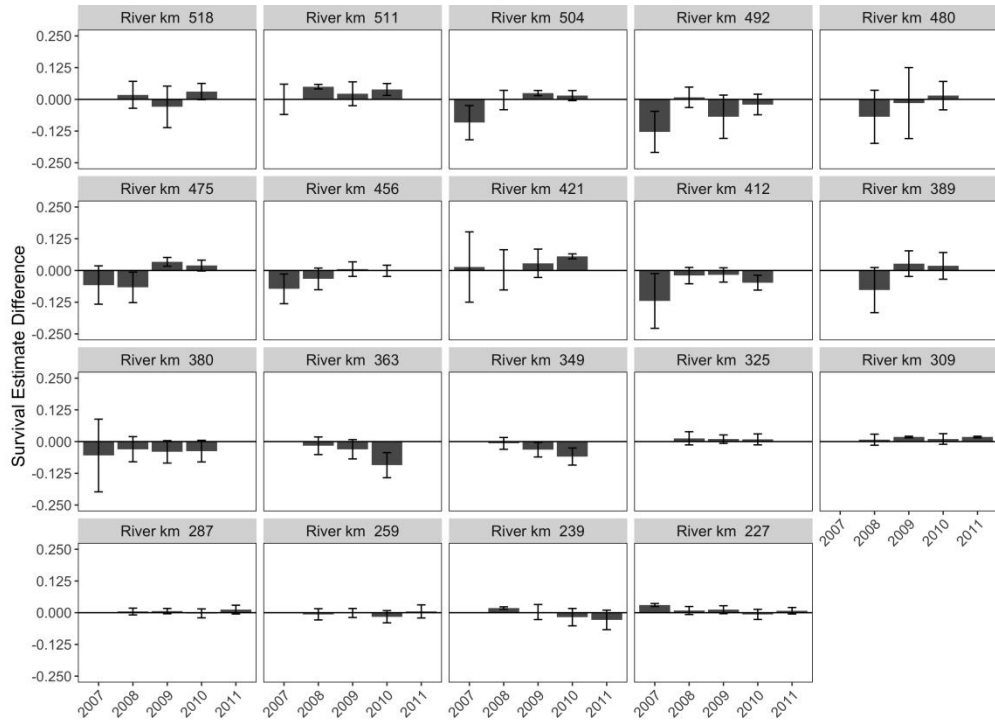
Figure 3. Difference between survival estimates in the spatial-temporal model and the covariate model for each reach (labeled as the distance (River km) between the upstream boundary and the Golden Gate Bridge). Negative values represent occasions when the covariate model had a larger estimate of survival and was presumably missing covariates that increased smolt mortality. Error bars represent the 95% confidence interval estimated with the delta method.

1164x846mm (72 x 72 DPI)
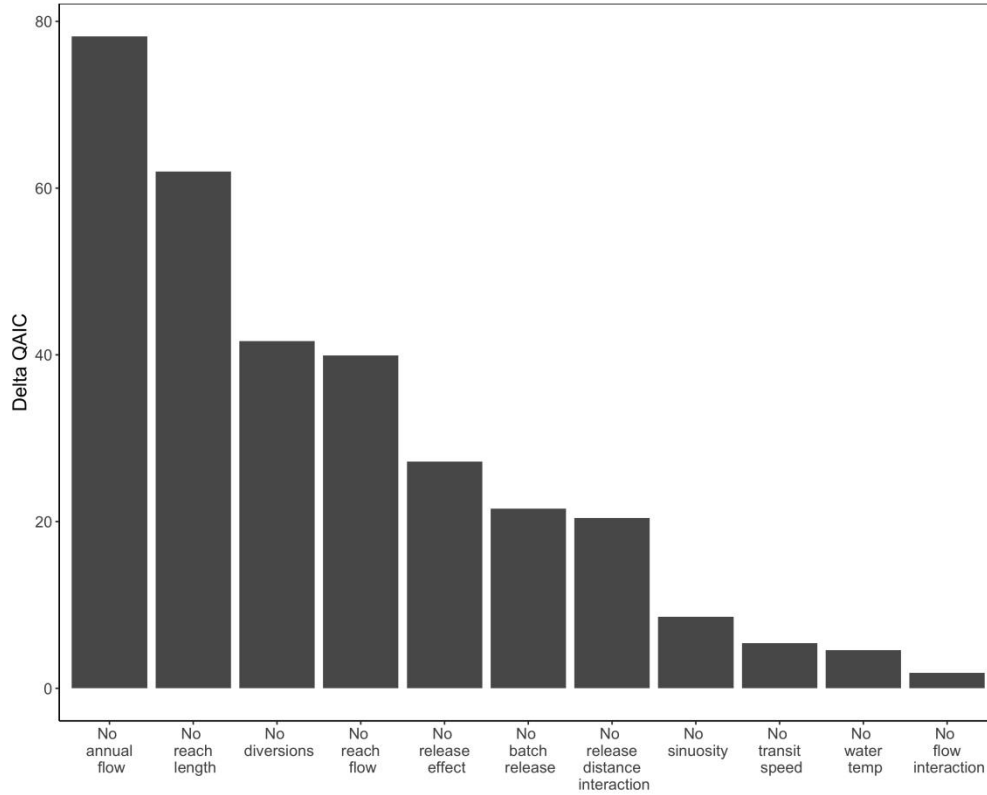
Figure 4: A barplot depicting the results of covariate importance analysis to determine how removing a single covariate influenced the fit of the selected model. Delta QAIC values represent the change in QAIC when specific variables are removed from the full model.

1058x846mm (72 x 72 DPI)
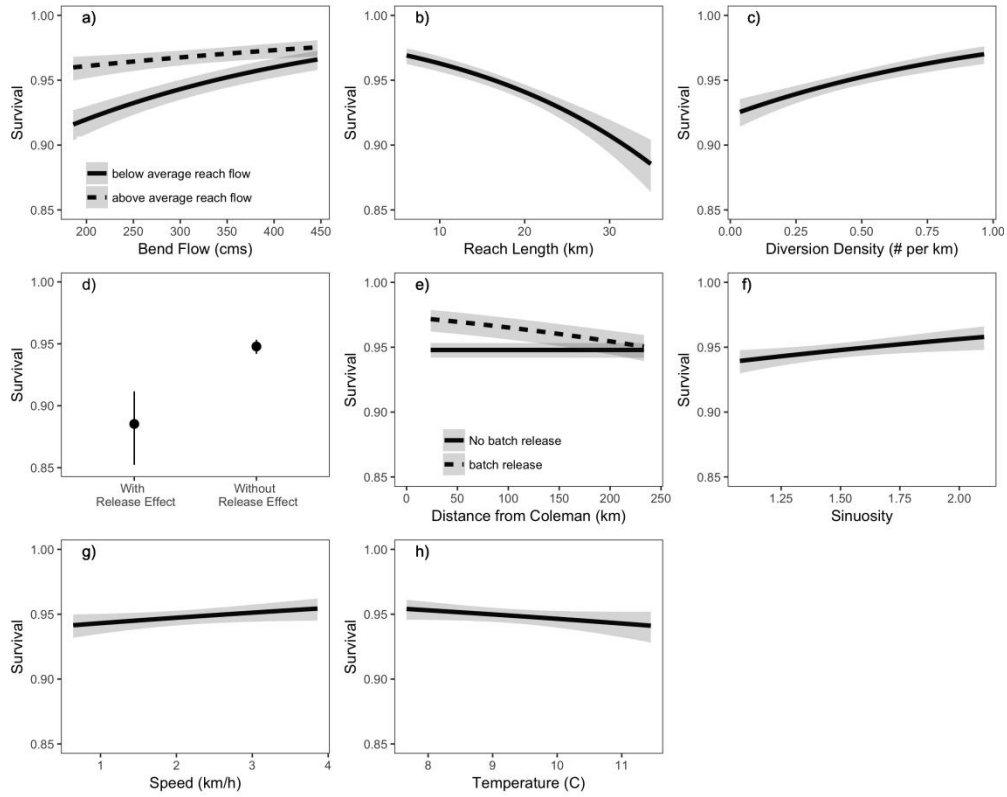
Figure 5: Covariate response plots showing the effect of the individual covariates on the apparent survival rate through a 10 km reach. The grey shaded region represent the 95% confidence interval.

1058x846mm (72 x 72 DPI)

Table 1: A description of the covariates included in the mark recapture model.

Category	Covariate	Range	Definition	Hypothesized relationship with survival
Individual	Fish Length[1]	135 - 204 mm	Fork length	Larger fish may exceed gape width of predators
	Fish Condition[1]	0.59 - 1.32	Fulton's K	Increased condition improves predator escape capability
	Transit speed[2]	0.02 - 8.25 km h^{-1}	Reach specific transit speed	Faster moving fish have less exposure to predators
Release group	Batch release[2]	Binary	Tagged fish released concurrently with large hatchery releases.	Predator swamping
	Release reach[1]	Binary	Difference in survival between newly released fish and those released upstream.	Newly released hatchery fish are naïve and susceptible to predation
	Annual flow[3]	179 - 499 cms	Mean flow measured at Bend Bridge throughout outmigration (December-March).	Increased flows produce more habitat and predator refugia throughout the river
Reach specific	Sinuosity[4]	1.04 - 2.74	River distance divided by Euclidean distance.	More natural habitats have more predator refugia
	Diversion density[5]	0 - 1.05 num km^{-1}	Number of diversions per reach length.	Increased predator densities near diversions
	Adjacent cover density[6]	0.2 - 0.76 %	Percent of non-armored river bank with adjacent natural woody vegetation.	Increased cover produces more predator refugia
	Off-channel habitat density[6]	0 - 1.62 %	Off-channel habitat within 50 m of river expressed as percentage of river area	Increased off-channel habitat produces more predator refugia
Time varying	Temperature[7]	6.2 - 12.9 °C	Mean water temperature per reach	Increased temperatures results in increased predation due to higher metabolic demands of predators
	Inter-annual Reach flow[7]	215 – 447 cms	Mean water flow per reach	Higher flows within a reach will produce more habitat and predator refugia within that reach
	Intra-annual Reach flow[7]	129 – 902 cms	Mean water flow per reach and year	Higher intra-annual flows (e.g., precipitation or dam releases) decreases predation due to increased turbidity and increased predator refugia.

[1]Measured during tagging and release; [2]Observed travel times and mixed effects model estimates; [3]California Water Data Library; [4]National Hydrography Dataset; [5]Passage Assessment Database - verified by field survey; [6]Department of Water Resources; [7]River Assessment for Forecasting Temperature (RAFT) model

Table 2. Beta estimates (standard errors) of covariates included in mark recapture models with a delta QAICc < 2. The Battle Creek, Sacramento-San Joaquin Delta (Sac-SJ Delta), and San Francisco Bay (SF Bay) covariate are beta estimates for the three reaches where habitat and predation related covariates were not included in the model. See Table 1 for definitions of the other covariates. The selected model is in bold.

Covariate	Model 1	**Model 2**	Model 3	Model 4	Model 5	Model 6	Model 7
Intercept	2.918 (0.050)	**2.900 (0.049)**	2.899 (0.049)	2.917 (0.050)	2.943 (0.049)	2.942 (0.049)	2.936 (0.049)
Battle Creek	-2.000 (0.141)	**-1.986 (0.140)**	-1.957 (0.141)	-1.969 (0.142)	-2.023 (0.141)	-1.992 (0.142)	-2.013 (0.141)
Sac-SJ Delta	-2.673 (0.096)	**-2.656 (0.095)**	-2.659 (0.095)	-2.678 (0.096)	-2.695 (0.096)	-2.698 (0.096)	-2.691 (0.096)
SF Bay	-2.888 (0.260)	**-2.868 (0.259)**	-2.899 (0.261)	-3.042 (0.240)	-2.926 (0.259)	-2.959 (0.261)	-2.913 (0.259)
Reach length	-0.463 (0.047)	**-0.446 (0.046)**	-0.444 (0.045)	-0.461 (0.047)	-0.445 (0.049)	-0.442 (0.049)	-0.457 (0.049)
Sinuosity	0.168 (0.050)	**0.147 (0.049)**	0.145 (0.049)	0.167 (0.050)	0.181 (0.051)	0.181 (0.051)	0.188 (0.051)
Adjacent cover					0.073 (0.053)	0.076 (0.053)	0.089 (0.052)
Diversion density	0.421 (0.057)	**0.382 (0.052)**	0.379 (0.052)	0.418 (0.057)	0.423 (0.056)	0.421 (0.056)	0.419 (0.056)
Off-channel habitat	0.118 (0.062)			0.120 (0.062)	0.143 (0.065)	0.147 (0.065)	0.147 (0.065)
Fish condition			0.050 (0.030)	0.054 (0.030)		0.054 (0.030)	
Annual flow	0.404 (0.039)	**0.406 (0.039)**	0.405 (0.039)	0.402 (0.039)	0.387 (0.038)	0.387 (0.038)	0.396 (0.038)
Reach flow (year)	0.320 (0.047)	**0.320 (0.047)**	0.315 (0.047)	0.314 (0.047)	0.309 (0.047)	0.304 (0.047)	0.327 (0.046)
Annual flow: Reach flow	-0.112 (0.046)	**-0.113 (0.046)**	-0.107 (0.046)	-0.106 (0.046)	-0.115 (0.046)	-0.109 (0.046)	-0.106 (0.046)
Temperature	-0.079 (0.041)	**-0.080 (0.041)**	-0.078 (0.041)	-0.077 (0.041)			
Transit speed	0.079 (0.034)	**0.078 (0.034)**	0.081 (0.034)	0.083 (0.035)	0.069 (0.035)	0.073 (0.035)	
Release reach	-0.821 (0.131)	**-0.857 (0.130)**	-0.865 (0.130)	-0.829 (0.131)	-0.781 (0.135)	-0.787 (0.135)	-0.781 (0.135)
Batch release	0.694 (0.147)	**0.701 (0.146)**	0.689 (0.147)	0.679 (0.147)	0.637 (0.143)	0.625 (0.143)	0.651 (0.143)
Batch release: Distance	-0.003 (0.000)	**-0.003 (0.000)**	-0.003 (0.000)	-0.003 (0.000)	-0.003 (0.000)	-0.003 (0.000)	-0.003 (0.000)
Survival covariates	16	**15**	16	17	16	17	15
Delta QAICc	0	**0.29**	0.71	1.20	1.27	1.38	1.63

Decoupling outmigration from marine survival indicates outsized influence of streamflow on cohort success for California's Chinook salmon populations

Cyril J. Michel[1][*]

* Corresponding author
cyril.michel@noaa.gov
Voice: 831-420-3986
Fax: 831-420-3977

[1] University of California, Santa Cruz
Institute of Marine Sciences
Affiliated with:
Fisheries Ecology Division
Southwest Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
110 McAllister Way, Santa Cruz, CA 95060

1

1   **Abstract**

2   Historically, marine survival estimates for salmon have been confounded with freshwater

3   seaward migration ("outmigration") survival. Telemetry studies have revealed low and variable

4   survival during outmigration, suggesting marine mortality may not be the primary source of

5   variability in cohort size as previously believed. Using a novel combination of tagging

6   technologies, survival during these two life stages was decoupled over five years for Sacramento

7   River Chinook salmon. Outmigration survival ranged from 2.6% to 17%, marine survival ranged

8   from 4.2% to 22.8%. Influential environmental drivers in both life stages were also compared to

9   smolt-to-adult ratios (SAR) for three Chinook salmon populations over 20 years. Streamflow

10   during outmigration had higher correlation with SAR (r-squared >0.34) than two marine

11   productivity indices (r-squared <0.08). The few SAR estimates that were poorly predicted by

12   flow occurred during years with the lowest marine productivity, suggesting most inter-annual

13   SAR fluctuations are explained by outmigration survival, but abnormally poor marine conditions

14   also reduce SAR. The outsized influence of flow on SAR provides managers with a powerful

15   mitigation tool in a watershed where flow is tightly regulated.

16   **Keywords**

17   **-Chinook salmon**

18   **-Survival**

19   **-California**

20   **-River regulation**

21   **-Marine productivity**

22   **-Smolt-to-adult**

23   **-Acoustic telemetry**

2

24 **Introduction**

25   Convention is that variability in salmon cohort success is set during the early marine

26 residence period. To date, direct evidence of how outmigration (freshwater plus estuarine)

27 survival might be affecting overall cohort success has been scarce throughout the range of

28 salmon populations. Historically, it has been difficult to parse out outmigration survival from

29 marine survival, further obfuscating the causes and magnitude of outmigration mortality. Recent

30 telemetry studies have estimated very low survival during the outmigration life stage of certain

31 salmon stocks (Buchanan et al. 2013; Michel et al. 2015; Clark et al. 2016), suggesting that

32 marine survival is likely higher than what the literature indicates. Many models attempting to

33 explain marine survival using marine environmental indicators suffer from large amounts of

34 unexplained variation in some years (Koslow et al. 2002; Logerwell et al. 2003; Sharma et al.

35 2013); and there is potential that variation due to outmigration survival has been incorrectly

36 attributed to marine survival in these models. Through the accurate partitioning of outmigration

37 and marine survival, it may be possible to identify new survival bottlenecks which will require

38 new and different management solutions.

39   Marine conditions are often blamed for poor cohort success of California's Central

40 Valley Chinook salmon (*Oncorhynchus tshawytscha*) populations, but there is a building body of

41 evidence to suggest that outmigration survival may be playing a large role (Buchanan et al. 2013;

42 Michel et al. 2015). Gross et al. (1988) posited that anadromous life history strategies evolve in

43 fishes when migration to the ocean provides gains to individual fitness that outweigh the costs of

44 the migration itself. It is believed that salmon have evolved this life history strategy because the

45 ocean provides a more favorable tradeoff between abundant food and predation risk. However,

46 the Central Valley may be an example of a system where the costs of outmigration are high

3

47   enough that the anadromous life history strategy is no longer sustainable, and is only persisting

48   through the assistance of humans (such as through hatcheries, or transporting outmigrants past

49   regions of poor survival). Three of the four distinct salmonid Evolutionarily Significant Units

50   (ESUs) that are found there are listed under the U.S. Endangered Species Act (ESA), and the

51   fourth is a "species of concern". Many inland stressors have been identified that have led to the

52   decline of these populations, including the loss of 47% of spawning and rearing habitat due to

53   dams without fish passage (Yoshiyama et al. 2001) and 97% of the productive floodplain rearing

54   habitat to diking (Whipple et al. 2012). These dams and levees are one-time historical

55   perturbations, but have ongoing impacts and will likely never be completely reversed. While it is

56   almost certain that populations will not return to pre-dam and pre-diking levels without reversing

57   these habitat changes, studies must also concentrate on the contemporary stressors that are

58   governing annual outmigration survival dynamics, such as warm stream and estuary

59   temperatures during outmigration, slow water velocities, low turbidity, and abundant predators

60   (Baker et al. 1995; Newman and Rice 2002; Grossman 2016). However, these are just the

61   symptoms of a larger problem: the fundamental alteration of the Central Valley hydrological

62   regime. The dams and diversions of the Central Valley have resulted in the reduction and

63   homogenization of river flows (Buer et al. 1989), which in turn can alter water temperatures,

64   slow water velocities associated with large flow events, lower turbidity and provide more

65   suitable habitat for warm-water predator species. These same dams and diversions give resource

66   managers tight control over streamflow and associated covariates. In contrast, managers have no

67   control over the environmental variables that are thought to govern marine survival. Therefore, if

68   outmigration survival is found to have a large influence on the magnitude and variability in

69   cohort success, this suggests that managers can likely do more to help these populations.

70   A novel method of pairing outmigration survival estimates derived from an acoustic

71   tagging study with smolt-to-adult ratio (SAR) estimates derived from coded-wire tag (CWT)

72   recoveries from the same cohorts was used to investigate the relative importance of (1)

73   freshwater and estuarine outmigration (hereafter simply termed "outmigration") survival versus

74   (2) marine survival rates for Central Valley Chinook salmon over the 5-year time series of the

75   acoustic tagging study. Expanding beyond this time series, many additional years of SAR

76   estimates were regressed against environmental drivers that are believed to be influential on

77   survival in each region to investigate the importance of these environmental drivers on smolt-to-

78   adult dynamics and ultimately gain insights on where the majority of mortality might be

79   occurring every year.

80   **Methods**

81   *Study system*

82   California's Central Valley includes the two largest rivers in the state. In the northern

83   portion of the valley, the Sacramento River flows north to south and in the southern portion of

84   the valley, the San Joaquin River flows south to north (Fig. 1). These two rivers meet to create

85   the freshwater portion of their shared estuary: the Sacramento-San Joaquin River Delta (hereafter

86   "Delta"), an expansive and complex network of tidal freshwater river channels and sloughs. It is

87   connected to the west by a series of increasingly saline bays, most notably the San Francisco

88   Bay, which comprise the brackish portion of the estuary ("Bays" in Fig. 1). The estuary connects

89   to the Pacific Ocean at the narrow passage at the Golden Gate, beyond which salmon have access

90   to the productive waters of the Gulf of the Farallones.

91   *Outmigration survival estimates*

92   In an attempt to decouple outmigration and marine survival of Central Valley Chinook

93 salmon, cohorts that were tagged using both acoustic tags (for estimation of outmigration

94 survival) and coded-wire tags ("CWT"; for estimation of overall cohort success) were identified.

95 Outmigration survival estimates were used from two acoustic tagging studies conducted on

96 hatchery-origin late-fall-run Chinook salmon from 2007 to 2011 (Michel et al. 2015; Iglesias et

97 al. 2017). These studies released their acoustic tagged fish as part of larger hatchery releases that

98 were also coded-wire tagged. CWTs are tiny, injectable, magnetized wire segments that are

99 embossed with a release group serial code, with release groups of thousands of fish often sharing

100 the same serial code. Recovery of tagged adults allows the estimation of smolt-to-adult ratio

101 (SAR) of these larger release groups. SAR represents the proportion of fish of a harvestable size

102 recovered from the total number of juveniles released into the wild and was therefore used as an

103 index of cohort success.

104   To assess the contribution of outmigration survival to overall SAR, and to factor out

105 estimates of marine survival, outmigration survival from acoustic tagged release groups were

106 associated to the SAR estimates from the most appropriate CWT release groups. However, some

107 of the acoustic tagged release groups were not released in exact synchrony with a respective

108 CWT release group. For these, if one or more CWT release groups were released within 7 days

109 of the acoustic tag group's release date, that acoustic tag group's outmigration survival was

110 associated to the respective CWT release group(s). For the purposes of these studies,

111 outmigration survival was estimated as total survival from release to the Golden Gate Bridge,

112 thereby including river and estuarine survival. For more information on the acoustic tagging,

113 tracking, and estimation of survival for the acoustic tagging studies, refer to Michel et al. (2015).

114 *Smolt-to-Adult estimates*

115   SAR is a survival metric often used for hatchery fish because of the fairly accurate

116   estimates of how many smolts are released. Hatchery Chinook salmon are often raised up to the

117   smolting stage before release, which is the beginning of the SAR period. The end of the SAR

118   period is when a fish either returns to the spawning grounds or hatchery, or is captured by

119   commercial or recreational fisheries. These various recapture scenarios ("strata"), and their

120   associated CWT recoveries, occur after Chinook salmon have spent at least one year in the ocean

121   (2+ year old), and can commonly occur for salmon that have spent as many as 3 years in the

122   ocean (4+ year old; Fig. 2). SAR therefore represents the survival of a cohort from smolting to

123   the point at which they reach harvestable and minimum reproductive (i.e. "adult") size. Thus,

124   survival during the SAR period for a CWT group will be the product of 1) "outmigration

125   survival" (S_O) and 2) "marine survival" (S_M), survival during the first year at sea plus an

126   amalgamation of year 2, 3, and 4 survival depending on recapture time of individuals within the

127   CWT group. Due to this complexity, SAR should be treated as an index of survival that primarily

128   represents survival from hatchery release to age 2, with some additional mortality from latter

129   periods (but that are thought to be relatively small contributions compared to critical survival

130   bottlenecks of outmigration and the first year at sea [Magnusson and Hilborn 2003; Quinn 2005

131   and references therein]).

132   The SAR in the Central Valley is most often calculated using CWT recoveries (CWT_R).

133   Approximately 25% of all hatchery-origin fall-run Chinook salmon (since 2007) and 100% of all

134   hatchery-origin late-fall-run and winter-run Chinook salmon (since 1992) in the Central Valley

135   have CWTs inserted into their snouts as juveniles. Once the salmon attain harvestable size

136   (hereafter "adults"), the CWTs are recovered from the fisheries through creel surveys, from the

137   spawning grounds through carcass surveys, and through the hatcheries (for additional details on

138   recovery sources, refer to Table 1). All CWT data were downloaded from the Pacific States

139   Marine Fisheries Commission's Regional Mark Processing Center's Regional Mark Information

140   System database (http://www.rmpc.org/).

141   The first brood year (i.e., the year the eggs were spawned; "BY" hereafter) for which

142   SAR could be accurately estimated was 1999 for both winter and fall-run Chinook salmon, and

143   1993 for late-fall-run Chinook salmon (despite the absence of spawning ground and recreational

144   river fishery recoveries until the late 1990s). Since an estimated 61 to 97% (mean 80%) of late-

145   fall-run Chinook salmon escapement are counted at hatcheries (using CWT data from recovery

146   years 2000-2016 when spawning ground and recreational river fishery recoveries occured), using

147   only hatchery returns in years prior to the late 1990s could bias SAR estimates low for those

148   years, but would likely still capture the major population trends.

149   For creel and carcass surveys, full coverage of all fishing areas and spawning grounds is

150   not possible; sampling fractions (r) are therefore estimated per stratum (i.e., unique recovery

151   type, area and year combinations). Sampling fractions are the fraction of estimated total number

152   of salmon caught (if a fishery) or that returned (if a hatchery or spawning area) that were

153   examined for presence of a CWT per stratum, with some additional nuances outlined in Palmer-

154   Zwahlen and Kormos (2015). Details on how total number of salmon per stratum were estimated

155   can be found in O'Farrell et al. (2012). Expansion factors, the reciprocal of sampling fractions,

156   are applied to the total CWTs observed per CWT release group that are recovered from that

157   respective stratum to produce expanded CWT recoveries ($eCWT_R$). Finally, since Chinook

158   salmon spawning age is variable (minimum age 2 years), SAR for the full cohort cannot be

159   estimated until the CWTs from the fifth year after release are processed. Thus, SAR estimates

160   beyond BY 2012 are not reported. Total expanded recoveries for each release group (N_e) is

161   therefore estimated as:

162    $N_e = \sum_{y=1}^{Y} [\text{eCWT}_R Ocean\ Fishery + \text{eCWT}_R River\ Fishery + \text{eCWT}_R Spawning\ Grounds + \text{CWT}_R Hatchery]$

163   ... (1)

164   where Y is total number of return years for which CWTs are observed for that CWT release

165   group. Note that hatchery CWT recoveries are not expanded because all CWTs are presumed to

166   be recovered from hatchery returns.

167   SAR is expressed as the proportion of expanded recoveries (N_e) out of all smolts released

168   from the hatchery for that CWT release group (N_r):

169    $SAR = \dfrac{N_e}{N_r}$ (2)

170   The standard error (SE) of the SAR for a CWT release group is a function of N_e, N_r, and

171   the total number of observed CWTs (before expansion, N_d) (Skalski and Townsend 2005):

172    $SE(SAR) = \sqrt{\dfrac{\dfrac{N_e}{N_r}\left(1 - \dfrac{N_e}{N_r}\right)}{N_r} + \dfrac{\left(\dfrac{1-r}{r^2}\right)N_d}{N_r^2}}$ (3)

173   For proper variance calculation, sampling fractions are needed per stratum. However,

174   protocols for estimating sampling fractions differed substantially by year and recapture type.

175   Overall, the sampling fraction for all CWTs recovered (across the strata) per brood year and per

176   population in this analysis was never below 0.21, and the mean was 0.35 for winter-run, 0.49 for

177   fall-run, and 0.63 for late-fall-run. Therefore, a global sampling fraction (r) was applied to

178   equation 3 using a conservative estimate of 0.2:

179    $SE(SAR) = \sqrt{\dfrac{\dfrac{N_e}{N_r}\left(1 - \dfrac{N_e}{N_r}\right)}{N_r} + \dfrac{\left(\dfrac{1-0.2}{0.2^2}\right)N_d}{N_r^2}}$ (4)

180   When calculating SAR and standard error for more CWT release groups that were

181   released on the same day, N_e, N_r, and N_d were totaled among those CWT release groups.

182   However, because there can be large heterogeneity in SAR estimates for different CWT release

183   groups released in the same year, annual SAR and standard errors are calculated differently

184   (Skalski and Townsend 2005). Annual SAR is a weighted average across CWT release groups:

185    $$\widehat{SAR} = \frac{\sum_{k=1}^{K} N_{ek}}{\sum_{k=1}^{K} N_{rk}} \tag{5}$$

186   Where K is the number of CWT release groups in a year. Standard error of the annual

187   SAR is estimated as:

188    $$SE(\widehat{SAR}) = \sqrt{\frac{\sum_{k=1}^{K} N_{rk}(SAR_k - SAR)^2}{(K-1)\sum_{k=1}^{K} N_{rk}}} \tag{6}$$

189   For the late-fall-run and winter-run populations, the only hatcheries that release smolts in

190   the Central Valley are the United States Fish and Wildlife Service's (USWFS) Coleman National

191   Fish Hatchery (CNFH) and Livingston Stone National Fish Hatchery (LSH), respectively. Both

192   of these hatcheries release the majority of their fish into the uppermost portions of the

193   Sacramento River that is available to anadromy, more than 500 river km from the Pacific Ocean.

194   Because multiple hatcheries in the Central Valley release fall-run smolts, to compare fall-run

195   release groups over the same outmigration corridor as the late-fall-run and winter-run, only fall-

196   run CWT recoveries from CNFH release groups were used. All CWT release groups that were

197   trucked and released downstream, a management strategy intended to artificially increase SARs

198   (by reducing outmigration mortality) of hatchery smolts, were also excluded. This is because one

199   of the main objectives of this study was to explicitly measure the magnitude and variability in

200   natural outmigration survival.

201   SAR estimates are the combination of survival over a finite outmigration period and non-

202   discrete marine period (due to various CWT recapture times). To ascertain the magnitude of the

203   bias introduced by the latter periods of the non-discrete marine period on overall SAR, SAR

204   estimates were compared to survival rates from hatchery release to the end of age 2 for winter-

205   run Chinook salmon for the same brood years, as estimated from a Sacramento River winter-run

206   Chinook salmon cohort reconstruction model ([O'Farrell et al. 2012]; data provided by M.

207   O'Farrell, NOAA-NMFS). This was done using a linear regression model fitted between the two

208   variables, after logit-transformation (due to the range of both variables being bound by 0 and 1).

209   Currently, a salmon cohort reconstruction model does not exist for Central Valley fall or late-

210   fall-run Chinook salmon.

211   *Outmigration vs. Marine Survival comparison*

212   The outmigration survival component of SAR, as estimated from acoustic telemetry, was

213   factored out to get an estimate of marine survival for those brood years:

214    $S_M = \frac{SAR}{S_O}$ (7)

215   To incorporate error in estimates of both SAR and S_O, parametric bootstrapping was

216   employed. SAR was assumed to have a normal distribution on the real scale and S_O was assumed

217   to have a normal distribution on the logit scale. Given these distributions, SAR and S_O were

218   generated 1000 times each and transformed back to the real scale, such that (SAR_1^*, SAR_2^*, ...,

219   SAR_{1000}^*) and ($S_{O_1}^*$, $S_{O_2}^*$, ..., $S_{O_{1000}}^*$) yielded $S_{M_1}^*$, $S_{M_2}^*$, ..., $S_{M_{1000}}^*$. Mean S_M and standard error of

220   the mean were estimated from these values on the logit scale and back transformed to the real

221   scale. The 95% confidence intervals were also generated given:

222    $logit^{-1}\left[logit(\widehat{S_M}) \pm 1.96 \times SE[logit(\widehat{S_M})]\right]$ (8)

223   This was done for late-fall-run Chinook salmon only, and not for fall-run or winter-run

224   Chinook salmon due to the lack of acoustic tag data old enough to estimate respective SAR

225   values.

226   *Freshwater outmigration survival vs. SAR*

227   Michel et al. (2015) demonstrated that much of the annual variability in outmigration

228   survival may be occurring during the freshwater portions of the outmigration. To evaluate the

229   effect of annual freshwater outmigration survival (S_{FW}) dynamics on SAR, a linear model was

230   fitted to survival rates estimated from acoustic tags and the CWT-based SAR. The acoustic tag-

231   estimated survival rates encompassed the river and Delta regions combined (i.e., from release to

232   Chipps Island; data from Michel et al. [2015]).

233   In order to incorporate error, parametric bootstrapping was employed for both *SAR* and

234   S_{FW}. *SAR* data was generated 1000 times on the real scale, then transformed to the logit scale

235   due to *SAR* being bounded by 0 and 1, such that $[logit(SAR_1^*), logit(SAR_2^*), ..., logit(SAR_{1000}^*$

236     $)]$ datasets were created. S_{FW} was generated 1000 times on the logit scale, again because S_{FW} is

237   bounded by 0 and 1, such that $[logit(S_{FW_1}^*), logit(S_{FW_2}^*), ..., logit(S_{FW_{1000}}^*)]$ datasets were

238   created. The *SAR* datasets were fitted to their respective S_{FW} datasets per iteration of 1000

239   different linear models, such that 1000 estimates of r-squared values were generated. The

240   median, 5% and 95% percentile values (i.e., 95% confidence intervals) of the r-squared estimates

241   were then calculated.

242   *Environmental covariates vs. SAR*

243   The relationship between SAR and variables that characterize the river and ocean

244   environments were evaluated for each of the three Chinook salmon populations. Linear

245   regression models were fitted between logit-transformed SAR estimates and environmental

246 indices. Because extreme outliers can mask strong and persistent trends, Cook's distances were

247 estimated for all points in all models (Cook 1977) to determine if any annual SAR values exert

248 excessive leverage on the linear regressions. The linear regression model was fitted with and

249 without any annual SAR value with a Cook's distance > 1.

250 Environmental covariates thought to influence survival during the outmigration and

251 marine survival life stages were selected in an attempt to determine the relative contribution of

252 these factors on cohort success. For the river environment, the literature suggests that flow may

253 have the greatest influence on outmigration survival (Newman and Rice 2002; Smith et al. 2003;

254 Michel et al. 2015). Flow values (cubic feet per second) were used from the United States

255 Geological Survey's Bend Bridge gauging station on the Sacramento River (USGS station

256 number 11377100). This gauge is located approximately 20 and 60 river kilometers downstream

257 from the release locations used by the CNFH and LSFH, respectively. Distribution of flow

258 values were right-skewed, and thus log-transformed for normality.

259 A single variable (upwelling) and a multivariate index of productivity were chosen for

260 the marine environment. Upwelling is a key variable in determining the quality of marine

261 conditions for salmon (Kope and Botsford 1990; Scheuerell and Williams 2005; Wells et al.

262 2016). Mean monthly coastal upwelling index as computed by the National Oceanic and

263 Atmospheric Administration's National Marine Fisheries Service for the 39° N 125° W station,

264 the closest station to the Gulf of the Farallones

265 (https://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html) was

266 used as the single covariate. The upwelling index represents wind-driven cross-shore transports

267 computed from surface pressure analyses (in cubic meters per second along each 100 meters of

268 coastline). The Multivariate Ocean Climate Indicator (MOCI) as described in Garcia-Reyes and

269   Sydeman (2017) was used as the multivariate index of productivity. This unitless environmental

270   indicator, specific to California's continental shelf, synthesizes numerous ocean and atmospheric

271   variables to give an index of the state of the ecosystem productivity

272   (http://www.faralloninstitute.org/moci). The MOCI is estimated for both the Northern California

273   region (38 to 42°N latitude) and the Central California region (34.5 to 38°N latitude). Since

274   juvenile salmon from the Central Valley are known to occupy both these regions (MacFarlane

275   2010), the mean seasonal MOCI between these regions was used. Low MOCI values represent

276   high marine productivity, and high MOCI values represent low marine productivity.

277   Daily mean flow at Bend Bridge was averaged over a 14-day window, starting the day of

278   release, for each CWT release group, to represent the mean river travel time from release to

279   Delta entry (as estimated for acoustic tagged hatchery-origin late-fall-run Chinook salmon smolts

280   [Michel et al. 2012]). These release group-specific 14-day mean flows were then averaged per

281   year and weighted to the size of each CWT release group. For the marine environment, the first

282   few months at sea is the most critical survival period of the marine phase of a salmon's life

283   history (Kilduff et al, 2014), specifically during the first spring at sea for Central Valley salmon

284   stocks and mediated through environmental drivers such as upwelling (Wells et al. 2012;

285   Woodson et al. 2013). Therefore, the mean monthly upwelling index across the months of

286   March, April, and May for the year of outmigration were used, as well as the mean of the

287   Northern and Central California spring MOCI.

288   The residuals of the flow linear models were graphically compared to upwelling and

289   MOCI to evaluate if any variability in SAR that was unexplained by flow could be explained by

290   the marine environmental covariates. Two contour plots were generated by interpolating the

291   known SAR values (all three salmon populations combined, to increase resolution) across a grid

14

292   of flow and either upwelling or MOCI values (using Akima interpolation [Akima 1970]),

293   bounded by the limits of the current dataset. Because SAR values could be influenced by

294   population-specific life history strategies, annual logit-scale SAR values were standardized

295   within populations (i.e., z-score: subtracted the mean and divided by the standard deviation for

296   each SAR value), and then combined. All analyses were performed using program R (version

297   3.5.1, R Core Team 2016) along with the "akima" package (Akima and Gebhardt 2016).

298   **Results**

299   *Smolt-to-Adult estimates*

300   Annual SAR values were estimated for 20 consecutive years for late-fall-run, and 14

301   consecutive years for winter-run and fall-run Chinook. The number of CWTs released per run

302   and per year ranged from 30,451 to 3,128,686. Annual SAR ranged from 0.02% to 3.29%

303   overall, and mean annual SAR for these years were 1.00% (0.1 SE) for late-fall-run Chinook

304   salmon, 0.64% (0.18 SE) for winter-run Chinook salmon, and 0.81% (0.26 SE) for fall-run

305   Chinook salmon (Table 2).

306   There was a strong positive relationship between the winter-run Chinook salmon SAR

307   values and hatchery release to end of age-2 survival, as estimated by cohort reconstruction (r-

308   squared 0.95; Fig. 3). Because the two variables are approximately equal under the same

309   conditions (95% confidence intervals of the linear model between these two variables overlap the

310   1:1 line), SAR was used to represent the combined outmigration and marine survival during the

311   first year at sea.

312   *Outmigration vs. Marine Survival comparison*

313   Overall, outmigration survival ranged from 2.6% to 17%, and marine survival ranged

314   from 4.2% to 19% for eight late-fall-run Chinook salmon CWT release groups (or cluster of

315   release groups) from brood years 2007 through 2010 (Fig. 4). For the eight CWT release groups,

316   five were estimated to have higher marine survival than the respective outmigration survival

317   estimate, two groups had the opposite pattern, and one group had approximately equal survival in

318   both periods. SAR estimates were distributed above and below the BY 1993-2012 long-term

319   median SAR (0.81%; represented by the black dashed line in Fig. 4), suggesting that these

320   release groups experienced overall survival that was roughly representative of the larger pool of

321   CWT release group SAR estimates.

322   *Freshwater outmigration survival vs. SAR*

323   Freshwater survival had a strong positive relationship with overall SAR for these same

324   eight CWT release group clusters (r-squared 0.62; Fig. 5), indicating freshwater outmigration

325   survival was an important factor in overall SAR for those cohorts.

326   *Environmental covariates vs. SAR*

327   Flow during outmigration was a strong predictor of SAR in all three of the Chinook

328   salmon runs (r-squared 0.45 for late-fall-run, 0.57 for winter-run, and 0.35 for fall-run Chinook

329   salmon, after removing the extreme outliers identified by Cook's distance), while both upwelling

330   and MOCI during the first spring at sea had little influence over SAR (Fig. 6). All points in all

331   linear models had Cook's distances <1 with the exception of 20.0 and 1.9 for outmigration year

332   (i.e., brood year +1; "OY" hereafter) 2006 in both the fall-run and winter-run Chinook salmon

333   linear models between SAR and flow (red labeled points in Fig. 6. d and g). The r-squared of the

334   linear regressions with the outlier included was 0.08 for fall-run and 0.16 for winter-run (linear

335   regressions shown in Fig. 6. d and g do not include the OY 2006 year). In both cases, these

336   outliers had lower SAR than what would be predicted by flow during outmigration given the

337   remainder of the datasets.

338   The residuals from the three flow regressions were plotted against spring upwelling

339   index, and spring MOCI. For fall-run and winter-run Chinook salmon OY 2006, the residual was

340   predicted based on the linear regression that was fitted to the dataset that did not include OY

341   2006 (due to having a Cook's distance > 1). Model performance was poorest in predicting annual

342   SAR in years with some of the lowest upwelling and MOCI indices (Fig. 7). Specifically, for

343   late-fall-run Chinook salmon, model performance was poor in OYs 1998 and 2005; years with

344   the lowest spring upwelling indices and the highest MOCI indices (i.e., low productivity) from

345   the 20-year time series. For winter-run Chinook salmon, the flow model performed poorly in

346   explaining the low SAR that occurred for salmon outmigrating during OY 2005 and 2006; these

347   same years also had the first and third lowest spring upwelling index values and the highest

348   MOCI index values for the 14-year time series. For fall-run Chinook salmon, the model poorly

349   explained the low SAR for outmigrating salmon in OY 2006; the year with the third lowest

350   spring upwelling index and the second highest MOCI index for the 14-year time series.

351   For all three runs, flow was the primary driver of year-to-year variation in SAR for the

352   variables tested (Fig. 6), with marine productivity only playing a major role in annual dynamics

353   when productivity was at low levels (Fig. 7). High SAR values tended to only occur when flow

354   was higher than average and productivity was not near abnormally low levels (Fig. 8). The OY

355   2014-2017 cohorts (for which SAR values are not yet available) are predicted to have poor SAR

356   based on the trends seen in the existing data with the exception of the OY 2015 late-fall Chinook

357   salmon and all three runs in OY 2017 as predicted by the upwelling contour plot (Fig. 8). The

358   MOCI contour plot has all three runs in OY 2017 falling outside the bounds of the contour plot.

359   **Discussion**

360   This study indicates that outmigration survival, and the conditions that affect it, are the

361   primary drivers of SAR dynamics, and marine survival likely only plays a critical role in years

362   with abnormally unfavorable marine conditions for salmon. Lindley et al. (2009) also suggested

363   that ocean conditions can have infrequent and yet drastic effects on salmon cohorts, while the

364   long-term, steady degradation of the freshwater environment likely plays a larger role in

365   population health of Central Valley Chinook salmon populations. In a sense, these populations

366   are extremely stressed due to the degraded freshwater environment, and cumulative to this, poor

367   marine conditions can then result in extremely low survival rates.

368   This study used a novel combination of short-term acoustic tagging data paired with

369   long-term coded-wire tag recovery data to estimate marine survival rates for California Chinook

370   salmon populations. The results indicated that marine survival for California Chinook salmon

371   populations is similar in scale to outmigration survival. Given that these marine survival

372   estimates are confounded with return river survival, net marine survival is likely higher than

373   outmigration survival in most years. Two studies have found exceptionally low outmigration

374   survival rates for California Central Valley Chinook salmon stocks compared to other large West

375   Coast rivers (Buchanan et al. 2013; Michel et al. 2015). Given these low outmigration survival

376   rates, it would be mathematically impossible for these fished populations to be sustainable if

377   marine survival was much lower than outmigration survival and hatchery propagation did not

378   exist (Michel et al. 2015). Indeed, the average annual SAR estimates in this study were below

379   1% for all three populations; for Upper Columbia and Snake River Chinook salmon populations,

380   the Columbia River Basin Fish and Wildlife Program suggests that a minimum of 2% SAR is

381   required for population survival and 4% for population recovery (NPCC 2009). This study is an

382   additional line of evidence suggesting that for California Central Valley Chinook salmon

383 populations, the risks of outmigration may now be too high and these populations are likely no

384 longer sustainable.

385   That the contribution of marine survival to cohort success has been overestimated over

386 the past decades of salmon research is an emerging concept, and one that is not unique to

387 California or Chinook salmon. It has been suggested for Atlantic salmon (*Salmo salar*) in the

388 Bay of Fundy, Canada (Lacroix 2008), for steelhead (*Oncorhynchus mykiss*) in the Cheakamus

389 River, British Columbia (Melnychuk et al. 2014), and for sockeye salmon (*Oncorhynchus nerka*)

390 in the Fraser River, British Columbia (Clark et al. 2016). The emergence of this concept is

391 fundamentally linked to the advent of acoustic tags small enough for tagging juvenile salmon;

392 because accurate estimates of outmigration survival before acoustic tags was difficult if not

393 impossible. Without an estimate of outmigration survival, outmigration survival and marine

394 survival cannot be parsed, which may lead researchers to believe that marine survival was

395 driving population declines. Potential factors leading to this misconception include the fact that

396 less is known about marine survival dynamics, marine residency is substantially longer in

397 duration than the outmigration period, and recruitment is set during early marine residence for

398 many strictly marine fishes and this concept was transferred to salmon. Managers and biologists

399 should ensure that salmon life-cycle and forecast models incorporate some index of outmigration

400 survival.

401   Streamflow during outmigration was found to have a large influence on SAR dynamics.

402 Over 35% of all variability in annual SAR dynamics can be explained by flow during

403 outmigration for three different Chinook salmon populations (after removal of an extreme

404 outlier). Flow has been found by numerous studies to have strong influences on outmigration

405 survival of salmon populations worldwide, including Central Valley Chinook salmon

406 populations (Kjelson and Brandes 1989; Zeug et al. 2014). Increases in flow usually cause or are

407 coincident with changes in many other river conditions that are beneficial to the survival of

408 outmigrating salmon, such as increased water velocities (Hogasen 1998), decreased water

409 temperatures (Smith et al. 2003), increased turbidity (Gregory and Levings 1998), and increases

410 in habitat area that reduce exposure to predators and increase growth opportunities (Sommer et

411 al. 2001). Among existing studies, this is one of only a few studies have demonstrated that flow

412 can ultimately have a strong influence on overall cohort success in the Central Valley (Sturrock

413 et al. 2015; Wells et al. 2017).

414   These results demonstrate that marine survival is also a major contributor to overall

415 cohort strength. While the indices used for marine productivity in this analysis did not show

416 strong relationships with SAR, this is not evidence of a lack of influence of marine survival on

417 SAR variability, as they cannot capture all the relevant factors (e.g., abundance of predators,

418 alternative prey, etc.). Moreover, the magnitude of marine survival was found to be as large a

419 contributor to SAR as outmigration survival. Furthermore, three of the study years showed

420 evidence of poor marine productivity leading to low SAR, all of which were corroborated with

421 existing literature. The first of these three years, 1998, was a record El Nino-Southern Oscillation

422 (ENSO) event with drastic effects on the California marine ecosystem (Lynn et al. 1998), which

423 likely had a strong negative impact on marine survival of salmon (Pearcy and Schoener 1987;

424 Johnson 1988). In 2005, during the well-documented delayed spring upwelling and resulting

425 poor productivity of the northern California Current (Schwing et al. 2006; Barth et al. 2007),

426 there was evidence of strong size and growth-rate selective early-marine mortality of Central

427 Valley Chinook salmon (Woodson et al. 2013). In 2006, spring upwelling was similarly delayed

428 as in 2005, especially off the coast of Central California where juvenile Central Valley Chinook

429 salmon first recruit to after leaving the San Francisco Bay, leading to a similar situation of poor

430 productivity (Lindley et al. [2009] and references therein). It is widely accepted that the poor

431 early-marine survival of Central Valley fall-run Chinook salmon in the springs of 2005 and 2006

432 were the proximate causes of the collapse of that stock and the temporary closure of the fishery

433 (Lindley et al. 2009), and in this analysis, the otherwise strong positive relationship between

434 flow and SAR for fall-run and winter-run Chinook salmon was likely overshadowed by

435 abnormally poor early-marine survival in OY 2006, as demonstrated by the high Cook's

436 distances of those points.

437 　　　These results also provide insights into how river and marine conditions might have

438 varied influences on different salmon populations. High flows during outmigration benefited all

439 three populations, despite the juveniles leaving at different sizes and at different times of the

440 year. However, marine productivity seems to have affected the different runs differently in some

441 years. For example, the late-fall-run Chinook salmon did not experience the OY 2006 crash,

442 while the winter-run and fall-run did, despite all three benefitting from relatively high flows

443 during outmigration. This could be due to the late-fall-run's predisposition to a larger size at

444 ocean entry, especially if size-selective mortality is at play (which is often seen during poor

445 ocean conditions [Holtby et al. 1990; Saloniemi et al. 2004; Woodson et al. 2013]). Lindley et al.

446 (2009) reported on this discrepancy between the fall-run and late-fall-run Chinook salmon in

447 those years: "Curiously, Sacramento River late-fall-run Chinook salmon escapement has

448 declined only modestly since 2002, while the [Sacramento River fall-run] in the same river basin

449 fell to record low levels." This is strong support for the concept of allowing Central Valley

450 salmon to exhibit many life-history strategies and thereby diversifying the Central Valley

451 salmon's portfolio and increasing population stability (Schindler et al. 2010; Carlson and

452 Satterthwaite 2011).

453   As with many large-scale correlative survival studies, there are noteworthy caveats.

454 Firstly, the survival estimates used in this analysis are for hatchery-origin fish only. While the

455 trends discovered in this analysis likely effect wild populations similarly, empirical estimates of

456 SAR for wild Central Valley Chinook salmon do not currently exist. Secondly, the effects of

457 acoustic tagging on juvenile salmon can bias survival estimates low, through mortality related to

458 the tag or surgery, mortality due to behavioral changes, or tag shedding. A subset of the fish used

459 to generate the acoustic tag survival estimates used here from Michel et al. (2015) were also

460 submitted to a laboratory tag effects study. In that study, no fish shed their tags over 160 days

461 (exceeding the maximum outmigration time) and tagged fish growth and survival was not

462 significantly different than untagged fish (Ammann et al. 2013). However, no tests were

463 conducted to address mortality related to behavioral changes, and therefore it is conceivable that

464 outmigration survival estimates used in this study were biased low. Thirdly, the strong

465 relationship between flow during outmigration and SAR may be mediated in some part through

466 marine survival. Climatic dynamics that led to increases or decreases in precipitation over the

467 inland portions of the salmon's range may have also influenced marine conditions in a manner

468 not captured by the marine productivity indices, but had an influence on SAR nonetheless. A

469 similar scenario was demonstrated by Lawson et al. (2004) with coho salmon populations in the

470 Pacific Northwest. One potential avenue for a post-hoc investigation of this concept would be to

471 look for correlation between flow during outmigration and the marine productivity indices.

472 Using the combined datasets, the r-squared for a linear model between flow during outmigration

473 and spring upwelling was 0.07, and 0.19 between flow and spring MOCI, showing some

474   evidence of relationships between these freshwater and marine indices. These relationships are

475   likely driven by the trend that years with extremely high flows typically have low spring

476   productivity (see conspicuous lack of points in upper-right quadrant of figure 8a and lower-right

477   quadrant of figure 8b). This phenomenon may be in part explained by the effects of ENSO,

478   which often manifests itself in California with heavy precipitation and low productivity of

479   coastal waters (Schonher and Nicholson 1989; Jacox et al. 2015). In the one year that

480   contradicted this trend in this dataset, OY 2005, when flow during outmigration and ocean

481   productivity were both extremely low, SAR values were at their lowest levels (1st lowest for late-

482   fall-run, 2nd lowest for winter-run, and 3rd lowest for fall-run). For salmon, it is perhaps a

483   fortunate climatic concurrence that low marine productivity seems to be frequently associated

484   with high outmigration flows in California.

485   The management implications of this study are important: while we do not have the

486   luxury of mitigation actions when it comes to marine conditions, we have some control over

487   conditions in the freshwater environment, and therefore potentially control over 35% of the

488   annual variability in salmon population abundances, and thus can somewhat buffer these

489   populations from the negative effects of poor marine conditions. Managers should explore

490   approaches to increase river flow and other associated beneficial river conditions during the

491   outmigration season of Central Valley Chinook salmon populations.

Acknowledgements

I would like to thank A. Osterback and S. Hayes for thoughtful discussions that led to the genesis

of this study. I would also like to thank B. Wells and N. Mantua for further discussions that led

to a refinement of the manuscript. I am indebted to A. Ammann who was instrumental in

developing the different acoustic tag studies that have allowed this analysis. The Red Bluff

USFWS office, in particular K. Offill, R. Null and K. Niemela, provided additional data where

the RMIS database was lacking. Finally, I would like to thank E. Danner, S. Lindley, M.

O'Farrell, W. Satterthwaite, and the anonymous reviewers for insightful reviews of the

manuscript. Support for this project was provided by the National Marine Fisheries Service –

Southwest Fisheries Science Center. Funding for the project that generated acoustic tag survival

estimates (as part of Michel et al. [2015]) was provided by a CALFED Bay Delta program grant,

project U-05-SC-047.

Akima, H. 1970. A New Method of Interpolation and Smooth Curve Fitting Based on Local Procedures. Journal of the Association for Computing Machinery 17:589-602.

Akima, H., and Gebhardt, A. 2016. akima: Interpolation of Irregularly and Regularly Spaced Data. R package version 0.6-2. https://CRAN.R-project.org/package=akima

Ammann, A.J., Michel, C.J., and MacFarlane, R.B. 2013. The effects of surgically implanted acoustic transmitters on laboratory growth, survival and tag retention in hatchery yearling Chinook salmon. Environmental Biology of Fishes 96:135-143.

Baker, P.F., Speed, T.P., and Ligon, F.K. 1995. Estimating the influence of temperature on the survival of chinook salmon smolts(Oncorhynchus tshawytscha) migrating through the Sacramento- San Joaquin River Delta of California. Canadian Journal of Fisheries and Aquatic Sciences 52:855-863.

Barth, J.A., Menge, B.A., Lubchenco, J., Chan, F., Bane, J.M., Kirincich, A.R., McManus, M.A., Nielsen, K.J., Pierce, S.D., and Washburn, L. 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. Proceedings of the National Academy of Sciences 104:3719-3724.

Buchanan, R.A., Skalski, J.R., Brandes, P.L., and Fuller, A. 2013. Route Use and Survival of Juvenile Chinook Salmon through the San Joaquin River Delta. North American Journal of Fisheries Management 33:216-229.

Buer, K., Forwalter, D., Kissel, M., and Stohler, B. 1989. The Middle Sacramento River: Human impacts on physical and ecological processes along a meandering river. USDA Forest Service General Technical Report.

Carlson, S.M., and Satterthwaite, W.H. 2011. Weakened portfolio effect in a collapsed salmon population complex. Canadian Journal of Fisheries and Aquatic Sciences 68:1579-1589.

Clark, T.D., Furey, N.B., Rechisky, E.L., Gale, M.K., Jeffries, K.M., Porter, A.D., Casselman, M.T., Lotto, A.G., Patterson, D.A., Cooke, S.J., Farrell, A.P., Welch, D.W., and Hinch, S.G. 2016. Tracking wild sockeye salmon smolts to the ocean reveals distinct regions of nocturnal movement and high mortality. Ecological Applications 26:959-978.

Cook, R.D. 1977. Detection of Influential Observation in Linear Regression. Technometrics 19:15-18.

Garcia-Reyes, M., and Sydeman, W.J. 2017. California Multivariate Ocean Climate Indicator (MOCI) and marine ecosystem dynamics. Ecological Indicators 72:521-529.

Gregory, R.S., and Levings, C.D. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions of the American Fisheries Society 127:275-285.

Gross, M.R., Coleman, R.M., and McDowall, R.M. 1988. Aquatic Productivity and the Evolution of Diadromous Fish Migration. Science 239:1291-1293.

Grossman, G.D. 2016. Predation on Fishes in the Sacramento–San Joaquin Delta: Current Knowledge and Future Directions. San Francisco Estuary and Watershed Science 14.

Hogasen, H.R. 1998. Physiological changes associated with the diadromous migration of salmonids. Canadian Special Publication of Fisheries and Aquatic Sciences 127:i-viii, 1-128.

Holtby, L.B., Andersen, B.C., and Kadowaki, R.K. 1990. Importance of Smolt Size and Early Ocean Growth to Interannual Variability in Marine Survival of Coho Salmon (Oncorhynchus kisutch). Canadian Journal of Fisheries and Aquatic Sciences 47:2181-2194.

Iglesias, I.S., Henderson, M.A., Michel, C.J., Ammann, A.J., and Huff, D.D. 2017. Chinook salmon smolt mortality zones and the influence of environmental factors on out-migration success in the Sacramento River Basin. NOAA-National Marine Fisheries Service Report prepared for United States Fish and Wildlife Service.

Jacox, M.G., Fiechter, J., Moore, A.M., and Edwards, C.A. 2015. ENSO and the California Current coastal upwelling response. Journal of Geophysical Research: Oceans 120:1691-1702.

Johnson, S.L. 1988. The effects of the 1983 El Niño on Oregon's Coho (Oncorhynchus kisutch) and Chinook (O. tshawytscha) Salmon. Fisheries Research 6:105-123.

Kilduff, D.P., Botsford, L.W., and Teo, S.L.H. 2014. Spatial and temporal covariability in early ocean survival of Chinook salmon (Oncorhynchus tshawytscha) along the west coast of North America. ICES Journal of Marine Science: Journal du Conseil.

Kjelson, M.A., and Brandes, P.L. 1989. The use of smolt survival estimates to quantify the effects of habitat changes on salmonid stocks in the Sacramento-San Joaquin River, California. Pages 100-115 *in* C. D. Levings, L. B. Holtby, and M. A. Henderson, editors. Proceedings of the National Workshop on the effects of habitat alteration on salmonid stocks. Canadian Special Publication of Fisheries and Aquatic Sciences.

Kope, R.G., and Botsford, L.W. 1990. Determination of Factors Affecting Recruitment of Chinook Salmon Oncorhynchus-Tshawytscha in Central California. Fishery Bulletin 88:257-269.

Koslow, J.A., Hobday, A.J., and Boehlert, G.W. 2002. Climate variability and marine survival of coho salmon (Oncorhynchus kisutch) in the Oregon production area. Fisheries Oceanography 11:65-77.

Lacroix, G.L. 2008. Influence of origin on migration and survival of Atlantic salmon (Salmo salar) in the Bay of Fundy, Canada. Canadian Journal of Fisheries and Aquatic Sciences 65:2063-2079.

Lawson, P.W., Logerwell, E.A., Mantua, N.J., Francis, R.C., and Agostini, V.N. 2004. Environmental factors influencing freshwater survival and smolt production in Pacific Northwest coho salmon (Oncorhynchus kisutch). Canadian Journal of Fisheries and Aquatic Sciences 61:360-373.

Lindley, S.T., Grimes, C.B., Mohr, M.S., Peterson, W., Stein, J., Anderson, J.T., Botsford, L.W., Bottom, D.L., Busack, C.A., Collier, T.K., Ferguson, J., Garza, J.C., Grover, A.M., Hankin, D.G., Kope, R.G., Lawson, P.W., Low, A., MacFarlane, R.B., Moore, K., Palmer-Zwahlen, M., Schwing, F.B., Smith, J., Tracy, C., Webb, R., Wells, B.K., and Williams, T.H. 2009. What caused the Sacramento River fall Chinook stock collapse? NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-447.

Logerwell, E.A., Mantua, N., Lawson, P.W., Francis, R.C., and Agostini, V.N. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (Oncorhynchus kisutch) marine survival. Fisheries Oceanography 12:554-568.

Lynn, R.J., Baumgartner, T., Garcia, J., Collins, C.A., Hayward, T.L., Hyrenback, K.D., Mantyla, A.W., Murphree, T., Shankle, A., Schwing, F.B., Sakuma, K.M., and Tegner, M.J. 1998. The State of the California Current, 1997-1998: Transition to El Nino Conditions. California Cooperative Oceanic Fisheries Investigations Report 39.

MacFarlane, R.B. 2010. Energy dynamics and growth of Chinook salmon (Oncorhynchus tshawytscha) from the Central Valley of California during the estuarine phase and first ocean year. Canadian Journal of Fisheries and Aquatic Sciences 67:1549-1565.

Magnusson, A., and Hilborn, R. 2003. Estuarine influence on survival rates of Coho (Oncorhynchus kisutch) and Chinook salmon (Oncorhynchus tshawytscha) released from hatcheries on the US Pacific Coast. Estuaries 26:1094-1103.

Melnychuk, M.C., Korman, J., Hausch, S., Welch, D.W., McCubbing, D.J.F., and Walters, C.J. 2014. Marine survival difference between wild and hatchery-reared steelhead trout determined during early downstream migration. Canadian Journal of Fisheries and Aquatic Sciences 71:831-846.

Michel, C.J., Ammann, A.J., Chapman, E.D., Sandstrom, P.T., Fish, H.E., Thomas, M.J., Singer, G.P., Lindley, S.T., Klimley, A.P., and Macfarlane, R.B. 2012. The effects of environmental factors on the migratory movement patterns of Sacramento River yearling late-fall run Chinook salmon (Oncorhynchus tshawytscha). Environmental Biology of Fishes 96:257-271.

Michel, C.J., Ammann, A.J., Lindley, S.T., Sandstrom, P.T., Chapman, E.D., Thomas, M.J., Singer, G.P., Klimley, A.P., and MacFarlane, R.B. 2015. Chinook salmon outmigration survival in wet and dry years in California's Sacramento River. Canadian Journal of Fisheries and Aquatic Sciences 72:1749-1759.

Newman, K.B., and Rice, J. 2002. Modeling the Survival of Chinook Salmon Smolts Outmigrating through the Lower Sacramento River System. Journal of the American Statistical Association 97:983-993.

NPCC (Northwest Power and Conservation Council). 2009. Columbia River Basin Fish and Wildlife Program. Council Document 2009-Appendix E: Subbasin Measures. Available at: https://www.nwcouncil.org/fw/program/program-2009-amendments

O'Farrell, M.R., Mohr, M.S., Grover, A.M., and Satterthwaite, W.H. 2012. Sacramento River winter Chinook cohort reconstruction: analysis of ocean fishery impacts. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-491:74 pp.

Palmer-Zwahlen, M., and Kormos, B. 2015. Recovery of Coded-Wire Tags from Chinook Salmon in California's Central Valley Escapement, Inland Harvest, and Ocean Harvest in 2012. California Dept. of Fish and Wildlife - Fisheries Administrative Report 2015-04.

Pearcy, W.G., and Schoener, A. 1987. Changes in the marine biota coincident with the 1982–1983 El Niño in the northeastern Subarctic Pacific Ocean. Journal of Geophysical Research: Oceans 92:14417-14428.

Quinn, T.P. 2005. The Behavior and Ecology of Pacific Salmon and Trout. 1st edition. University of Washington press, Seattle.

Saloniemi, I., Jokikokko, E., Kallio-Nyberg, I., Jutila, E., and Pasanen, P. 2004. Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. Ices Journal of Marine Science 61:782-787.

Scheuerell, M.D., and Williams, J.G. 2005. Forecasting climate-induced changes in the survival of Snake River spring/summer Chinook salmon (Oncorhynchus tshawytscha). Fisheries Oceanography 14:448-457.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609-612.

Schonher, T., and Nicholson, S.E. 1989. The Relationship between California Rainfall and ENSO Events. Journal of Climate 2:1258-1269.

Schwing, F.B., Bond, N.A., Bograd, S.J., Mitchell, T., Alexander, M.A., and Mantua, N. 2006. Delayed coastal upwelling along the U.S. West Coast in 2005: A historical perspective. Geophysical Research Letters 33.

Sharma, R., Velez-Espino, L.A., Wertheimer, A.C., Mantua, N., and Francis, R.C. 2013.
    Relating spatial and temporal scales of climate and ocean variability to survival of Pacific
    Northwest Chinook salmon (Oncorhynchus tshawytscha). Fisheries Oceanography 22:14-
    31.

Skalski, J.R., and Townsend, R.L. 2005. Pacific Northwest Hatcheries Smolt-to-Adult Ratio
    (SAR) Estimation using Coded Wire Tags (CWT) Data. Technical Report to Bonneville
    Power Administration, Project No. 1991-051-00, Contract No. 00013690.

Smith, S.G., Muir, W.D., Hockersmith, E.E., Zabel, R.W., Graves, R.J., Ross, C.V., Connor,
    W.P., and Arnsberg, B.D. 2003. Influence of river conditions on survival and travel time
    of Snake River subyearling fall chinook salmon. North American Journal of Fisheries
    Management 23:939-961.

Sommer, T.R., Nobriga, M.L., Harrell, W.C., Batham. W., and Kimmerer, W.J. 2001. Floodplain
    rearing of juvenile chinook salmon: evidence of enhanced growth and survival. Canadian
    Journal of Fisheries and Aquatic Sciences 58:325-333.

Sturrock, A.M., Wikert, J.D., Heyne, T., Mesick, C., Hubbard, A.E., Hinkelman, T.M., Weber,
    P.K., Whitman, G.E., Glessner, J.J., and Johnson, R.C. 2015. Reconstructing the
    Migratory Behavior and Long-Term Survivorship of Juvenile Chinook Salmon under
    Contrasting Hydrologic Regimes. PLoS One 10:e0122380.

Wells, B.K., Santora, J.A., Field, J.C., MacFarlane, R.B., Marinovic, B.B., and Sydeman, W.J.
    2012. Population dynamics of Chinook salmon Oncorhynchus tshawytscha relative to
    prey availability in the central California coastal region. Marine Ecology Progress Series
    457:125-137.

Wells, B.K., Santora, J.A., Schroeder, I.D., Mantua, N., Sydeman, W.J., Huff, D.D., and Field,
    J.C. 2016. Marine ecosystem perspectives on Chinook salmon recruitment: a synthesis of
    empirical and modeling studies from a California upwelling system. Marine Ecology
    Progress Series 552:271-284.

Wells, B.K., Santora, J.A., Henderson, M.J., Warzybok, P., Jahncke, J., Bradley, R.W., Huff,
    D.D., Schroeder, I.D., Nelson, P., Field, J.C., and Ainley, D.G. 2017. Environmental
    conditions and prey-switching by a seabird predator impact juvenile salmon survival.
    Journal of Marine Systems 174:54-63.

Whipple, A.A., Grossinger, R.M., Rankin, D., Stanford, B., and Askevold, R.A. 2012.
    Sacramento-San Joaquin Delta Historical Ecology Investigation: Exploring Pattern and
    Process. San Francisco Estuary Institute - Aquatic Science Center, Richmond, CA.

Woodson, L.E., Wells, B.K., Weber, P.K., MacFarlane, R.B., Whitman, G.E., and Johnson, R.C.
    2013. Size, growth, and origin-dependent mortality of juvenile Chinook salmon

Oncorhynchus tshawytscha during early ocean residence. Marine Ecology Progress Series 487:163-175.

Yoshiyama, R.M., Gerstung, E.R., Fisher, F.W., and Moyle, P.B. 2001. Historical and present distribution of chinook salmon in the Central Valley drainage of California. Pages 71-176 *in* R. L. Brown, editor. Contributions to the Biology of Central Valley Salmonids. California Department of Fish and Game, Sacramento, California.

Zeug, S.C., Sellheim, K., Watry, C., Wikert, J.D., and Merz, J. 2014. Response of juvenile Chinook salmon to managed flow: lessons learned from a population at the southern extent of their range in North America. Fisheries Management and Ecology 21:155-168.

Table 1. The different sources of CWT recoveries and the agency, method, and first collection year for each. In the last column, years highlighted in black represent the first brood year for which SAR was estimated.

Chinook salmon run	Recovery type	Recovery Agency[c]	Collection methods	Brood Year when first available
Winter	Ocean recreational fishery[a]	CDFW	Creel surveys	1991[b]
Winter	Ocean commercial fishery[a]	CDFW	Creel surveys	1991[b]
Winter	River recreational fishery	CDFW	Creel surveys	*No fishery*
Winter	Spawning ground	USFWS	Carcass surveys	**1999**
Winter	Hatchery	USFWS	Hatchery returns	1991[b]
Late-fall	Ocean recreational fishery[a]	CDFW	Creel surveys	1993[b]
Late-fall	Ocean commercial fishery[a]	CDFW	Creel surveys	1993[b]
Late-fall	River recreational fishery	CDFW	Creel surveys	1998
Late-fall	Spawning ground	CDFW	Carcass surveys	1999
Late-fall	Hatchery	USFWS	Hatchery returns	**1993[b]**
Fall	Ocean recreational fishery[a]	CDFW	Creel surveys	1979[b]
Fall	Ocean commercial fishery[a]	CDFW	Creel surveys	1979[b]
Fall	River recreational fishery	CDFW	Creel surveys	1998
Fall	Spawning ground	CDFW	Carcass surveys	**1999**
Fall	Hatchery	USFWS	Hatchery returns	1979[b]

[a] Some ocean fishery recoveries are received from out-of-state sources
[b] First year of consistent Coded-wire tagging
[c] CDFW refers to the California Department of Fish and Wildlife, and USFWS refers to the United States Fish and Wildlife Service.

Table 2. The estimated annual SAR (%), standard errors (SE), and total number of release days

for each run and each brood year. Standard errors were calculated using equation 6.

Brood Year	Late-fall run			Winter run			Fall run		
	SAR (%)	SE	Total Release Days	SAR (%)	SE	Total Release Days	SAR (%)	SE	Total Release Days
1993	0.50	0.07	3						
1994	1.80	0.42	5						
1995	1.02	0.13	5						
1996	1.64	0.23	5						
1997	0.69	0.10	6						
1998	0.85	0.08	3						
1999	1.03	0.14	5	2.23	0.21	1	3.29	0.14	3
2000	0.77	0.11	4	0.34	0.03	1	0.78	0.05	4
2001	1.10	0.19	4	0.24	0.02	1	0.70	0.06	5
2002	1.44	0.25	4	1.88	0.09	1	0.94	0.12	2
2003	1.44	0.16	4	1.38	0.07	1	0.30	0.04	1
2004	0.26	0.07	4	0.08	0.01	1	0.10	0.03	2
2005	1.72	0.24	3	0.11	0.01	1	0.02	0.01	2
2006	0.87	0.16	3	0.29	0.04	1	0.04	0.01	4
2007	0.79	0.16	3	0.28	0.05	1	0.13	0.01	4
2008	0.56	0.05	4	0.05	0.01	1	0.59	0.04	3
2009	0.58	0.10	3	0.59	0.04	2	2.39	0.09	3
2010	1.21	0.14	3	0.43	0.06	1	1.46	0.08	4
2011	0.91	0.09	5	0.42	0.03	1	0.45	0.04	3
2012	0.88	0.10	4	0.62	0.07	1	0.15	0.02	3

Figure Captions

Figure 1. Map of the Central Valley, including portions of major rivers accessible to Chinook salmon populations delineated by major regions, major cities and points of interest, and salmon hatcheries relevant to this study.

Figure 2. A schematic representing the various recapture points for CWTs along the salmon life cycle that contribute to the estimation of a SAR for a given CWT group. The colored arrows represent life stage transitions, each with inherent levels of natural mortality. The circle shape represents hatchery release and rectangles represent CWT recoveries. Green-filled shapes represent events that occur in freshwater, and blue-filled shapes represent events that occur in the ocean. While recoveries of 5+ year old salmon are possible, they are extremely rare and therefore not represented in this schematic.

Figure 3. The relationship between winter-run Chinook salmon SAR values (%) and survival from hatchery release to the end of age-2 (%). The solid black line represents the 1:1 line. The black dotted line represents the linear model between these two variables, and the grey shaded area the 95% confidence interval around the linear model. The intercept, slope, r-squared and significance of the linear model is provided in the top left corner of the plot frame.

Figure 4. The range of possible relationships between outmigration survival and marine survival given known CWT release group SAR values for late-fall-run Chinook salmon. Each grey line represents the SAR value for a specific CWT release group, and the point along each line that represents the actual outmigration and marine survival for each release group is unknown, with the exception of the years for which acoustic tagging data outmigration survival estimates existed (black points, respective marine survival estimates with bootstrapped 95% confidence

intervals represented alongside). The black dashed line represents the median SAR for all CWT release groups. The black dotted line represents the location where outmigration and marine survival are equal (i.e., 1:1 line): if a point falls above this line, marine survival was higher than outmigration survival.

Figure 5. The relationship between freshwater outmigration survival (i.e., release to Chipps Island) for acoustic-tagged late-fall-run Chinook salmon release groups and their associated % SAR. The red lines represents 1000 linear models between 1000 parametric bootstrapped samples of these two variables, with the mean r-squared (and bootstrapped 95% confidence intervals) of these models represented in the top left corner of the plot frame.

Figure 6. The relationship between annual SAR and (1) flow during outmigration (a, d, g), (2) upwelling during the first spring at sea (b, e, h), and (3) MOCI during the first spring at sea (c, f, i), for late-fall-run Chinook salmon (a, b, c) winter-run Chinook salmon (d, e, f) and fall-run Chinook salmon (g, h, i). The solid lines in all panels represent the linear model for that relationship, as well as the r-squared value. Note that the r-squared values in plots d and g did not include the OY 2006 because it was determined to be an outlier (datapoint represented in red).

Figure 7. The relationship between the residuals from the flow versus SAR linear model and spring upwelling during the first spring at sea (a, c, e), and between the residuals from the flow versus SAR linear model and spring MOCI during the first spring at sea (b, d, f). The dotted lines in all panels represent the zero line for residuals. The points with the largest negative residual values have been labeled with their year of ocean entry. The closer points fall to the zero line, the better they were predicted by the flow model. The three different runs of Chinook salmon are represented: late-fall-run (a, b); winter-run (c, d) and fall-run (e, f).

Figure 8. The influence of (1) flow during outmigration and spring upwelling during the first year at sea on SAR (a), and (2) flow during outmigration and spring MOCI during the first year at sea on SAR (b). Logit-scale SAR values have been standardized; yellow colors represent low SAR values, and blue colors represent high SAR values. Empty symbols represent the location of actual data that were interpolated across; size of these symbols increase proportionally with standardized SAR values. Solid black symbols represent conditions experienced by cohorts for which SAR values are not yet available, spanning OY 2014-2017. Square symbols represent late-fall-run Chinook salmon, circle symbols are for fall-run Chinook salmon, and triangle symbols are for winter-run Chinook salmon (no point exists for OY 2015 fall-run because no CNFH salmon were released in the river that year).

Figure 1.

Figure 2.

$y = 0.67 + 1.11x$, $r^2 = 0.97$, $p < 0.001$
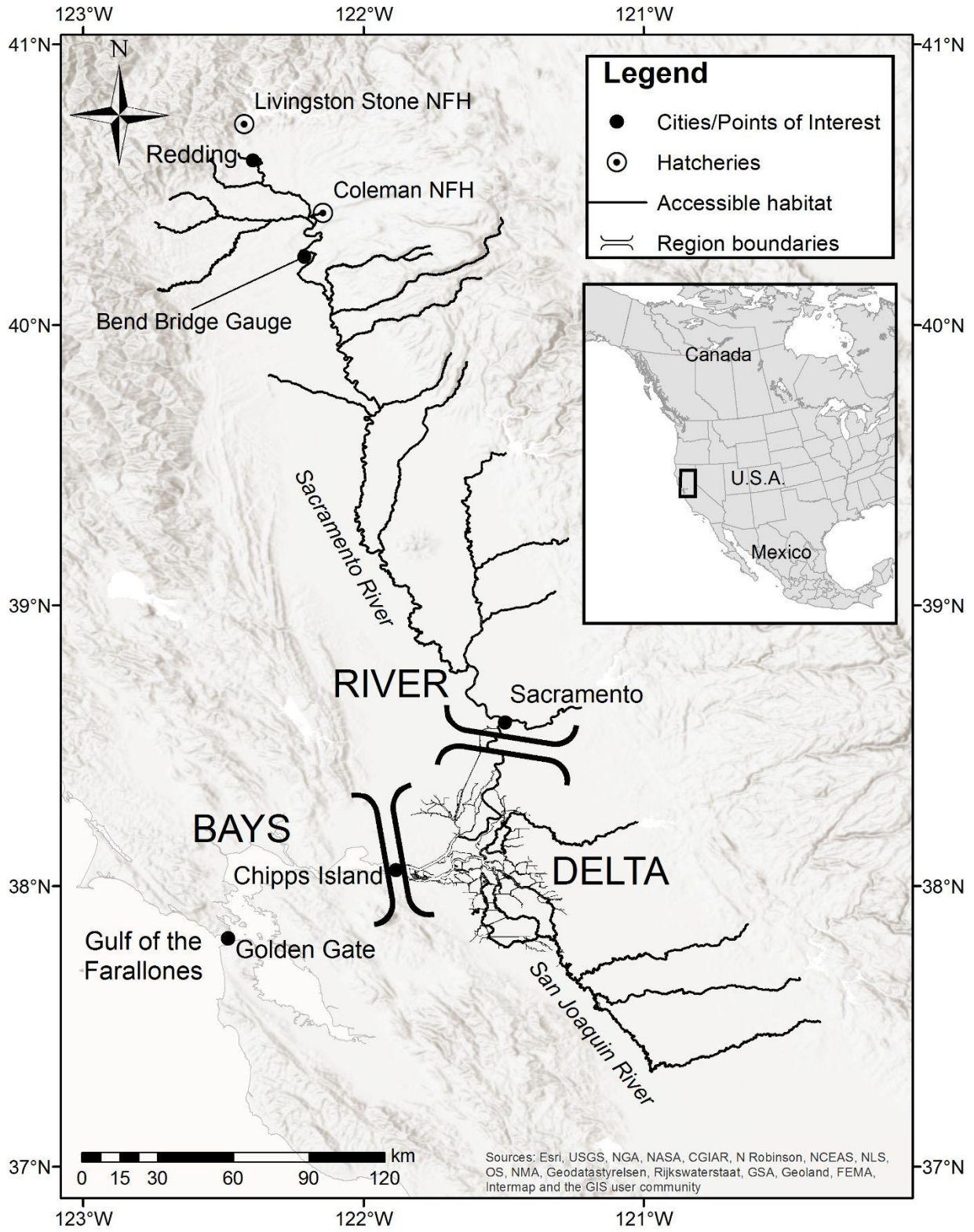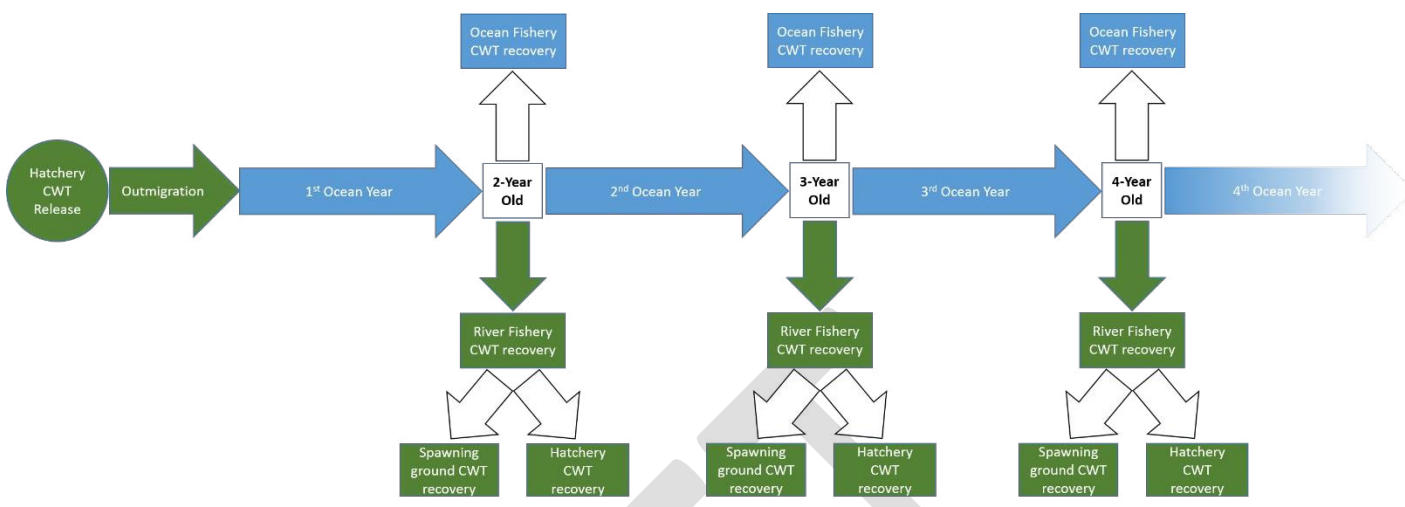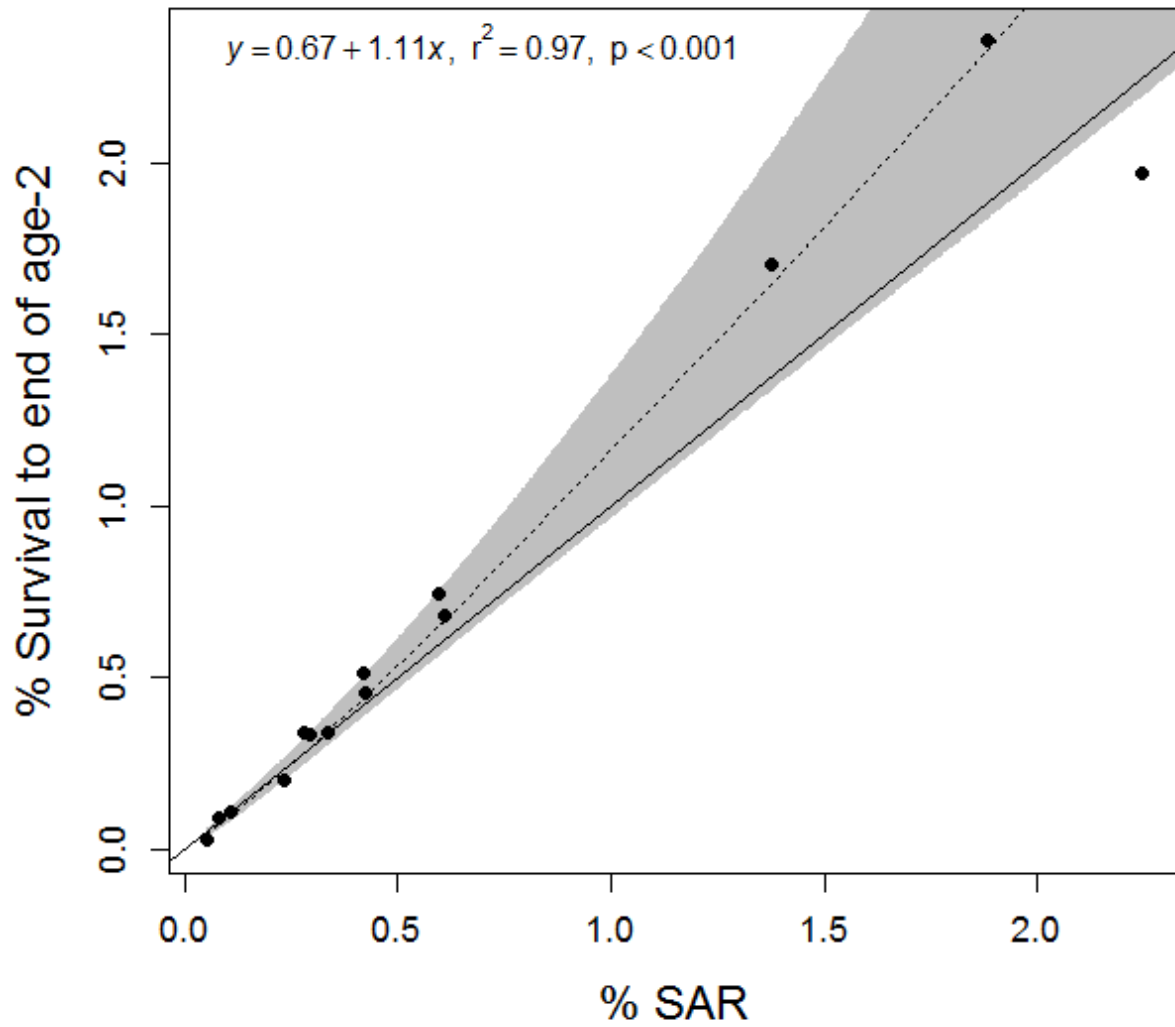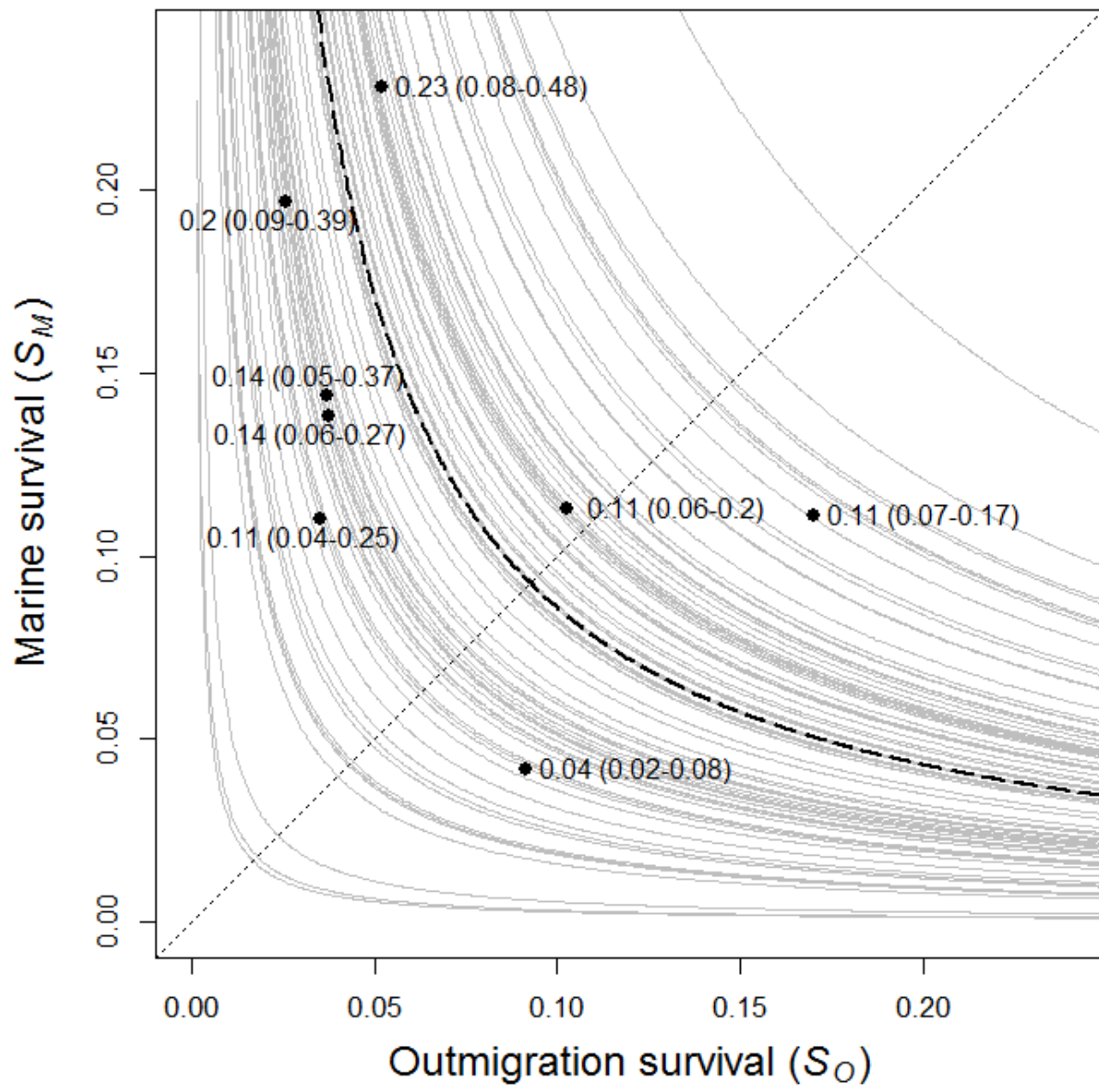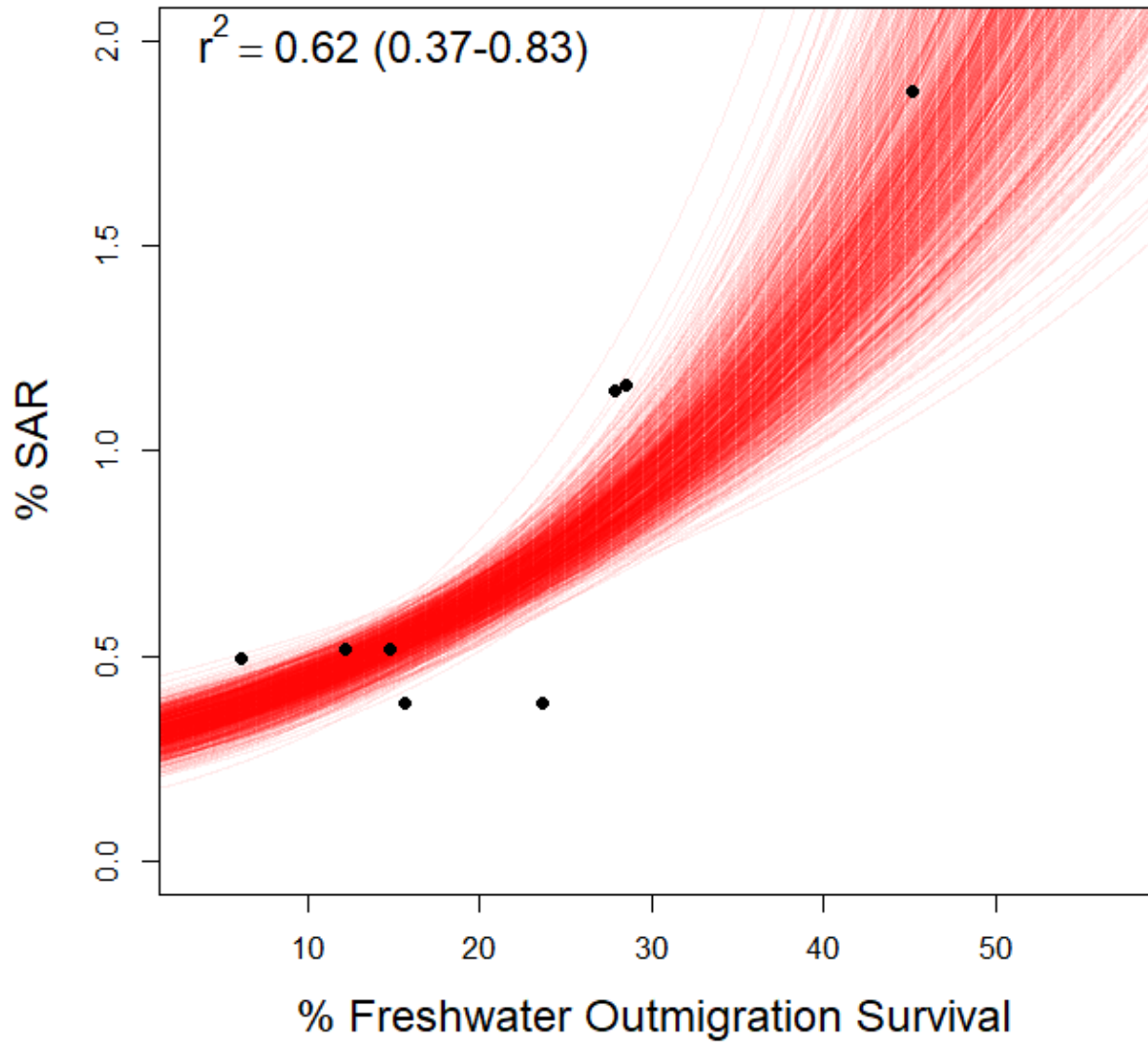
Figure 3.

Figure 4.

Figure 5.

Figure 6.

Figure 7.

Figure 8.

NRC Research Press

ARTICLE

Fishery collapse, recovery, and the cryptic decline of wild salmon on a major California river

Malte Willmes, James A. Hobbs, Anna M. Sturrock, Zachary Bess, Levi S. Lewis, Justin J.G. Glessner, Rachel C. Johnson, Ryon Kurth, and Jason Kindopp

Abstract: Fall-run Chinook salmon (*Oncorhynchus tshawytscha*) from the Sacramento–San Joaquin River system form the backbone of California's salmon fishery and are heavily subsidized through hatchery production. Identifying temporal trends in the relative contribution of hatchery- versus wild-spawned salmon is vital for assessing the status and resiliency of wild salmon populations. Here, we reconstructed the proportion of hatchery fish on natural spawning grounds in the Feather River, a major tributary to the Sacramento River, using strontium isotope ($^{87}Sr/^{86}Sr$) ratios of otoliths collected during carcass surveys from 2002 to 2010. Our results show that prior to the 2007–2008 salmon stock collapse, 55%–67% of in-river spawners were of hatchery origin; however, hatchery contributions increased drastically (89%) in 2010 following the collapse. Data from a recent hatchery marking program corroborate our results, showing that hatchery fish continued to dominate (~90%) in 2011–2012. Though the rebound in abundance of salmon in the Feather River suggests recovery of the stock po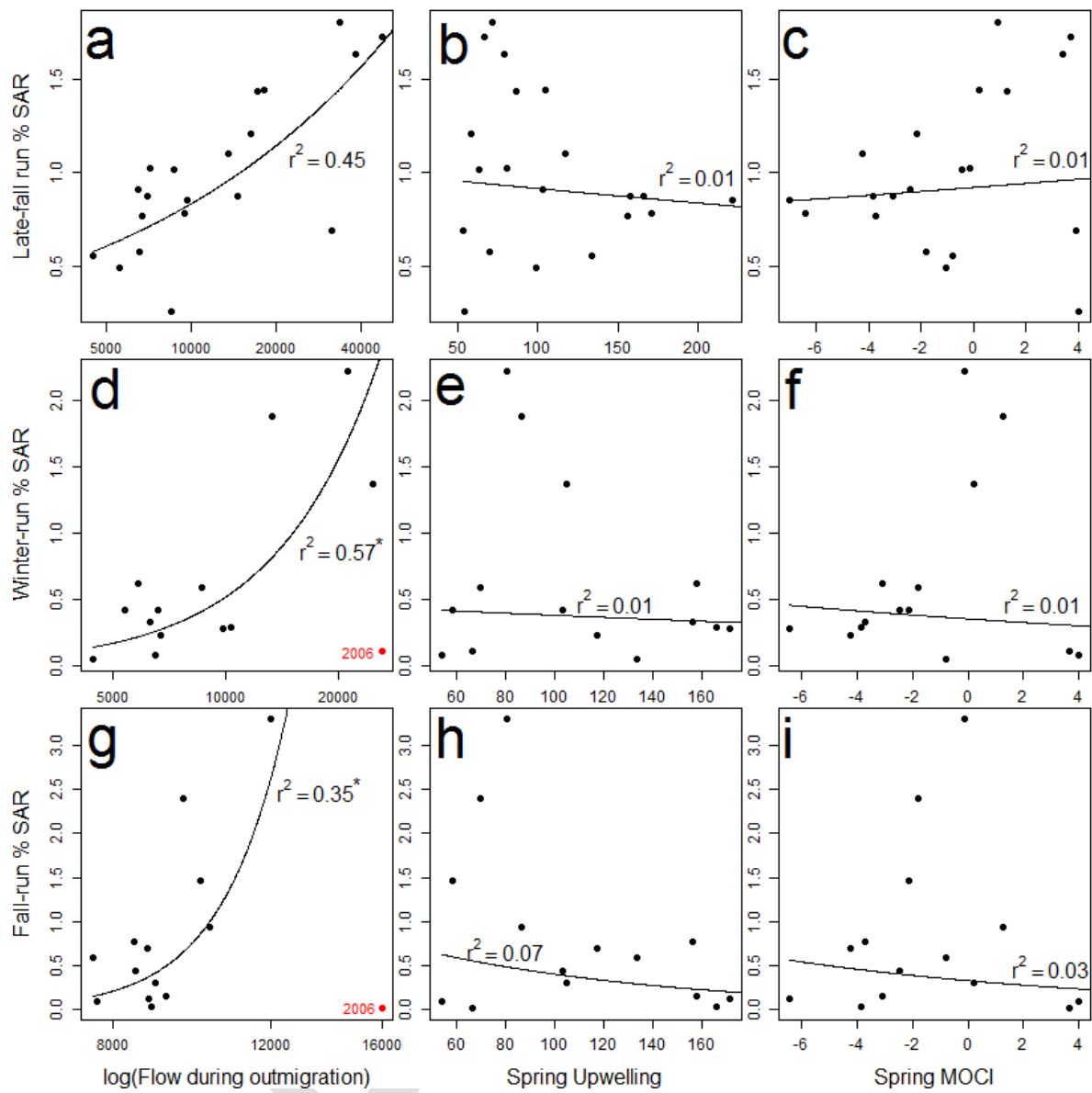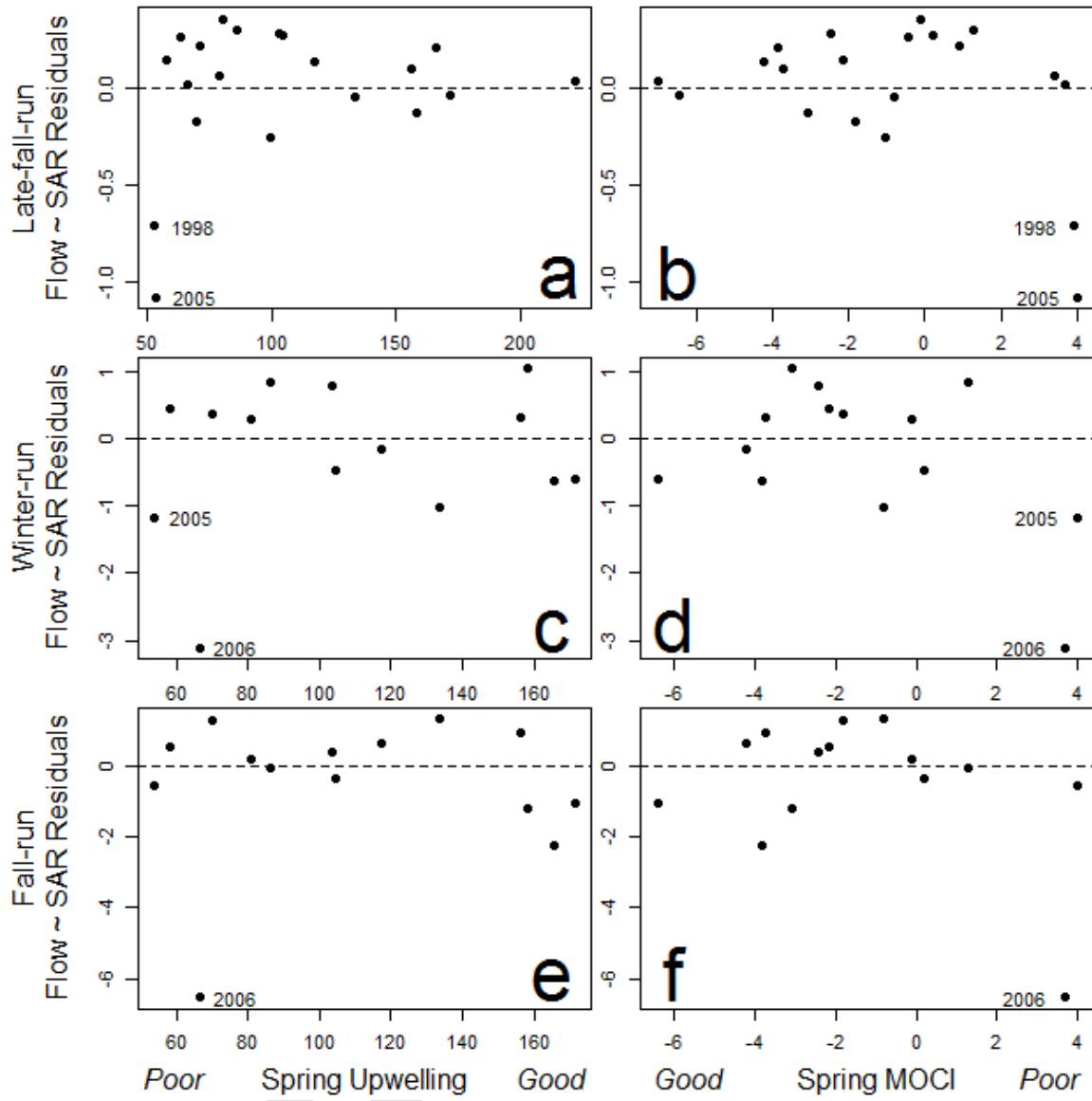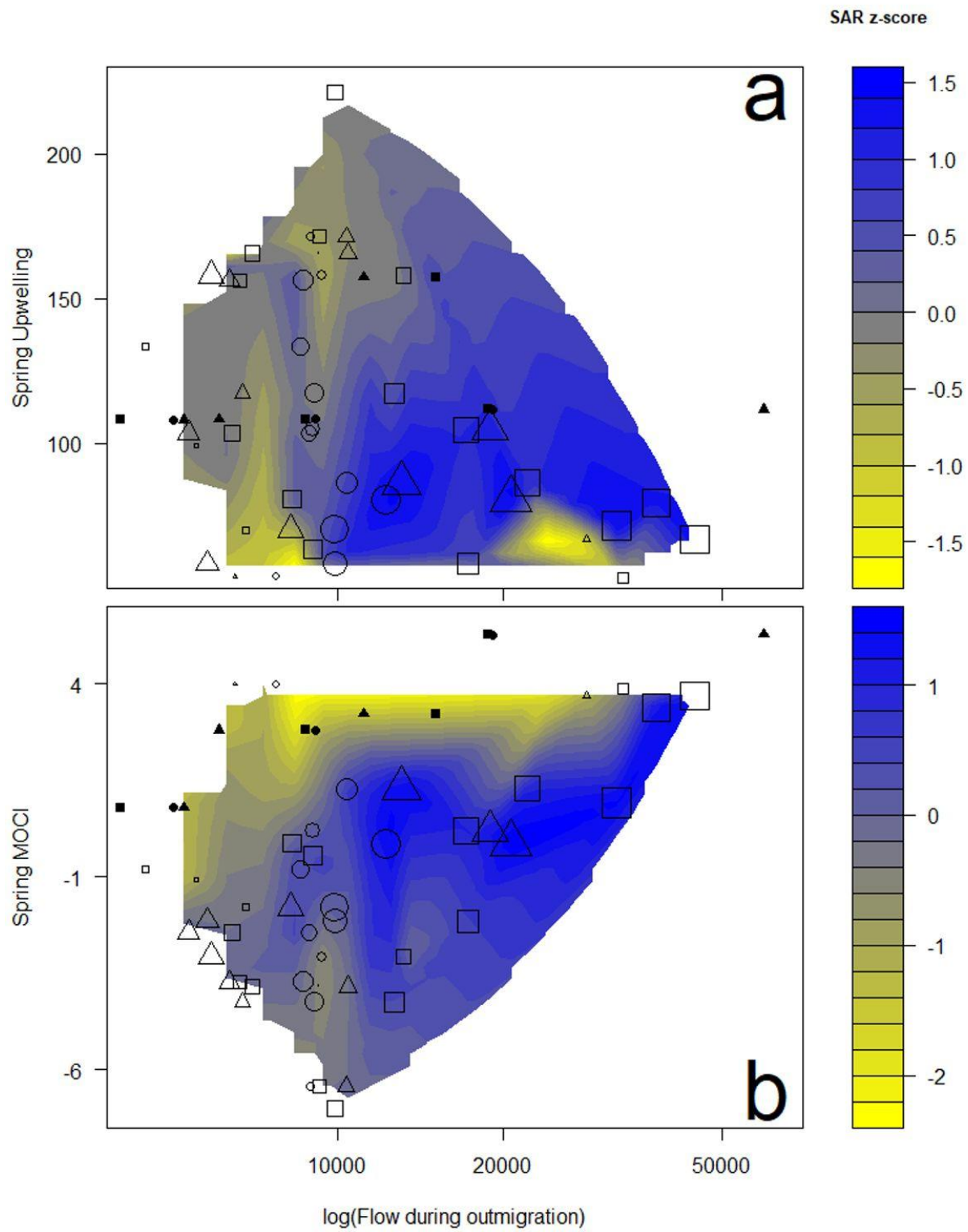stcollapse, our otolith chemistry data document a persistent decline of wild spawners, likely leading to the erosion of locally adapted Feather River salmon populations.

Résumé : Les saumons quinnats (*Oncorhynchus tshawytscha*) à migration automnale du réseau du fleuve Sacramento et de la rivière San Joaquin forment l'épine dorsale de la pêche aux saumons en Californie et sont fortement soutenus par la production en alevinières. La détermination des tendances dans le temps des apports relatifs de saumons issus d'alevinières et de saumons nés dans la nature est cruciale pour évaluer l'état et la résilience des populations de saumons sauvages. Nous avons reconstitué la proportion de poissons issus d'alevinières dans des aires de frai naturelles dans la rivière Feather, un important affluent du fleuve Sacramento, en utilisant les rapports d'isotopes de strontium ($^{87}Sr/^{86}Sr$) d'otolites prélevés durant des relevés de carcasses de 2002 à 2010. Les résultats montrent que, avant l'effondrement des stocks de saumons de 2007–2008, de 55 % à 67 % des frayeurs dans la rivière provenaient d'alevinières; toutefois, l'apport d'alevinières a connu une augmentation très marquée (89 %) en 2010 dans la foulée de l'effondrement. Les données tirées d'une campagne récente de marquage en alevinière corroborent ces résultats, démontrant que les poissons issus d'alevinières sont toujours prédominants (~90 %) en 2011–2012. Si la remontée de l'abondance des saumons dans la rivière Feather semble indiquer un rétablissement du stock à la suite de l'effondrement, nos données sur la chimie des otolites documentent un déclin soutenu des géniteurs sauvages, qui mène vraisemblablement à l'érosion des populations de saumons adaptées aux conditions locales de la rivière Feather. [Traduit par la Rédaction]

Introduction

The Sacramento–San Joaquin River system in California's Central Valley (CV) is the foundation of California's water supply, providing water for approximately 35 million residents and supporting a multibillion dollar agriculture industry, and is home to the southernmost spawning runs of Chinook salmon (*Oncorhynchus tshawytscha*) in the Northern Hemisphere (Fisher 1994; Yoshiyama et al. 1998; Moyle 2002; Williams 2006). Chinook salmon populations have persisted in California's highly variable Mediterranean climate by exhibiting a diverse portfolio, expressed as distinct run types (spring, fall, late-fall, winter) and plastic life history strategies (Yoshiyama et al. 1998; Hilborn et al. 2003; Williams 2006), which buffers population abundance against stochastic environmental variability. However, habitat loss and degradation, water

diversions, fish harvest, and the construction of dams, which blocked large areas (>80%) of spawning habitat and rearing grounds, have resulted in population decline threatening the long-term survival of salmon in the CV (Yoshiyama et al. 2000, 2001). Spring- and winter-run Chinook salmon are listed as threatened and endangered, respectively, under the federal Endangered Species Act (NMFS 1999, 2005), while fall–late-fall-run salmon are considered species of concern and are targeted for harvest in the ocean fishery.

Hatcheries were built along CV tributaries to mitigate for dam construction and habitat loss, and many salmon populations in the CV are heavily subsidized by hatchery production (HSRG 2012, 2014; Palmer-Zwahlen and Kormos 2015). Fall-run Chinook salmon from the Sacramento–San Joaquin River system form the backbone of California's ocean salmon fishery, contributing sub-

M. Willmes, J.A. Hobbs, Z. Bess, and L.S. Lewis. University of California Davis Wildlife, Fish and Conservation Biology, One Shields Avenue, Davis, CA, 95616, USA.
A.M. Sturrock. University of California Davis Center for Watershed Sciences, One Shields Avenue, Davis, CA, 95616, USA.
J.J.G. Glessner. University of California Davis Interdisciplinary Center for Plasma Mass Spectrometry, Davis, CA 95616, USA.
R.C. Johnson. University of California Davis Center for Watershed Sciences, One Shields Avenue, Davis, CA, 95616, USA; Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 McAllister Way, Santa Cruz, CA 95060, USA.
R. Kurth and J. Kindopp. Department of Water Resources, Division of Environmental Services, 460 Glen Drive, Oroville, CA 95966, USA.
Corresponding author: Malte Willmes (email: mwillmes@ucdavis.edu).

Pagination not final (cite DOI) / Pagination provisoire (citer le DOI)

2

Can. J. Fish. Aquat. Sci. Vol. 00, 0000

Fig. 1. Fall-run escapement estimates for the Sacramento River System (grey) and the Feather River (hatchery and in-river spawning population; black) from 1975 to 2016. Data from GrandTab2017.04.07, California Central Valley Chinook Population Database Report. An asterisk (*) indicates that there is no in-river escapement data available for 1990, 1998, and 1999 for the Feather River.
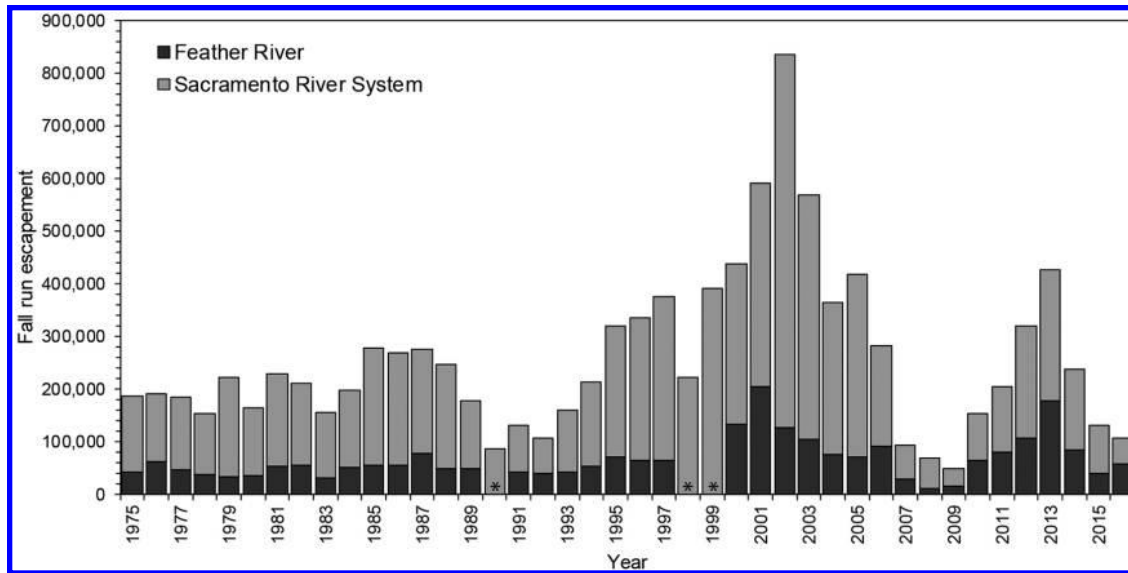
stantially to the fisheries off Oregon and Washington (Lindley et al. 2009; Satterthwaite et al. 2015), and are an integral part of the present and past culture in this region (Yoshiyama et al. 1998). However, wild stocks in several California rivers are now dominated by hatchery fish (Barnett-Johnson et al. 2007; Johnson et al. 2012; Quiñones and Moyle 2014), potentially eroding the long-term resiliency of wild, locally adapted populations by disrupting selection for heritable traits that improve lifetime reproductive success in variable environments.

In 2007, record low numbers of adult salmon returned to the CV (Fig. 1), and forecasted low escapement resulted in the closure of the commercial ocean fishery off the coast of California and Oregon in 2008 and 2009 for the first time in over 100 years, causing major economic impact (Schwarzenegger 2008; Michael 2010). While the proximate cause of this stock collapse was attributed to low food availability in the coastal ocean in spring 2005 and 2006 (Lindley et al. 2009), the effect of hatchery practices likely contributed to a weakened CV salmon portfolio through increasing synchrony in fall-run population dynamics, further exacerbating the impact of climatic variability (Satterthwaite and Carlson 2015). After 2009, Chinook salmon fall-run escapement numbers rebounded, suggesting a quick and successful recovery of the salmon stock, before the decreases in 2014 and 2015 that were potentially linked to the recent prolonged drought period (Dettinger and Cayan 2014). Owing to the continued declines in wild salmon abundance, lack of hatchery management reform, and impending climate change, the fate of wild salmon in California are in jeopardy, and extinction in the wild is deemed likely if drastic management actions are not taken (Katz et al. 2012; Franks and Lackey 2015; Moyle et al. 2017).

Effective management, monitoring, and status assessment of wild salmon populations require reliable estimates of hatchery fish abundance on the natural spawning grounds (Araki et al. 2008; HSRG 2012, 2014; Christie et al. 2014; Quiñones et al. 2014). However, only recently have hatchery fish been consistently physically marked (adipose fin clip) and tagged (coded wire tags) in California rivers (Lindley et al. 2007; HSRG 2014). The California Constant Fractional Marking Program (CFM) began marking 25% of fall-run hatchery releases in 2007, providing a method to estimate hatchery contributions to natural spawning grounds since 2010 (Kormos et al. 2012; Palmer-Zwahlen and Kormos 2013, 2015). The results of the CFM program showed that most CV rivers have

a high contribution of hatchery-origin fish in their natural spawning grounds, particularly those co-located with hatcheries, such as the Feather River (Palmer-Zwahlen and Kormos 2013). However, the CFM data cannot provide estimates prior to 2010 and thus does not inform stock composition prior to and during the salmon stock collapse. Without such estimates, it is impossible to quantify trends in the abundance of natural-origin fish (Johnson et al. 2012) or to evaluate population extinction risk (Lindley et al. 2007; Katz et al. 2012). Ultimately, understanding the extent of gene flow between hatchery- and natural-origin spawners is critical, since the influence of too many hatchery adults can reduce the fitness of subsequent generations in the wild (Waples 1991; McGinnity et al. 2003; Araki et al. 2008; Christie et al. 2014).

A variety of methods have been used to discriminate between hatchery- and natural-origin salmonids, including physical tags (Palmer-Zwahlen and Kormos 2015), genetics (Hauser et al. 2006), otolith microstructure (Barnett-Johnson et al. 2007), and otolith chemistry (Johnson et al. 2012, 2016). Otoliths (i.e., ear stones) consist of calcium carbonate and are found in the inner ear of bony fishes. They are metabolically inert and accrete continuously, producing a unique record of fish age and growth. Chemical elements from the environment are incorporated into the otolith, resulting in a chemical composition that can reflect the habitat occupied during deposition (Campana 1999). Strontium (Sr) is readily substituted for calcium in the mineral lattice, resulting in element concentrations and isotope ratios ($^{87}Sr/^{86}Sr$) that reflect environmental abundances and are frequently used to reconstruct individual movements (Rooker et al. 2001; Walther and Limburg 2012). In the CV, $^{87}Sr/^{86}Sr$ can be a powerful natural tag of fish origin, because the water $^{87}Sr/^{86}Sr$ isotope ratios vary among many of the salmon-producing rivers and hatcheries (Ingram and Weber 1999; Barnett-Johnson et al. 2008; Sturrock et al. 2015).

Here, we use otolith $^{87}Sr/^{86}Sr$ isotope ratios to identify natal origin of adult Chinook salmon spawning in the Feather River to determine the annual contribution of hatchery-produced fish to escapement years 2002–2010, encompassing the years of stock collapse and recovery. We refer to individuals that reared in the river as wild fish and fish that reared in the hatchery as hatchery fish, independent of their parental or genetic origin. Furthermore, we focused only on phenotypic fall-run salmon, defined as returning to in-river spawning grounds after 1 September, and did not examine the genetic run identity of these fish.

Fig. 2. Overview map of the study region and the hatcheries producing Chinook salmon. The Feather River is further divided into the High Flow and Low Flow channels. Data from the National Hydrography Dataset, US Geological Survey.
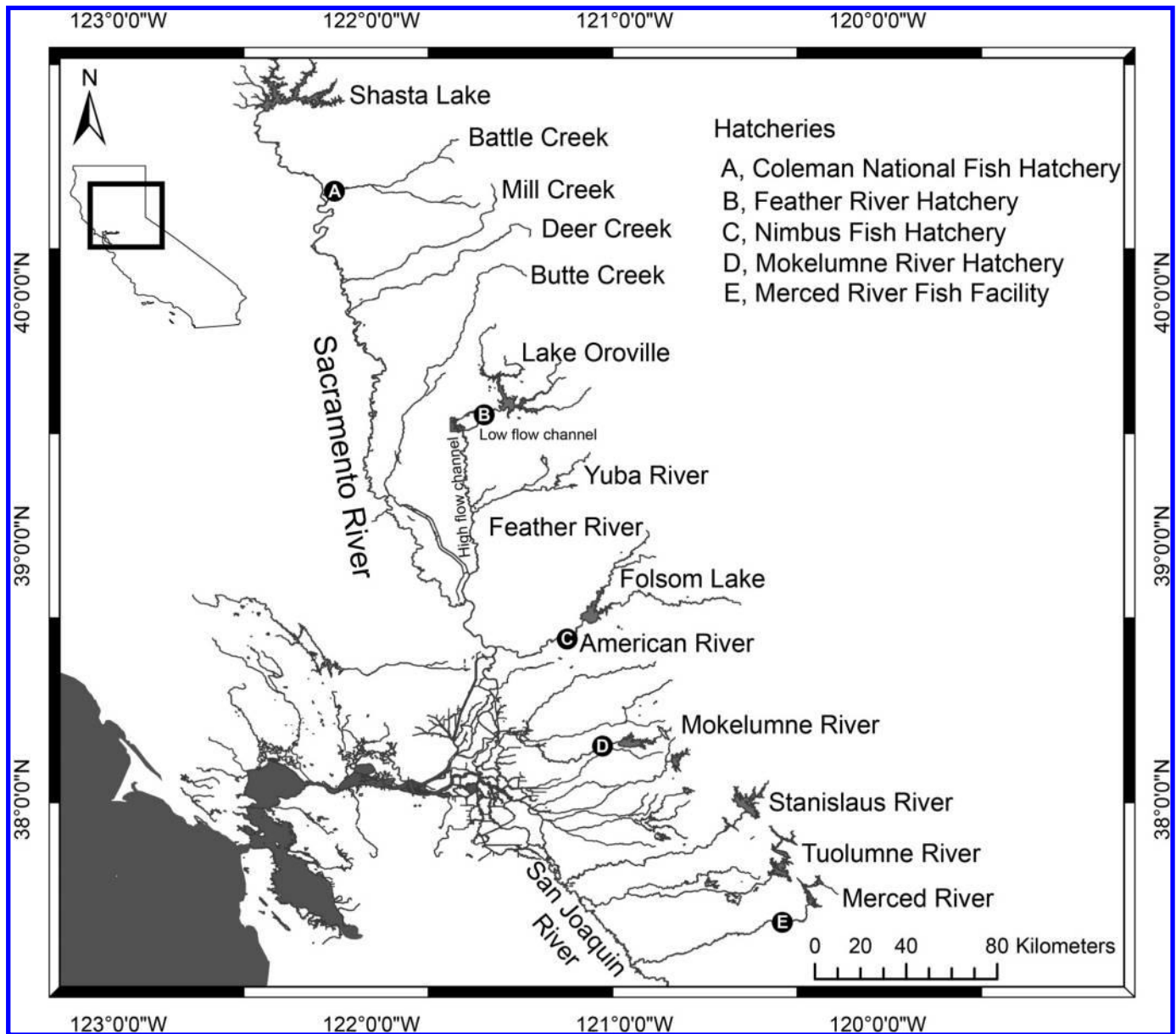
Materials and methods

The Feather River

The Feather River Basin is located in the foothills of the western Sierra Nevada (Fig. 2). The basin is a major contributor to the California State Water Project, and Lake Oroville, created by the completion of Oroville Dam in 1967, plays an important role in flood management, water storage, water quality, power generation, and recreation. The Fish Barrier Dam represents the uppermost barrier to upstream fish migration, as well as the location of the fish ladder entering the Feather River Hatchery (FRH). In addition to the main hatchery, there is an annex hatchery located along Highway 99, about 2 km south of Oroville Dam Blvd., with warmer water temperatures that provide opportunities for increased growth rates.

The Feather River Hatchery is one of the largest producers of CV Chinook salmon, supporting both spring- and fall-run populations (Fisher 1994; Yoshiyama et al. 1998). Historically, spring-run salmon returned from the ocean in spring–early summer and then held over summer and spawned in the uppermost reaches of small tributaries to the Feather River, while fall-run fish returned later in the fall and spawned in the lower foothill reaches of the mainstem river. Spawning for both populations is concentrated in approximately 12 river kilometres below Oroville Dam (Mercer and Kurth 2014). Hatchery broodstock management has attempted to separate the two runs; however, considerable mixing has occurred, resulting in substantial genetic introgression (Clemento et al. 2014; Meek et al. 2016*b*), and spring-run fish have hybridized with fall-run fish, resulting in overlapping run timings and frequent examples of "run-switching" between parents and offspring (Sommer et al. 2001).

The FRH maintains an integrated hatchery program resulting in considerable mixing of hatchery and wild fish in the fall-run hatchery broodstock and in-river spawning population (Williamson and May 2005; HSRG 2012). To reduce in-river mortality during seaward migration, juveniles produced by the FRH (and many other hatcheries in the CV) are trucked directly to San Pablo Bay

Pagination not final (cite DOI) / Pagination provisoire (citer le DOI)

4

Can. J. Fish. Aquat. Sci. Vol. 00, 0000

Table 1. Number of otoliths sampled and analyzed by recovery location (High Flow and Low Flow channels).

Year	Population estimates			Analyzed otoliths			Proportion of population sampled by otoliths		
	High Flow	Low Flow	Total	High Flow	Low Flow	Total	High Flow	Low Flow	Total
2002	34 125	71 038	105 163	41	70	111	0.15	0.12	0.13
2003	37 643	52 303	89 946	41	54	95	0.11	0.10	0.11
2004	17 113	37 058	54 171	35	64	99	0.24	0.17	0.19
2005	12 583	36 577	49 160	33	70	103	0.27	0.19	0.21
2006	16 990	59 424	76 414	23	49	72	0.14	0.08	0.09
2007	876	21 033	21 909	33	76	109	3.78	0.36	0.50
2008	297	5 642	5 939	27	62	89	9.09	1.10	1.50
2009	223	4 624	4 847	7	38	45	3.14	0.80	0.91
2010	2 201	42 713	44 914	4	28	32	0.18	0.07	0.07

Note: Population estimates are from GrandTab2017.04.07, California Central Valley Chinook Population Database Report and California Department of Water Resources (unpublished data, contact Jason.Kindopp@water.ca.gov).

and acclimatized in net pens prior to release. Since 2000, FRH has released 80%–100% of its fall-run production directly into the San Francisco Estuary or Bay (Huber and Carlson 2015). Because of a lack of olfactory imprinting during juvenile emigration, juveniles that are trucked stray disproportionately as adults to other rivers, resulting in increased gene flow among salmon populations (Palmer-Zwahlen and Kormos 2013, 2015; Huber and Carlson 2015; Meek et al. 2016a). Hatchery fish are also released over a relatively short time window, leading to reduced diversity in emigration phenology and increased risk of mismatch with optimal ocean conditions (Satterthwaite et al. 2014; Huber and Carlson 2015).

Otolith collection

Otoliths were collected from postspawned Chinook salmon between 2002 and 2010 as part of the annual carcass survey. For this survey, the Feather River is divided into 40 stream sections, each section corresponding to a single riffle–pool complex. The Low Flow Channel includes the Feather River from the Fish Barrier Dam to the Thermalito Outlet, and the High Flow Channel extends from the Thermalito Outlet downstream to the Gridley Bridge (Fig. 2). Otoliths were collected from a total of 50 fish per week, among 10 river sections randomly selected each week, five in the Low Flow Channel and five in the High Flow Channel. To ensure that these fish are representative of the overall population, the first five salmon carcasses, irrespective of size, sex, and presence or lack of adipose fin, were sampled within each of these randomly selected locations. This stratification of the river into sections ensures that the entire river's spawning grounds are surveyed equally (Table 1).

From this set of collected fish, a subset ($n = 755$) was selected for otolith analysis in proportion to fish abundances in the High Flow and Low Flow channels for each year. However, this was not possible for all years, leading to an uneven sample distribution between the High Flow and Low Flow channels. We used the escapement estimates for each recovery location as a weighting factors to incorporate this variation in subsampling into our estimations of hatchery and wild contributions to the overall escapement. In addition to these stratified samples, fish with coded wire tags (CWT, $n = 110$) were randomly selected and used to validate the otolith isotope assignments (natal origins).

Otolith sample preparation

Sagittal otoliths were extracted from each fish, cleaned, dried, labeled, and transferred to the Department of Wildlife, Fish, and Conservation Biology, University of California Davis. Otoliths were mounted in Epocure (Buehler Scientific) epoxy resin and thin-sectioned with an Isomet diamond cutting saw in the transverse plane. Thin sections were adhered to glass microscope slides with Crystal Bond thermoplastic resin (Crystalbond 509, Ted Pella Inc., Redding, California), sanded to the core on both sides with 1200–2000 grit sandpaper, and polished with 0.3 µm alumina and a polishing cloth, following methods from Wells et al. (2003).

Digital images of otoliths were taken at 6× magnification on a CH30 Olympus compound microscope. Otoliths sections were washed with 1 mol·L⁻¹ chemical grade nitric acid for 5 to 10 s, rinsed in an ultrasonic water bath for 5 min, and dried under a class 100 laminar flow hood.

Otolith aging

Otoliths contain a unique time series of opaque and translucent bands that are deposited on a daily and seasonal basis in response to photoperiod, temperature, diet, and endogenous rhythms (Neilson and Geen 1982; Campana and Neilson 1985). On adult otoliths, an opaque zone followed by a translucent zone (Fig. 3) represents 1 year of otolith growth (Welch et al. 1993). Annual ages were estimated from digital images along the transverse plane of the ventral lobe (Fig. 3), counting the summer bands. We used the transverse section instead of the sagittal preparation typically used for juvenile habitat use and growth reconstructions (Woodson et al. 2013; Sturrock et al. 2015) to preserve the outer rings in the convex adult otoliths. Otoliths that were completely vateritic, or broken along the ventral lobe by the sanding process, were not aged. Ages were validated by comparing age counts with those of hatchery fish with physical tag information and known age ($n = 74$) and between two age readers following the methods proposed by Campana (2001) and using the FSA package (Ogle 2018) in R (R Core Team 2017). All fish were aged as either 2-, 3-, 4-, or 5-year-olds, consistent with the currently understood life history of the species (Fisher 1994).

Otolith Sr isotopic analysis

For laser ablation, otoliths were remounted on petrographic glass slides, with 20 individual otoliths per slide. ⁸⁷Sr/⁸⁶Sr isotope ratios were measured at the University of California Davis Interdisciplinary Center for Plasma Mass Spectrometry. For the in situ Sr isotope analysis, an Nd:YAG 213 nm laser (New Wave Research UP213) was coupled to a Nu Plasma HR MC-ICP-MS (Nu032). A laser beam of 55 µm diameter was traversed across the otolith from the core to the edge at 10 µm·s⁻¹, with the laser pulsing at 10 Hz frequency and 5–15 J·cm⁻² photon output. The ⁸⁷Sr/⁸⁶Sr isotope ratio was normalized for instrumental mass discrimination by monitoring the ⁸⁶Sr/⁸⁸Sr isotope ratio (assuming ⁸⁶Sr/⁸⁸Sr = 0.1194), and ⁸⁷Rb was corrected by monitoring the ⁸⁵Rb signal. Krypton interference originating in the argon supply (⁸⁶Kr) was subtracted using the on peak zero method before each analysis. Kr contribution was monitored throughout the analyses, as increasing amounts of Kr would lead to an increased uncertainty of the individual measurement. Operating conditions and reproducibility of standards on the LA-MC-ICP-MS were evaluated using a modern marine coral from the South China Sea and a modern marine otolith from a white seabass (*Atractoscion nobilis*) collected offshore of Baja California. Replicate analyses for the coral yielded a mean ($\pm 2\sigma$) ⁸⁷Sr/⁸⁶Sr isotope ratio of 0.70921 ± 0.00008 ($n = 61$) and for the

Fig. 3. (A) Image of a transverse section of an adult otolith in transmitted light, showing growth increments used to estimate ages as well as the laser trajectory (white dotted line) from the strontium isotopic analysis. (B) Corresponding $^{87}Sr/^{86}Sr$ isotope profile with a loess smooth (span = 0.1) applied; grey bands represent the 95% confidence intervals. Green box indicates the approximate region used for the natal origin assignment. [Colour online.]
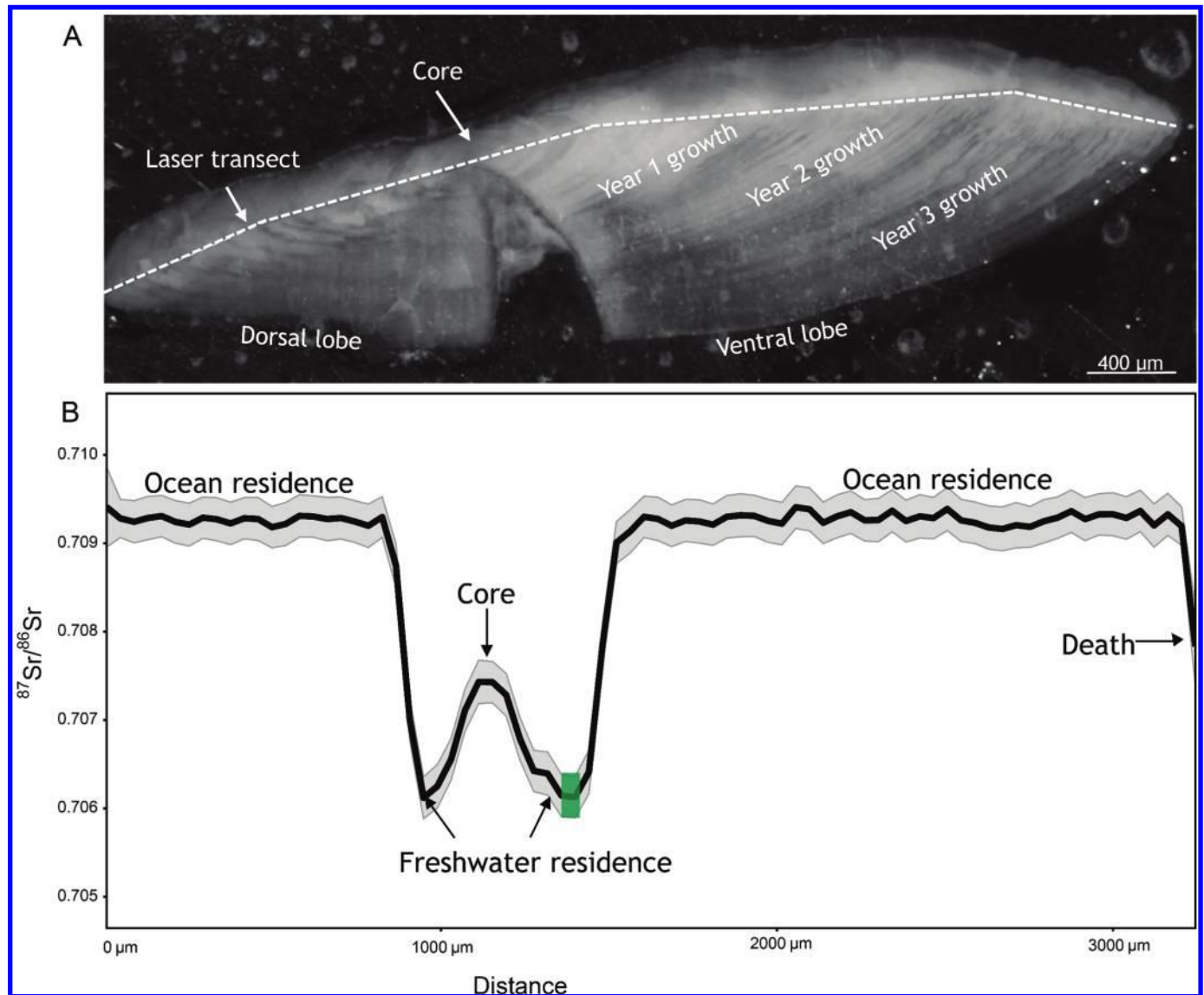
otolith of 0.70919 ± 0.00003 ($n = 63$). These values are in good agreement with the mean modern $^{87}Sr/^{86}Sr$ isotope value of seawater, 0.70918 (McArthur et al. 2001).

Baseline Sr isotope data

The $^{87}Sr/^{86}Sr$ isotope ratio baseline for the Sacramento River System was compiled from published data (Ingram et al. 1999; Barnett-Johnson et al. 2008; Sturrock et al. 2015) and newly collected water and otolith samples of known origin from five locations along the Feather River, from the FRH, and from the Thermalito Annex.

Water samples were collected at base flow conditions during the fall of 2013, in the direct flow of water using 50 mL polypropylene tubes, acidified with 1 mol·L⁻¹ nitric acid and filtered with a 0.45 μm filter. The samples were transported to a class 100 clean room facility at the UC Davis Interdisciplinary Center for Plasma Mass Spectrometry. An aliquot of each water sample was made at a volume totaling approximately 1 μg of Sr. This volume was evaporated to dryness in an acid-leached polytetrafluoroethylene

(Teflon) vial on a hotplate, and Sr was isolated from all other aqueous constituents by selective ion exchange chromatography (Horwitz et al. 1992). Sr separates were reconstituted in 2% HNO_3 and introduced in the MC-ICP-MS (Nu Plasma HR) using a desolvating nebulizer introduction system (Nu Instruments DSN-100). $^{87}Sr/^{86}Sr$ data were internally normalized by the measured $^{86}Sr/^{88}Sr$ ratio (assuming $^{86}Sr/^{88}Sr = 0.1194$). ^{85}Rubidium was monitored to correct for ^{87}Rb if present, but all were well below the Rb correction threshold due to the selective ion exchange chromatography beforehand. $^{84}Sr/^{86}Sr$ was monitored to estimate the $^{84}Kr/^{86}Kr$ isotope ratio. ^{86}Kr was subtracted until the $^{84}Sr/^{88}Sr$ ratio equalled the canonical value of 0.006755, while iterating the mass-bias correction. Procedural blank was measured and contributed <0.002% of total Sr processed per sample. Replicated analyses of NIST SRM 987 were conducted every six samples, normalizing for instrument drift over the course of the day and for analytical artifacts among sessions. An in-house modern marine coral standard was processed in parallel with water samples and

resulted in a mean (2σ) $^{87}Sr/^{86}Sr$ isotope ratio of 0.70918 ± 0.00002 ($n = 8$).

Sr isotope ratios from the natal region of hatchery-reared otoliths (Fig. 3) were analyzed by LA-MC-ICP-MS, following the same protocols as the samples collected from the spawning grounds, to determine the range of isotope ratios indicative of rearing in the FRH. We examined otoliths from 10 fall-run Chinook salmon reared at the Feather River's main hatchery facility in two raceways collected on 19 April 2012 and ranging in fork length from 43 to 78 mm and 10 fish reared at the Thermalito Annex from two raceways removed on 19 March 2012 and ranging in fork length from 88 to 90 mm.

Natal origin assignments

To assign natal origin, the otolith material deposited immediately following onset of exogenous feeding (i.e., with no isotopic influence of the maternal yolk) was visually identified in the Sr isotope profile and matched to the distance from the otolith core (typically ~250 μm). The mean $^{87}Sr/^{86}Sr$ isotopic ratio for this natal portion of the profile (Fig. 3) was then assigned to a source location by matching it to the established Sr isotopic baseline for the Sacramento River System (Ingram and Weber 1999; Barnett-Johnson et al. 2008) using single-factor quadratic discriminant function analysis (QDFA) in R (R Core Team 2017). We used the quadratic function instead of a linear function because it relaxes the assumption that all the variances of the $^{87}Sr/^{86}Sr$ values from groups are the same. There are some $^{87}Sr/^{86}Sr$ overlaps between natal sources in the San Joaquin and Sacramento basins (particularly Mokelumne versus Feather River Hatcheries and Merced versus Yuba rivers; Sturrock et al. 2015), which could result in strays from the San Joaquin basin potentially being misclassified by our Sacramento-focused QDFA. However, given the large production differences among basins, San Joaquin origin strays have little numerical effect, with the combined contribution of Merced and Mokelumne Hatchery strays to the Feather River and FRH escapements being <1% in 2010–2012 (Kormos et al. 2012; Palmer-Zwahlen and Kormos 2013, 2015). Given that CV hatchery fish are likely to stray at much higher rates than natural-origin fish due to the extensive trucking program, we assumed that the potential error rate attributable to misclassified San Joaquin origin strays was below 1%. We made no attempt to adjust prior probabilities in the QDFA based on annual hatchery production estimates.

Otolith subsample sizes among weekly surveys and channel strata were too small to calculate proportion of hatchery fish at fine spatial and temporal scales; therefore, samples were pooled by survey year retaining the stratification by High Flow and Low Flow channels. To provide a robust estimate of the proportion of hatchery-origin fish on the spawning grounds, we estimated the mean and standard deviation using bootstrapping with 1000 iterations and sample sizes equal to the number of otoliths collected in each channel for each year. The annual contribution and number of hatchery-origin fish on the spawning grounds was estimated by expanding the bootstrapped mean proportion by the escapement estimates in the High Flow and Low Flow channels for each year. The accuracy of our hatchery classifications was evaluated using otoliths of known hatchery origin ($n = 110$) that were included in the sample set without prior decoding of their origin.

Emigration timing

To investigate the difference in timing of ocean entry of wild- and hatchery-origin fish, we compared fall-run hatchery release data from Huber and Carlson (2015) with catch data from the USFWS Chipps Island Midwater Trawl Survey. The hatchery release data were filtered to include only fall-run FRH-produced fish that were released into San Pablo Bay from 2002 to 2012 and normalized for each day of the year by the total number of fish released that year. Chipps Island Survey data was filtered to include only fall-run sized, unmarked fish captured in 2002–2012 and then normalized

for each Julian day using catch per unit effort and total catch for that year. Note that the latter will therefore include unmarked hatchery fish released upstream of Chipps Island, for example from the Coleman National Fish Hatchery (75% unmarked), and thus likely represents a lower estimate for the true emigration timing variability of wild fish. This allows us to compare emigration timing irrespective of differences in interannual abundance.

Results

Ages

Otolith annual band counts provided a reliable determination of fish age. Otolith age estimates of known-age fish showed high accuracy: 92% ($n = 74$). Fish incorrectly aged were ±1 year of known age, 5% were estimated to be 1 year older, and 3% were estimated to be 1 year younger than their known age. Age estimations between the two age readers across all otoliths ($n = 755$) reached an agreement of 92% (ACV = 1.771, APE = 1.252). This level of agreement between readers is comparable to that of other otolith aging studies (Flain and Glova 1988; Murray 1994; Secor et al. 1995). Of the individuals aged, 6.1%, 68.6%, 24.6%, and 0.7% were estimated as 2-, 3-, 4-, and 5-year-old fish, respectively. This age distribution was similar to age class distribution estimates for the Feather River (Grover and Kormos 2008). Similarly, of the CWT retrieved from fish at FRH from 2002 through 2007, 15.58% were 2-year-olds, 56.07% were 3-year-olds, 28.23% were 4-year-olds, and 0.13% were 5-year-olds (Mesick et al. 2009).

Natal origins

The baseline $^{87}Sr/^{86}Sr$ isotope ratios for the Sacramento River System varied significantly between different rivers and hatcheries (Fig. 4; Table 2). Using QDFA, we achieved an overall classification success rate of 96%, providing a robust baseline to determine the natal origins of Chinook salmon in this river system. Furthermore, 95% of known-origin (CWT) fish were correctly assigned to the FRH (Table 3). Classification success rate varied by collection year, ranging from 75% in 2002 to 100% in 2006, 2009, and 2010.

Sr isotope profiles from the core to the edge of otoliths for 755 individuals revealed distinct patterns in natal origins and life histories (Fig. 5). All otoliths examined reached $^{87}Sr/^{86}Sr$ isotope ratios equivalent to the global ocean value 0.70918 (McArthur et al. 2001) prior to the first annual band, indicating that all individuals had entered the ocean in their first year of life. Each otolith was classified based on its natal origin, escapement year, and recovery location (Table 4). A majority of fish were classified as FRH fish ($n = 373$), with a small contribution from the Thermalito Annex ($n = 15$) or as wild fish from the Feather River ($n = 292$). The remaining fish were classified as strays within the Sacramento River System, most originating from the Yuba River ($n = 32$) and the Nimbus Fish Hatchery ($n = 35$) on the American River, with minor contributions from the Coleman National Fish Hatchery ($n = 6$) and the Northern Tributaries ($n = 2$). The relatively large presence of Yuba River strays is likely explained by the fact that the Feather–Yuba confluence is only about 40 river miles (1 mile = 1.609 km) downstream from the FRH, with well-documented exchange occurring between the two tributaries (Yuba Accord RMT 2013).

Changes in spawning composition over time

The proportion of hatchery- and wild-origin fish varied throughout the time series (2002–2010; Fig. 6; Table 5). Since stray fish are included in the overall CFM estimates of hatchery and wild contributions in the CV, we combined them with the FRH- or wild-origin fish, based on their natal assignment (hatchery strays or wild strays).

The contribution of hatchery origin fish on the Feather River spawning grounds before the stock collapse (2002–2006) varied from 55% ± 7% (±1σ) to 67% ± 9% (±1σ) (Fig. 6). During the collapse (2007–2008), the proportion of hatchery fish decreased to 40% ± 7% (±1σ) in 2008. After the collapse (2009), the contribution of hatchery

Fig. 4. Boxplot showing the $^{87}Sr/^{86}Sr$ isotope ratios of natal sources in the Sacramento River System assumed to potentially contribute to the Feather River escapement. Note that the northern tributaries (Upper Sacramento, Mill Creek, Deer Creek, Battle Creek, Butte Creek) were combined and treated as a single source. The acronyms are NT (northern tributaries), CNH (Coleman National Fish Hatchery), THE (Thermalito Annex), FEA (Feather River), FRH (Feather River Hatchery), YUB (Yuba River), NIH (American River Nimbus Fish Hatchery), AME (American River). [Colour online.]
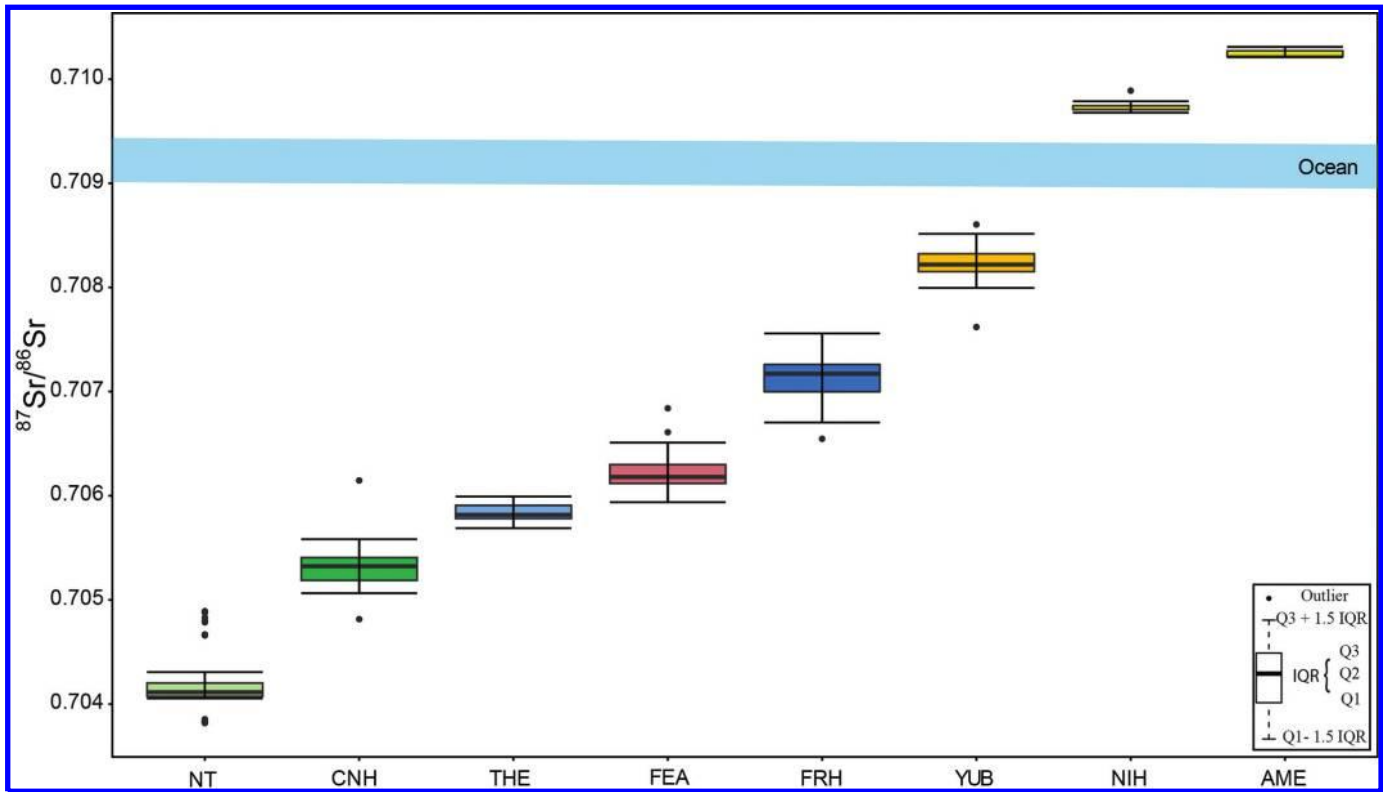
Table 2. Summary statistics for the baseline $^{87}Sr/^{86}Sr$ isotope ratios for the Sacramento River System.

	Northern tributaries	Coleman National Fish Hatchery	Feather River	Feather River Fish Hatchery	Thermalito Annex	Yuba River	Nimbus Fish Hatchery	American River
Min.	0.70382	0.70481	0.70594	0.70655	0.70569	0.70762	0.70968	0.71021
Q_1	0.70407	0.70519	0.70612	0.70700	0.70578	0.70815	0.70971	0.71022
Median	0.70411	0.70532	0.70618	0.70717	0.70582	0.70822	0.70971	0.71023
Mean	0.70421	0.70533	0.70623	0.70712	0.70584	0.70823	0.70974	0.71025
Q_2	0.70420	0.70541	0.70630	0.70726	0.70591	0.70832	0.70975	0.71027
Max.	0.70489	0.70615	0.70684	0.70756	0.70599	0.70861	0.70989	0.71031
n	41	13	31	37	10	19	9	5

Note: Data from Ingram and Weber (1999), Barnett-Johnson et al. (2008), Sturrock et al. (2015), and this study.

Table 3. Classification success rate of known-origin (coded wire tags, CWT) Feather River Hatchery fish using quadratic discriminant function analysis and the Sacramento River basin $^{87}Sr/^{86}Sr$ isotope baseline.

Collection year	No. of fish with CWT	Assigned to		Correct assignment (%)
		Hatchery	River	
2002	8	6	2	75
2003	7	6	1	86
2004	8	7	1	88
2005	16	15	1	94
2006	6	6	0	100
2007	11	10	1	91
2008	—	—	—	—
2009	5	5	0	100
2010	49	49	0	100
Total	110	104	6	95

fish increased rapidly to 89% ± 8% (±1σ) in 2010 and, according to CFM data, remained at 90% for 2011–2012 (Kormos et al. 2012; Palmer-Zwahlen and Kormos 2013, 2015).

For 2010, both CFM and microchemistry data are available, with CFM estimates yielding 78% hatchery fish and otolith estimates 89% ± 8% (±1σ). However, CFM data from 2010 is thought to underestimate the proportion of hatchery fish due to problems in the identification of hatchery fish from decayed carcasses (Mohr and Satterthwaite 2013). Given the directionality of bias in the CFM estimate, the otolith microchemistry and CFM estimates appear compatible.

Emigration timing

During this time series (2002–2012), Feather River fall-run hatchery fish were almost exclusively (~95%) trucked and released directly into San Pablo Bay (Huber and Carlson 2015). The timings of the hatchery fish releases overlap within their interquartile range with the timing of wild emigration, suggesting that most of the fish enter the ocean at a similar time. However, the

8

Can. J. Fish. Aquat. Sci. Vol. 00, 0000

Fig. 5. Example otolith $^{87}Sr/^{86}Sr$ isotope profiles of Chinook salmon with different natal origins. The cores show an influence of the marine strontium isotopic signature, indicating that the parents of these fish matured in the ocean and that this marine signature was incorporated into the organism prior to hatching, typical for fall-run Chinook salmon. Shaded bars are the $^{87}Sr/^{86}Sr$ isotope ranges of the different freshwater source regions from Fig. 4. The acronyms are NT (northern tributaries), CNH (Coleman National Fish Hatchery), THE (Thermalito Annex), FEA (Feather River), FRH (Feather River Hatchery), YUB (Yuba River), NIH (American River Nimbus Fish Hatchery), AME (American River). No fish were classified as American River natal origin. [Colour online.]
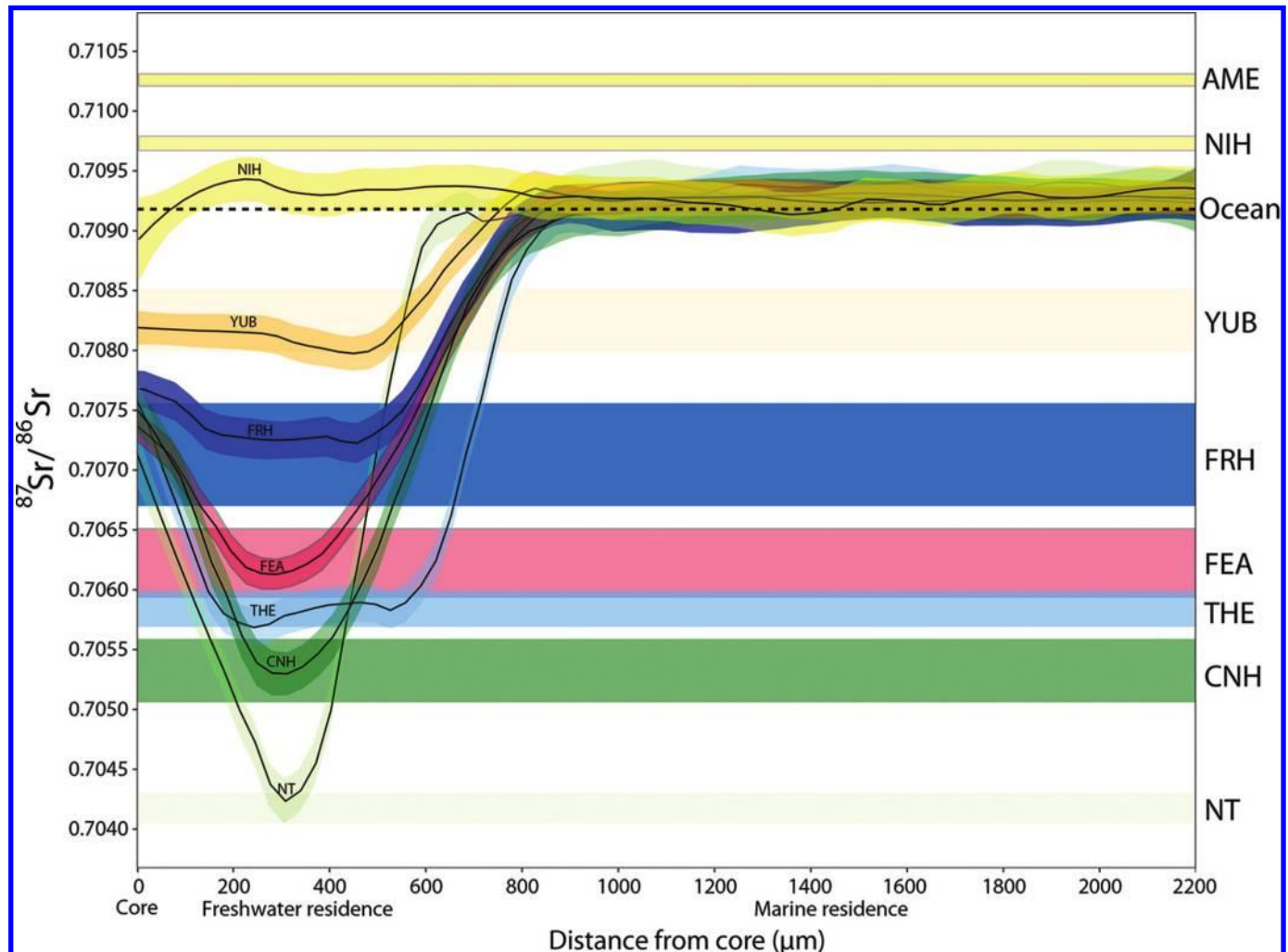
variance of the wild emigrating fish is larger, with both earlier and later emigrants, than the hatchery releases, which occur over a shorter time period (Fig. 7).

Discussion

Identifying the contribution of hatchery-origin fish to a population is essential for assessing the status, fitness, and resilience of locally adapted wild salmon populations (Lindley et al. 2007; Williams et al. 2016). Numerous studies have documented reduced fitness (Araki et al. 2008; Christie et al. 2014) and loss of diversity (portfolio) in populations with supplementation from hatchery-reared fish, causing overall reduced resilience (Schindler et al. 2010). In this study, otolith Sr isotope analysis was highly successful in identifying natal origin and discerning hatchery from wild origins of Chinook salmon in the Feather River. Combining our otolith-based approach with CFM data allowed us to reconstruct an 11-year record of hatchery contributions to the in-river escapement. Temporal trends in the contribution of hatchery- and wild-origin fish in our time series document an increase in the proportion of hatchery-origin fish on the natural spawning grounds after the salmon stock collapse (Figs. 6 and 8).

This substantial change in the proportion of hatchery fish was likely the result of relatively stable hatchery production from the small numbers of returning fish during stock collapse and either poor production or survival of wild offspring in-river during the 2007–2009 drought (DWR 2010).

The proximate cause of the 2007–2009 salmon stock collapse has been attributed to poor ocean conditions and food availability in the ocean after emigration (Lindley et al. 2009; Wells et al. 2016). Ocean conditions off the Californian coast are highly variable, with wind patterns driving the intensity and timing of coastal upwelling, influencing food production and survival of young salmon during ocean entry (Mantua et al. 1997; Satterthwaite et al. 2014; Sabal et al. 2016; Wells et al. 2016). Hatchery-produced smolts entering the ocean in 2005 and 2006 experienced weakly upwelled ocean conditions with variable timing of the spring transition (Lindley et al. 2009), which led to elevated ocean mortality and decline in hatchery contributions and stock abundance on the Feather River in 2008 (Huber and Carlson 2015). Meanwhile, wild fish exhibited a broader ocean arrival window during emigration (Fig. 7), increasing the odds that at least part of the population would be matched with optimal feeding opportunities

Table 4. Number of otoliths by escapement year and recovery location classified to their natal origin.

Escapement year	Recovery location	Hatchery-origin fish (otolith n)					Wild-origin fish (otolith n)		Total (otolith n)	
		FRH	THE	NIH	CNH	FEA	YUB	NT	Hatchery	Wild
2002	High Flow	18	2	2	—	19	—	—	22	19
	Low Flow	25	3	11	—	28	2	1	39	31
2003	High Flow	18	3	2	1	17	—	—	24	17
	Low Flow	29	1	2	—	20	2	—	32	22
2004	High Flow	17	1	2	—	12	3	—	20	15
	Low Flow	31	—	5	—	22	6	—	36	28
2005	High Flow	12	1	—	—	16	3	1	13	20
	Low Flow	47	1	1	1	17	3	—	50	20
2006	High Flow	13	—	—	—	9	1	—	13	10
	Low Flow	34	—	—	—	14	1	—	34	15
2007	High Flow	11	1	—	1	19	1	—	13	20
	Low Flow	42	—	3	3	24	4	—	48	28
2008	High Flow	7	—	—	—	20	—	—	7	20
	Low Flow	21	1	3	—	35	2	—	25	37
2009	High Flow	2	—	—	—	5	—	—	2	5
	Low Flow	19	1	3	—	11	4	—	23	15
2010	High Flow	3	—	—	—	1	—	—	3	1
	Low Flow	24	—	1	—	3	—	—	25	3

Note: The northern tributaries (Upper Sacramento, Mill Creek, Deer Creek, Battle Creek, Butte Creek) were combined and treated as a single source. The acronyms are NT (northern tributaries), CNH (Coleman National Fish Hatchery), THE (Thermalito Annex), FEA (Feather River), FRH (Feather River Hatchery), YUB (Yuba River), and NIH (American River Nimbus Fish Hatchery).

Fig. 6. Time series of the proportions of fall-run Chinook salmon on the Feather River assigned to each of the seven natal habitats. No fish were assigned to the American River. [Colour online.]
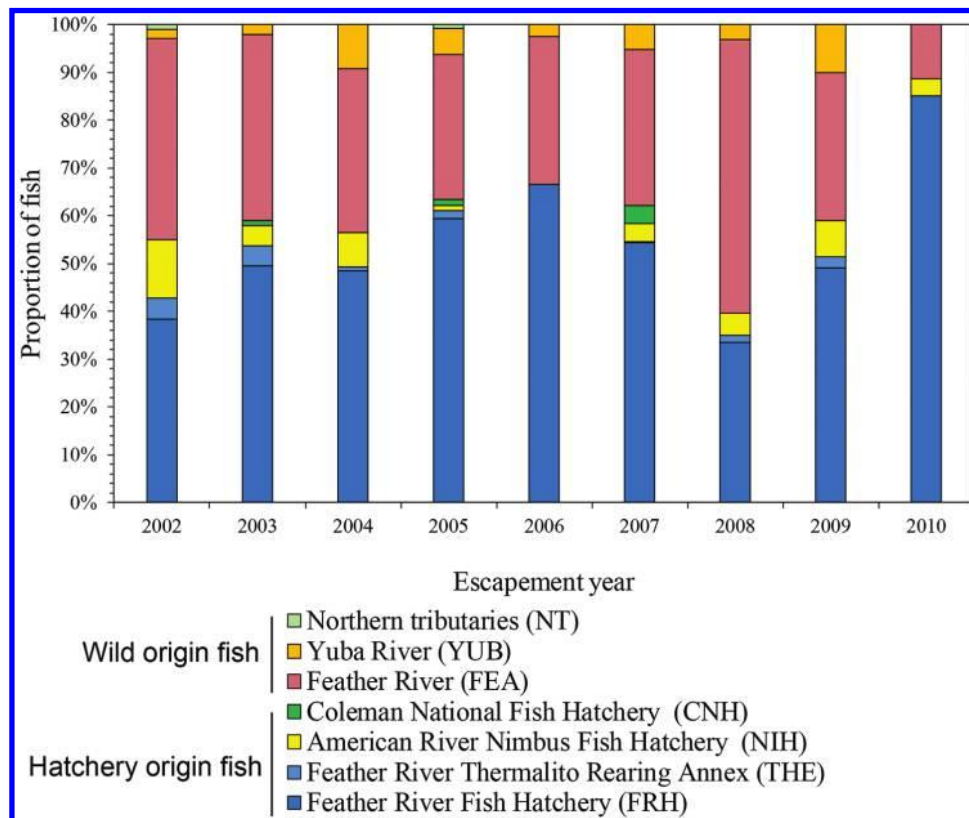
(Wells et al. 2016). We hypothesize that this diversity in outmigration timing may have led to the observed increase in the wild component of the 2008 returns. However, even with this apparent difference in the resiliency of hatchery and wild populations, all populations declined precipitously during this period. Thus, the population collapse can be attributed to poor ocean survival for both hatchery- and wild-origin smolts from the 2005 and 2006 emigration years (Lindley et al. 2009).

Total escapement to the Feather River and the Sacramento Valley increased rapidly from 2009 to 2013 (Fig. 8), reaching near prestock collapse abundances in just 3 years. Our analysis showed that ~90% of these fish returning to the Feather River were of

Pagination not final (cite DOI) / Pagination provisoire (citer le DOI)

10

Can. J. Fish. Aquat. Sci. Vol. 00, 0000

Table 5. Contributions of hatchery origin fish on the Feather River spawning grounds from 2002 to 2010.

Escapement year	Recover location	Population estimate	Hatchery origin (%)	Hatchery origin (1σ)	Hatchery fish (n)	Hatchery fish (1σ)	Combined hatchery origin (% ± 1σ)	Combined hatchery fish (n ± 1σ)
2002	High Flow	34 125	54	8	18 348	2 700		
2002	Low Flow	71 038	56	6	39 508	4 295	55±7	57 863±7 106
2003	High Flow	37 643	59	8	22 115	2 951		
2003	Low Flow	52 303	59	7	31 014	3 506	59±7	53 127±6 483
2004	High Flow	17 113	57	8	9 781	1 451		
2004	Low Flow	37 058	56	6	20 748	2 239	56±7	30 505±3 700
2005	High Flow	12 583	39	9	4 923	1 078		
2005	Low Flow	36 577	71	6	26 118	2 034	63±15	31 117±7 576
2006	High Flow	16 990	56	10	9 578	1 753		
2006	Low Flow	59 424	70	6	41 317	3 853	67±9	50 930±7 075
2007	High Flow	876	40	8	347	72		
2007	Low Flow	21 033	62	5	13 011	1 134	61±7	13 358±1 544
2008	High Flow	297	26	9	78	25		
2008	Low Flow	5 642	40	6	2 269	357	40±7	2 347±424
2009	High Flow	223	28	17	63	39		
2009	Low Flow	4 624	60	8	2 777	376	59±11	2 841±532
2010	High Flow	2 201	75	22	1 650	473		
2010	Low Flow	42 713	89	6	38 152	2 494	89±8	39 802±3 613

Note: Population estimates from GrandTab2017.04.07, California Central Valley Chinook Population Database Report, and California Department of Water Resources (unpublished data, contact Jason.Kindopp@water.ca.gov). Mean values and standard deviation (1σ) were calculated using bootstrapping for each recovery location (High Flow and Low Flow channels) and then expanded by the population estimate and combined for each year.

Fig. 7. Timing of ocean entry of fish released from the Feather River hatchery (blue) and wild out-migrating (red) from 2002 to 2010. The area of each violin represents the proportion of fish out-migrating at that Julian day and is normalized to the total abundance of outmigrants for that year. The black lines represent the interquartile range (first to third quantiles). Hatchery release data for the Feather River Hatchery (FRH) are from Huber and Carlson (2015). Data for "wild" (unmarked) fall-run sized outmigrants are from the USFWS Chipps Island Midwater Trawl. [Colour online.]
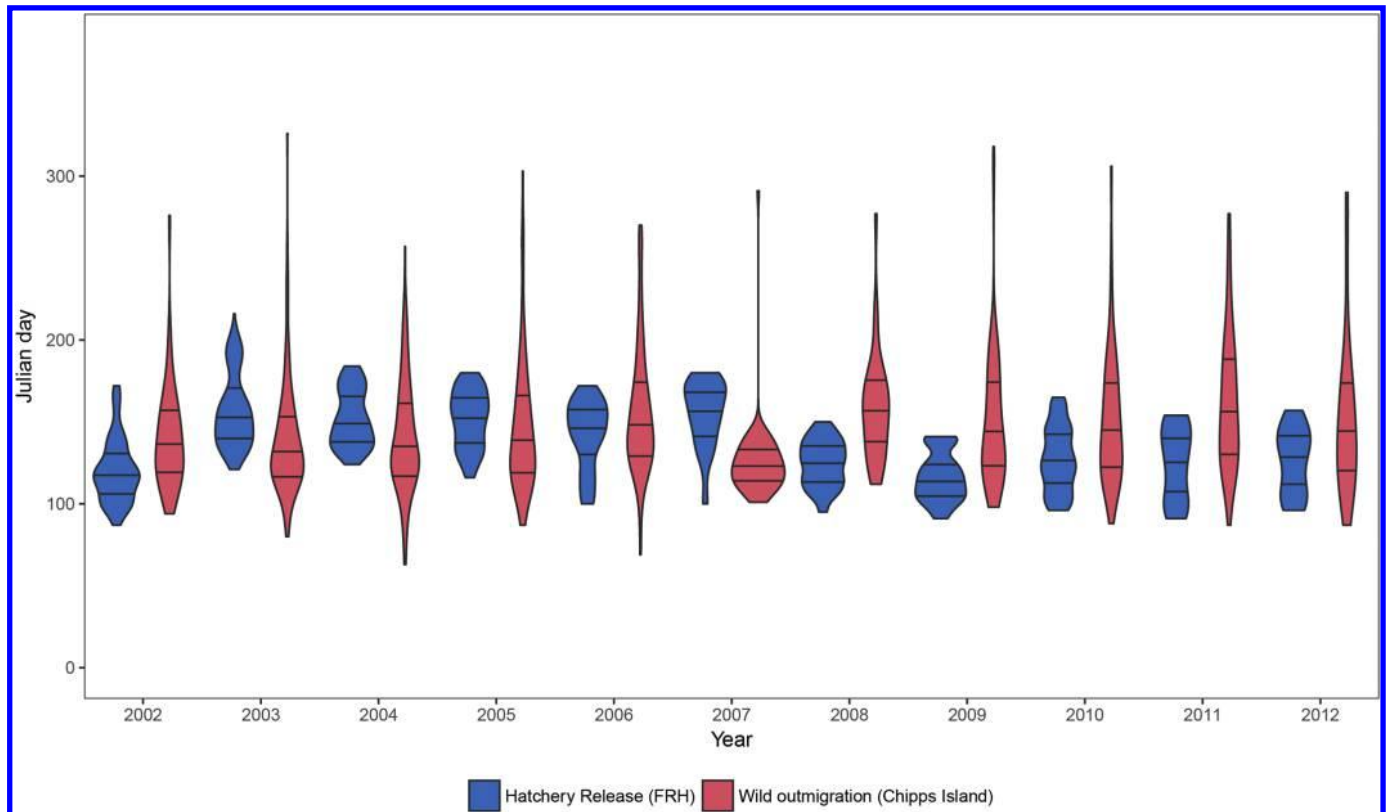
hatchery origin. This could in part be attributed to hatchery fish benefitting from improved ocean conditions as well the fishery closure, showing that hatchery and fishery management actions were highly effective at recovering fish stocks following the stock collapse. During this period, FRH release practices were relatively unchanged, with comparable numbers of juveniles produced and trucked directly to the bay relative to escapement (Fig. 8) (Huber and Carlson 2015). Wild populations likely take longer to recover from stock collapse because their population dynamics are reliant on spawning stock size more so than that of the hatchery. Fur-

Fig. 8. Feather River fall-run in-river escapement estimates split between hatchery- (blue) and wild-origin (red) fish based on otolith (2002–2010) and California Constant Fractional Marking Program (CFM) data (2011–2012). The time of the salmon stock collapse (2007–2009) is marked by low escapement numbers. Top panel shows the relative stability of hatchery releases over the time series. Escapement data are taken from the GrandTab2016.04.11, California Central Valley Chinook Population Database Report, and hatchery releases numbers are from Huber and Carlson (2015). [Colour online.]
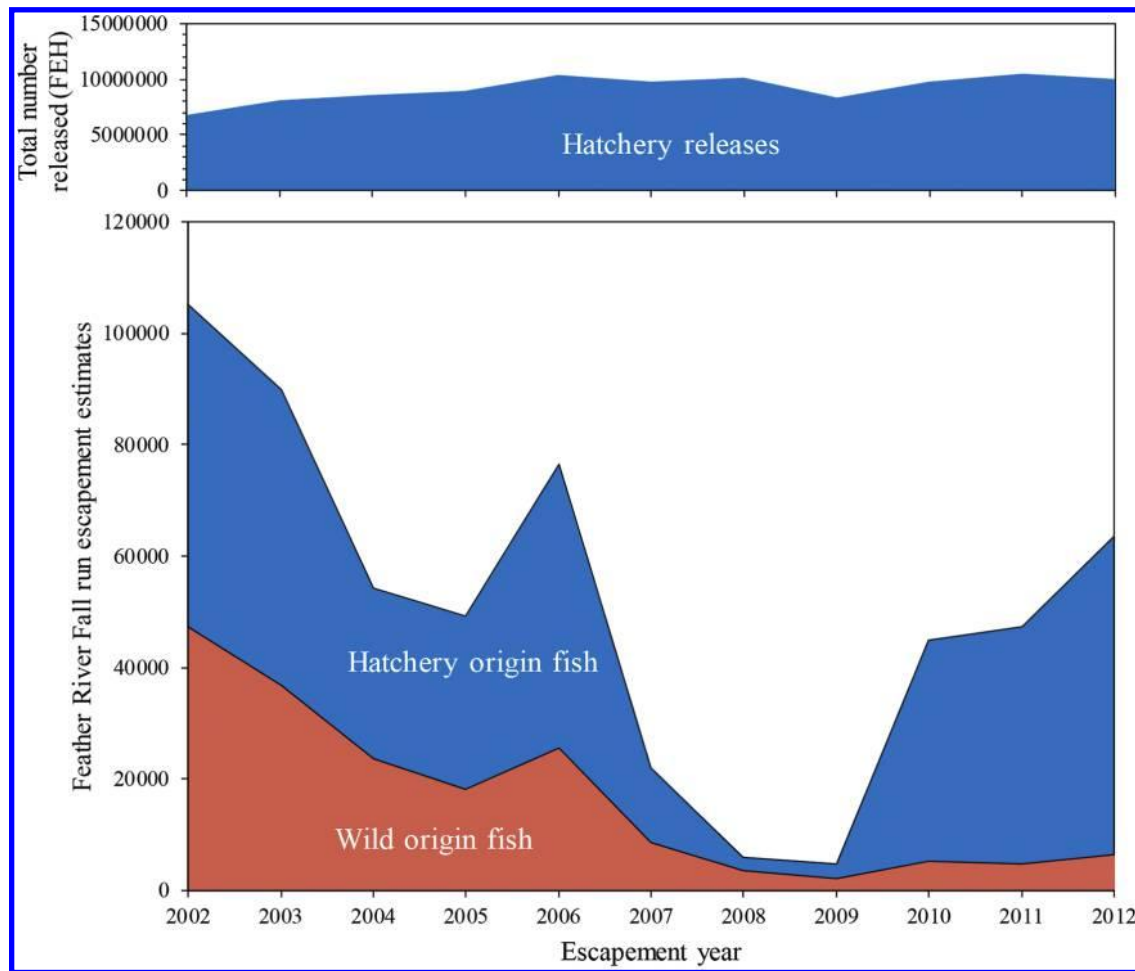
thermore, wild populations are subject to high early life mortality during emigration from CV rivers, which is exacerbated by periods of low-flow conditions during droughts (Zeug et al. 2014). In-river spawner abundance was greatly reduced during the stock collapse (J. Kindopp, unpublished data, Jason.Kindopp@water.ca.gov), which coincided with a period of drought in California (2007–2009), and their offspring likely experienced high mortality. Continued monitoring of proportion of hatchery-origin fish as part of this time series will be critical to determine the extent to which the observed pattern represents a fundamental shift towards hatchery dominance. The overwhelming presence of hatchery-origin adults on the spawning grounds would suggest that fall-run Chinook on the Feather River may now be dependent on hatchery fish. Thus, while management strategies for population supplementation of salmon have been successful, they may also facilitate synchronization of hatchery and wild populations (Satterthwaite and Carlson 2015), eroding their resilience to ocean and climate variability.

The dominance of hatchery fish on the Feather River spawning grounds in recent years suggests that interbreeding of hatchery and wild fish is likely and pervasive, particularly given that we did not consider cross-generational hatchery influence (treating all juveniles produced in-river as "wild", independent of parental origin). This is supported by unusually high hatchery contributions on most natural spawning grounds in the CV (Kormos et al.

2012; Palmer-Zwahlen and Kormos 2013, 2015) and a lack of genetic structuring in fall-run CV Chinook salmon, both hatchery and "wild" (Williamson and May 2005). This introgression of hatchery- and wild-origin fish may have reduced fitness (Araki et al. 2008) and weakened the Chinook salmon population portfolio, increasing synchrony among populations and eroding life history diversity and resilience (Carlson and Satterthwaite 2011; Satterthwaite and Carlson 2015). Given the environmental variability inherent to California and predictions of increased frequency of extreme events with future climate change (Cloern et al. 2011; Dettinger et al. 2011), loss of phenotypic diversity could have serious impacts on salmon stock resilience, increasing ecological and economic uncertainty.

The dominance of hatchery-origin fish is not limited to the Feather River. For example, 90% of in-river spawners on the Mokelumne River in 2004 were classified as hatchery fish (Johnson et al. 2012), and CFM data indicate high hatchery contributions (~80%–90%) to natural spawning grounds on Battle Creek, the Merced River, and the Stanislaus River (Kormos et al. 2012; Palmer-Zwahlen and Kormos 2013, 2015). Furthermore, the majority of the ocean fishery is supported by hatcheries, with 90% of the fishery supported by hatchery fish in 2001 (Barnett-Johnson et al. 2007). There is a growing concern that salmon populations in the CV of California are becoming dependent upon hatchery supplementation, a conservation status recently identified as "mitigated extinction"

Pagination not final (cite DOI) / Pagination provisoire (citer le DOI)

12 Can. J. Fish. Aquat. Sci. Vol. 00, 0000

(Baumsteiger and Moyle 2017). Further studies are needed basin-wide to better understand the role that hatcheries may be playing in "reseeding" in-river populations, masking their declines, and (or) depressing natural production.

It is likely that a number of factors have resulted in hatchery fish effectively replacing wild stocks in the CV, including high and sustained smolt production, largely independent of spawner abundance and freshwater conditions (Huber and Carlson 2015), increased straying rates of trucked fish onto natural spawning grounds (Palmer-Zwahlen and Kormos 2013, 2015), and inflated survival of hatchery smolts as a result of their larger size and the reduction in freshwater mortality for trucked individuals. Such management practices have synchronized the CV salmon stock complex, contributing to a weakened portfolio (Carlson and Satterthwaite 2011; Huber and Carlson 2015; Satterthwaite and Carlson 2015), increased genetic homogenization, and potentially reduced population productivity (Williamson and May 2005). Owing to the reliance on hatchery fish and the high synchrony among the hatcheries in the CV, salmon stock collapses are likely in the future, and compensating for these collapses by increasing hatchery salmon production is likely to prove ineffective (Lindley et al. 2009). We recommend implementation of hatchery practices designed to promote population diversity, such as varying the timing, size, and location of releases to facilitate greater expression of life history diversity in this region and, in turn, its productivity and resiliency (Greene et al. 2010). Moving forward, to reduce the vulnerability of the fishery to over-reliance on hatchery fish and reduce overall extinction risk to wild CV fall-run Chinook salmon, production hatcheries could implement practices that (i) reduce domestication selection through balanced gene flow between hatchery- and natural-origin fish in hatchery broodstock and in rivers (HSRG 2014), (ii) minimize the numbers of hatchery-origin fish interbreeding with wild fish on spawning grounds, and (iii) reduce straying of hatchery adults to support local adaptation in natural salmon populations. CV salmon are at a critical juncture, with many populations close to extinction and facing an increasingly volatile climatic future (Greene et al. 2010; Cloern et al. 2011). Hatcheries can play a key role in the recovery of wild stocks, supplementing the fishery, and the reestablishment of natural areas, but only with cautious and appropriate management.

Acknowledgements

References

Araki, H., Berejikian, B.A., Ford, M.J., and Blouin, M.S. 2008. Fitness of hatchery-reared salmonids in the wild. Evol. Appl. 1(2): 342–355. doi:10.1111/j.1752-4571.2008.00026.x. PMID:25567636.

Barnett-Johnson, R., Grimes, C.B., Royer, C.F., and Donohoe, C.J. 2007. Identifying the contribution of wild and hatchery Chinook salmon (Oncorhynchus tshawytscha) to the ocean fishery using otolith microstructure as natural tags. Can. J. Fish. Aquat. Sci. 64(12): 1683–1692. doi:10.1139/f07-129.

Barnett-Johnson, R., Pearson, T.E., Ramos, F.C., Grimes, C.B., and MacFarlane, R.B. 2008. Tracking natal origins of salmon using isotopes, otoliths, and landscape geology. Limnol. Oceanogr. 53(4): 1633–1642. doi:10.4319/lo.2008.53.4.1633.

Baumsteiger, J., and Moyle, P.B. 2017. Assessing extinction. Bioscience, 67(4): 357–366. doi:10.1093/biosci/bix001.

Campana, S.E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Mar. Ecol. Prog. Ser. 188: 263–297. doi:10.3354/meps188263.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. 59(2): 197–242. doi:10.1111/j.1095-8649.2001.tb00127.x.

Campana, S.E., and Neilson, J.D. 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. 42(5): 1014–1032. doi:10.1139/f85-127.

Carlson, S.M., and Satterthwaite, W.H. 2011. Weakened portfolio effect in a collapsed salmon population complex. Can. J. Fish. Aquat. Sci. 68(9): 1579–1589. doi:10.1139/f2011-084.

Christie, M.R., Ford, M.J., and Blouin, M.S. 2014. On the reproductive success of early-generation hatchery fish in the wild. Evol. Appl. 7(8): 883–896. doi:10.1111/eva.12183. PMID:25469167.

Clemento, A.J., Crandall, E.D., Garza, J.C., and Anderson, E.C. 2014. Evaluation of a single nucleotide polymorphism baseline for genetic stock identification of Chinook Salmon (Oncorhynchus tshawytscha) in the California Current large marine ecosystem. Fish. Bull. 112(2–3): 112–130. doi:10.7755/FB.112.2-3.2.

Cloern, J.E., Knowles, N., Brown, L.R., Cayan, D., Dettinger, M.D., Morgan, T.L., Schoellhamer, D.H., Stacey, M.T., van der Wegen, M., Wagner, R.W., and Jassby, A.D. 2011. Projected evolution of California's San Francisco bay–delta–river system in a century of climate change. PLoS ONE, 6(9): e24465. doi:10.1371/journal.pone.0024465. PMID:21957451.

Dettinger, M., and Cayan, D. 2014. Drought and the California Delta — a matter of extremes. San Fr. Estuary Watershed Sci. 12(2): 6p. doi:10.15447/sfews.2014v12iss2art4.

Dettinger, M.D., Ralph, F.M., Das, T., Neiman, P.J., and Cayan, D.R. 2011. Atmospheric rivers, floods and the water resources of California. Water, 3(2): 445–478. doi:10.3390/w3020445.

DWR. 2010. California's drought of 2007–2009: an overview [online]. Available from https://www.water.ca.gov/Water-Basics/Drought.

Fisher, F.W. 1994. Past and present status of Central Valley Chinook Salmon. Conserv. Biol. 8(3): 870–873. doi:10.1046/j.1523-1739.1994.08030863-5.x.

Flain, M., and Glova, G. 1988. A test of the reliability of otolith and scale readings of Chinook salmon (Oncorhynchus tshawytscha). N.Z. J. Mar. Freshw. Res. 22(4): 497–500. doi:10.1080/00288330.1988.9516319.

Franks, S., and Lackey, R. 2015. Forecasting the most likely status of wild salmon in the California Central Valley in 2100. San Fr. Estuary Watershed Sci. 13(1): 217–220. doi:10.15447/sfews.2015v13iss1art1.

Greene, C.M., Hall, J.E., Guilbault, K.R., and Quinn, T.P. 2010. Improved viability of populations with diverse life-history portfolios. Biol. Lett. 6: 382–386. doi:10.1098/rsbl.2009.0780. PMID:20007162.

Grover, A., and Kormos, B. 2008. The 2007 Central Valley chinook age specific run size estimates, scale aging program. California Department of Fish and Game.

Hauser, L., Seamons, T.R., Dauer, M., Naish, K.A., and Quinn, T.P. 2006. An empirical verification of population assignment methods by marking and parentage data: hatchery and wild steelhead (Oncorhynchus mykiss) in Forks Creek, Washington, USA. Mol. Ecol. 15(11): 3157–3173. doi:10.1111/j.1365-294X.2006.03017.x. PMID:16968262.

Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. 2003. Biocomplexity and fisheries sustainability. Proc. Natl. Acad. Sci. 100(11): 6564–6568. doi:10.1073/pnas.1037274100. PMID:12743372.

Horwitz, E.P., Chiarizia, R., and Dietz, M.L. 1992. A novel strontium-selective extraction chromatographic resin*. Solvent Extr. Ion Exch. 10(2): 313–336. doi:10.1080/07366299208918107.

HSRG. 2012. California Hatchery Review Statewide Report. Prepared for the US Fish and Wildlife Service and Pacific States Marine Fisheries.

HSRG. 2014. On the science of hatcheries: an updated perspective on the role of hatcheries in salmon and steelhead management in the Pacific Northwest. Edited by A. Appleby, H.L. Blankenship, D. Campton, K. Currens, T. Evelyn, D. Fast, T. Flagg, J. Gislason, P. Kline, and C. Mahnk.

Huber, E.R., and Carlson, S.M. 2015. Temporal trends in hatchery releases of fall-run Chinook Salmon in California's Central Valley. San Fr. Estuary Watershed Sci. 13(2). doi:10.15447/sfews.2015vol13iss2art3.

Ingram, B.L., and Weber, P.K. 1999. Salmon origin in California's Sacramento–San Joaquin river system as determined by otolith strontium isotopic composition. Geology, 27(9): 851–854. doi:10.1130/0091-7613(1999)027<0851:SOICSS>2.3.CO;2.

Johnson, R.C., Weber, P.K., Wikert, J.D., Workman, M.L., MacFarlane, R.B., Grove, M.J., and Schmitt, A.K. 2012. Managed metapopulations: Do salmon hatchery "sources" lead to in-river "sinks" in conservation? PLoS ONE, 7(2): e28880. doi:10.1371/journal.pone.0028880. PMID:22347362.

Johnson, R., Garza, J., MacFarlane, R., Grimes, C., Phillis, C., Koch, P., Weber, P., and Carr, M. 2016. Isotopes and genes reveal freshwater origins of Chinook salmon Oncorhynchus tshawytscha aggregations in California's coastal ocean. Mar. Ecol. Prog. Ser. 548: 181–196. doi:10.3354/meps11623.

Katz, J., Moyle, P.B., Quiñones, R.M., Israel, J., and Purdy, S. 2012. Impending extinction of salmon, steelhead, and trout (Salmonidae) in California. Environ. Biol. Fishes, 96(10–11): 1169–1186. doi:10.1007/s10641-012-9974-8.

Kormos, B., Palmer-Zwahlen, M.L., and Low, A. 2012. Recovery of coded-wire tags from Chinook Salmon in California's Central Valley Escapement and Ocean Harvest in 2010. In California Department of Fish and Game, Fisheries BranchAdministrative Report 2012-02.

Lindley, S.T., Schick, R.S., Mora, E., Adams, P.B., Anderson, J.J., Greene, S., Hanson, C., May, B.P., McEwan, D., MacFarlane, R.B., Swanson, C., and Williams, J.G. 2007. Framework for assessing viability of threatened and endangered Chinook Salmon and Steelhead in the Sacramento–San Joaquin Basin. San Fr. Estuary Watershed Sci. **5**(1).

Lindley, S.T.T., Grimes, C.B., Mohr, M.S.S., Peterson, W., Stein, J., Anderson, J.T., Botsford, L.W., Bottom, D.L., Busack, C.A., Collier, T.K., Ferguson, J., Garza, J.C., Grover, A.M., Hankin, D.G., Kope, R.G., Lawson, P.W., Low, A., MacFarlane, R.B., Moore, K., Palmer-Zwahlen, M., Schwing, F.B., Smith, J., Tracy, C., Webb, R., Wells, B.K., and Williams, T.H. 2009. What caused the Sacramento River fall Chinook stock collapse? *In* NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-447. Pacific Fishery Management Council.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., and Francis, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Am. Meteorol. Soc. **78**(6): 1069–1079. doi:10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2.

McArthur, J.M., Howarth, R.J., and Bailey, T.R. 2001. Strontium isotope stratigraphy: LOWESS Version 3: Best fit to the marine Sr-isotope curve for 0–509 Ma and accompanying look-up table for deriving numerical age. J. Geol. **109**(2): 155–170. doi:10.1086/319243.

McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R., Maoiléidigh, N.O., Baker, N., Cotter, D., O'Hea, B., Cooke, D., Rogan, G., Taggart, J., and Cross, T. 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proc. R. Soc. B Biol. Sci. **270**(1532): 2443–2450. doi:10.1098/rspb.2003.2520.

Meek, K., Derry, L., Sparks, J., and Cathles, L. 2016*a*. 87Sr/86Sr, Ca/Sr, and Ge/Si ratios as tracers of solute sources and biogeochemical cycling at a temperate forested shale catchment, central Pennsylvania, USA. Chem. Geol. **445**: 84–102. doi:10.1016/j.chemgeo.2016.04.026.

Meek, M.H., Baerwald, M.R., Stephens, M.R., Goodbla, A., Miller, M.R., Tomalty, K.M.H., and May, B. 2016*b*. Sequencing improves our ability to study threatened migratory species: genetic population assignment in California's Central Valley Chinook salmon. Ecol. Evol. **6**(21): 7706–7716. doi:10.1002/ece3.2493.

Mercer, M., and Kurth, R. 2014. An evaluation of otolith thermal marking at the Feather River Hatchery, California. San Fr. Estuary Watershed Sci. **12**(4): 1–14. doi:10.15447/sfews.2014v12iss4art3.

Mesick, C., Marston, D., and Heyne, T. 2009. Estimating the total number of coded-wire-tagged adult fall-run Chinook Salmon (*Oncorhynchus tshawytscha*) in California' S Central Valley Rivers. El Dorado, California. Manuscript submitted to the California Fish and Game Scientific Journal, October 2009. Excel file database: CV Summary August 2009 Fall-Run Surveys Final.xls.

Michael, J. 2010. Employment impacts of California salmon fishery closures in 2008 and 2009. Business Forecasting Center. pp. 1–6.

Mohr, M.S., and Satterthwaite, W.H. 2013. Coded-wire tag expansion factors for Chinook Salmon carcass surveys in California: estimating the numbers and proportions of hatchery-origin fish. San Fr. Estuary Watershed Sci. **11**(4). doi:10.15447/sfews.2013v11iss4art3.

Moyle, P.B. 2002. Inland fishes of California. University of California Press.

Moyle, P.B., Lusardi, R., Samuel, P., and Trout, C. 2017. State of the Salmonids II: Fish in hot water. UCDavis, Center for Watershed Sciences.

Murray, C.B. 1994. A method for preparing Chinook Salmon otoliths for age determination, and evidence of its validity. Trans. Am. Fish. Soc. **123**(3): 358–367. doi:10.1577/1548-8659(1994)123<0358:AMFPCS>2.3.CO;2.

Neilson, J.D., and Geen, G.H. 1982. Otoliths of Chinook Salmon (*Oncorhynchus tshawytscha*): daily growth increments and factors influencing their production. Can. J. Fish. Aquat. Sci. **39**(10): 1340–1347. doi:10.1139/f82-180.

NMFS. 1999. Endangered and threatened species; threatened status for two chinook salmon evolutionarily significant units (ESUs) in California. Federal Register. Vol. 64, No. 179: 50394–50415. National Marine Fisheries Service.

NMFS. 2005. Endangered and threatened species; designation of critical habitat for seven evolutionarily significant units of Pacific salmon and steelhead in California. Final Rule Federal Register. Vol. 70, No. 170: 52488. National Marine Fisheries Service.

Ogle, D.H. 2018. FSA: Fisheries Stock Analysis. R package version 0.8.20.

Palmer-Zwahlen, M.L., and Kormos, B. 2013. Recovery of coded-wire tags from Chinook salmon in California's Central Valley Escapement and Ocean Harvest in 2011. *In* California Department of Fish and Game, Fisheries Branch Administrative Report 2013-02.

Palmer-Zwahlen, M.L., and Kormos, B. 2015. Recovery of coded-wire tags from Chinook Salmon in California's Central Valley Escapement, Inland Harvest, and Ocean Harvest in 2012. *In* California Department of Fish and Game, Fisheries Branch Administrative Report 2015-4.

Quiñones, R., and Moyle, P. 2014. Climate change vulnerability of freshwater fishes in the San Francisco Bay Area. San Fr. Estuary Watershed Sci. **12**(3): 217–220. doi:10.15447/sfews.2014v12iss3art3.

Quiñones, R.M., Johnson, M.L., and Moyle, P.B. 2014. Hatchery practices may result in replacement of wild salmonids: adult trends in the Klamath basin, California. Environ. Biol. Fishes, **97**(3): 233–246. doi:10.1007/s10641-013-0146-2.

R Core Team. 2017. R: a language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.r-project.org/.

Rooker, J., Zdanowicz, V., and Secor, D. 2001. Chemistry of tuna otoliths: assess-

ment of base composition and postmortem handling effects. Mar. Biol. **139**(1): 35–43. doi:10.1007/s002270100568.

Sabal, M.C., Huff, D.D., Henderson, M.J., Fiechter, J., Harding, J.A., and Hayes, S.A. 2016. Contrasting patterns in growth and survival of Central Valley fall run Chinook salmon related to hatchery and ocean conditions. Environ. Biol. Fishes, **99**(12): 949–967. doi:10.1007/s10641-016-0536-3.

Satterthwaite, W.H., and Carlson, S.M. 2015. Weakening portfolio effect strength in a hatchery-supplemented Chinook salmon population complex. Can. J. Fish. Aquat. Sci. **72**(12): 1860–1875. doi:10.1139/cjfas-2015-0169.

Satterthwaite, W.H., Carlson, S.M., Allen-Moran, S.D., Vincenzi, S., Bograd, S.J., and Wells, B.K. 2014. Match–mismatch dynamics and the relationship between ocean-entry timing and relative ocean recoveries of Central Valley fall run Chinook salmon. Mar. Ecol. Prog. Ser. **511**: 237–248. doi:10.3354/meps10934.

Satterthwaite, W.H., Ciancio, J., Crandall, E., Palmer-Zwahlen, M.L., Grover, A.M., O'Farrell, M.R., Anderson, E.C., Mohr, M.S., and Garza, J.C. 2015. Stock composition and ocean spatial distribution inference from California recreational Chinook salmon fisheries using genetic stock identification. Fish. Res. **170**: 166–178. doi:10.1016/j.fishres.2015.06.001.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. Nature, **465**(7298): 609–612. doi:10.1038/nature09060. PMID:20520713.

Schwarzenegger, A. 2008. Executive Order S-14-08. Office of the Governor, California.

Secor, D.H., Trice, T.M., and Hornick, H.T. 1995. Validation of otolith-based ageing and a comparison of otolith and scale-based ageing in mark–recaptured Chesapeake Bay striped bass, *Morone saxatilis*. Fish. Bull. **93**(1): 186–190.

Sommer, T., McEwan, D., and Brown, R. 2001. Factors affecting Chinook Salmon spawning in the Lower Feather River. Fish Bull. Contrib. to Biol. Cent. Val. Salmonids, **1**: 269–297.

Sturrock, A.M., Wikert, J.D., Heyne, T., Mesick, C., Hubbard, A.E., Hinkelman, T.M., Weber, P.K., Whitman, G.E., Glessner, J.J., and Johnson, R.C. 2015. Reconstructing the migratory behavior and long-term survivorship of juvenile Chinook Salmon under contrasting hydrologic regimes. PLoS ONE, **10**(5): e0122380. doi:10.1371/journal.pone.0122380. PMID:25992556.

Walther, B.D., and Limburg, K.E. 2012. The use of otolith chemistry to characterize diadromous migrations. J. Fish Biol. **81**(2): 796–825. doi:10.1111/j.1095-8649.2012.03371.x. PMID:22803736.

Waples, R.S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. Can. J. Fish. Aquat. Sci. **48**(S1): 124–133. doi:10.1139/f91-311.

Welch, T.J., Van Den Avvle, M.J., Betsill, R.K., and Driebe, E.M. 1993. Precision and relative accuracy of striped bass age estimates from otoliths, scales, and anal fin rays and spines. N. Am. J. Fish. Manage. **13**: 616–620. [October 2016.] doi:10.1577/1548-8675(1993)013<0616:PARAOS>2.3.CO;2.

Wells, B., Friedland, K., and Clarke, L. 2003. Increment patterns in otoliths and scales from mature Atlantic salmon *Salmo salar*. Mar. Ecol. Prog. Ser. **262**: 293–298. doi:10.3354/meps262293.

Wells, B., Santora, J., Schroeder, I., Mantua, N., Sydeman, W., Huff, D., and Field, J. 2016. Marine ecosystem perspectives on Chinook salmon recruitment: a synthesis of empirical and modeling studies from a California upwelling system. Mar. Ecol. Prog. Ser. **552**: 271–284. doi:10.3354/meps11757.

Williams, J.G. 2006. Central Valley Salmon: a perspective on Chinook and Steelhead in the Central Valley of California. San Fr. Estuary Watershed Sci. **4**(3): 1–393. doi:10.5811/westjem.2011.5.6700.

Williams, T.H., Spence, B.C., Boughton, D.A., Johnson, R.C., Crozier, L.G., Mantua, N.J., O'Farrell, M.R., and Lindley, S.T. 2016. Viability assessment for Pacific Salmon and Steelhead listed under the Endangered Species Act: southwest. doi:10.7289/V5/TM-SWFSC-564.

Williamson, K.S., and May, B. 2005. Homogenization of fall-run Chinook Salmon gene pools in the Central Valley of California, USA. N. Am. J. Fish. Manage. **25**(3): 993–1009. doi:10.1577/M04-136.1.

Woodson, L.E., Wells, B.K., Weber, P.K., MacFarlane, R.B., Whitman, G.E., and Johnson, R.C. 2013. Size, growth, and origin-dependent mortality of juvenile Chinook salmon *Oncorhynchus tshawytscha* during early ocean residence. Mar. Ecol. Prog. Ser. **487**: 163–175. doi:10.3354/meps10353.

Yoshiyama, R.M., Fisher, F.W., and Moyle, P.B. 1998. Historical abundance and decline of Chinook Salmon in the Central Valley Region of California. N. Am. J. Fish. Manage. **18**(3): 487–521. doi:10.1577/1548-8675(1998)018<0487:HAADOC>2.0.CO;2.

Yoshiyama, R.M., Moyle, P.B., Gerstung, E.R., and Fisher, F.W. 2000. Chinook Salmon in the California Central Valley: an assessment. Fisheries, **25**(2): 6–20. doi:10.1577/1548-8446(2000)025<0006:CSITCC>2.0.CO;2.

Yoshiyama, R.M., Gerstung, E.R., Fisher, F.W., Moyle, P.B., Fisher Frank, W., and Moyle, P.B. 2001. Historical and present distribution of chinook salmon in the Central Valley drainage of California. Contrib. Biol. Cent. Val. Salmonids, Fish Bull. **179**: 71–176.

Yuba Accord RMT. 2013. Yuba Accord M&E Program Draft Interim Report.

Zeug, S.C., Sellheim, K., Watry, C., Wikert, J.D., and Merz, J. 2014. Response of juvenile Chinook salmon to managed flow: lessons learned from a population at the southern extent of their range in North America. Fish. Manage. Ecol. **21**(2): 155–168. doi:10.1111/fme.12063.

Flow-mediated effects on travel time, routing, and survival of juvenile Chinook salmon in a spatially complex, tidally forced river delta

Russell W. Perry[1*], Adam C. Pope[1], Jason G. Romine[1**], Patricia L. Brandes[2], Jon R. Burau[3], Aaron R. Blake[3], Arnold J. Ammann[4], and Cyril J. Michel[4]

[1] U.S. Geological Survey, Western Fisheries Research Center, 5501A Cook-Underwood Road, Cook, WA 98605, USA (RWP: rperry@usgs.gov; ACP: apope@usgs.gov; JRG: jason_romine@fws.gov)

[2] U.S. Fish and Wildlife Service, 850 Guild Ave, Suite 105, Lodi, CA 95240, USA (PLB: pat_brandes@fws.gov)

[3] U.S. Geological Survey, California Water Science Center, 6000 J Street, Placer Hall, Sacramento, CA 95819, USA (JRB: jrburau@usgs.gov; ARB: ablake@usgs.gov)

[4] National Marine Fisheries Service, Southwest Fisheries Science Center, 110 Shaffer Rd., Santa Cruz, CA 95060, USA (AJA: arnold.ammann@noaa.gov; CJM: cyril.michel@noaa.gov)

[*] Corresponding author:

Phone: 509-538-2942

Fax: 509-538-2843

[**] Present address: U.S. Fish & Wildlife Service, Mid-Columbia River National Wildlife Refuge Complex, 64 Maple St, Burbank, WA 99323, USA

1   **Abstract**

2   We evaluated the interacting influences of river flows and tides on travel time, routing, and

3   survival of juvenile late-fall Chinook salmon (*Oncorhynchus tshawytscha*) migrating through the

4   Sacramento-San Joaquin River Delta. To quantify these effects, we jointly modeled the travel

5   time, survival, and migration routing in relation to individual time-varying covariates of

6   acoustic-tagged salmon within a Bayesian framework. We used observed arrival times for

7   detected individuals and imputed arrival times for undetected individuals to assign covariate

8   values in each reach. We found travel time was inversely related to river inflow in all reaches,

9   yet survival was positively related to inflow only in reaches that transitioned from bidirectional

10   tidal flows to unidirectional flow with increasing inflows. We also found that the probability of

11   fish entering the interior Delta, a low-survival reach, declined as inflow increased. Our study

12   illustrates how river inflows interact with tides to influence fish survival during the critical

13   transition between freshwater and ocean environments. Furthermore, our analytical framework

14   introduces new techniques to formally integrate over missing covariate values to quantify effects

15   of time-varying covariates.

Introduction

Anadromous salmonids have evolved diverse life history strategies that capitalize on spatial and temporal variation in their habitat to maximize productivity. Understanding how salmonids use habitat over space and time can provide insight into population dynamics and help to identify particularly sensitive stages in their life history. Regulated rivers influence migrations of anadromous salmonids by altering the timing, magnitude, variation, and constituents of river discharge (e.g., temperature, turbidity), which in turn can affect their survival (Raymond 1988; Smith et al. 2003). Thus, interest often centers on how regulation of river flow affects survival of juvenile salmonids at different locations and times (Skalski et al. 2002; Michel et al. 2015).

Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in the Central Valley of California, USA, emigrate from natal tributaries of the Sacramento River through the Sacramento-San Joaquin River Delta (henceforth, "the Delta"), a network of natural and man-made channels linking the Sacramento and San Joaquin rivers to San Francisco Bay and the Pacific Ocean (Fig. 1). The Delta is the hub of California's water delivery system, providing agricultural and domestic water that supports California's economy, the eighth largest in the world (Healey et al. 2016). Water from the Sacramento River is diverted from the North through natural channels and gated man-made channels to the South where large pumping stations "export" water from the Delta in canals (Fig. 1). As juvenile salmon enter the Delta, they distribute among its complex channel network where they are subject to channel-specific abiotic and biotic factors that influence their migration timing, growth, and survival. For example, fish that enter the interior Delta, the region to the south of the mainstem Sacramento River (reach 8 in Fig. 1), survive at lower rates than fish migrating through northerly routes, likely owing to longer

3

38 travel times, longer travel distances, higher predation rates, and entrainment at the pumping

39 stations (Brandes and McLain 2001; Newman and Brandes 2010; Perry et al. 2010, 2013).

40   Survival of juvenile salmon has been positively related to river discharge at the Delta-wide

41 scale (Kjelson et al. 1982; Kjelson and Brandes 1989; Newman and Rice 2002; Newman 2003),

42 but the underlying factors driving this relationship remain unclear. Low river discharge has been

43 associated with a high proportion of fish entering the interior Delta, thereby decreasing overall

44 survival by subjecting a larger fraction of the population to low survival probabilities (Perry et al.

45 2015). What remains unclear is the extent to which within-reach survival contributes to the

46 overall flow-survival relationship. Is survival related to discharge in all reaches, or do a few key

47 reaches drive the overall flow-survival relationship? Given that the Delta transitions from

48 unidirectional flow in its upper reaches to tidally driven bidirectional flows in lower reaches, we

49 hypothesized that the reach-specific relationship between inflow and survival could vary along

50 this gradient. Understanding exactly which reaches contribute to the overall flow-survival

51 relation will help researchers to focus on specific mechanisms driving this relationship and help

52 managers to target specific actions to increase survival.

53   Here, we analyze acoustic telemetry data on juvenile Chinook salmon from 17 distinct

54 release groups collected from two studies conducted between 2007 and 2011 (Table 1) to

55 understand how reach-specific travel time, migration routing, and survival vary among reaches in

56 the Sacramento-San Joaquin River Delta. Because each release group spread out over time as

57 they migrated through the Delta, individuals entered a given reach over a wide range of

58 environmental conditions. Our interest therefore centered on quantifying factors affecting

59 individual variation in survival. However, time-varying individual covariates are a vexing

60 problem in conventional mark-recapture models (e.g., maximum likelihood estimation performed

4

61   in Program Mark, White and Burnham 1999) because the value of the covariate is unknown

62   when an individual is undetected, rendering the likelihood analytically intractable in most cases

63   (but see Catchpole et al. 2008). Therefore, we developed a Bayesian hierarchical model that

64   jointly modeled both travel times and survival of juvenile salmon. The travel time model was

65   used to impute arrival times of undetected fish in each reach, which allowed us to define

66   covariate values based on imputed arrival times for undetected individuals. We then used

67   Markov Chain Monte Carlo techniques to integrate the likelihood over the missing covariate

68   values while simultaneously estimating parameters associated with both travel time and survival.

69

70   **Methods**

71   *Study area and telemetry system*

72   The telemetry system was designed to accommodate requirements of a multistate mark-

73   recapture model that estimated reach- and route-specific survival for nine discrete reaches and

74   four primary migration routes through the Delta (Perry et al. 2010; Figs. 1 and 2). The nine

75   reaches separate the Delta into the three hydrodynamic zones: 1) riverine reaches with

76   unidirectional flows and the least influence of tidal forcing (reaches 0–2), 2) transitional reaches

77   that shift from unidirectional flow to tidally driven bidirectional flows as river flow entering the

78   Delta decreases (reaches 3–6), and 3) tidal reaches with bidirectional flows regardless of the

79   amount of river flow entering the Delta (reaches 7–8, Figs. 1 and 3). These nine reaches

80   comprise four distinct migration routes that constitute the states of the multistate model: the

81   Sacramento River (Route A = reaches 1, 2, 4, and 7), Sutter and Steamboat Slough (Route B =

82   reaches 1, 3, and 7), the Delta Cross Channel (Route C = reaches 1, 2, 6, and 8), and Georgiana

83   Slough (Route D = reaches 1, 2, 5, and 8; Figs. 1 and 2).

84   Each telemetry station consisted of single or multiple tag-detecting monitors (Vemco

85   Model VR2, Amirix Systems, Inc., Halifax, Nova Scotia, Canada), depending on the number of

86   monitors needed to maximize detection probabilities at each station. Migration routes A, B, C,

87   and D were monitored with 7, 1, 1, and 2 telemetry stations, respectively, labeled according to

88   migration route r at sampling occasion j (Figs. 1 and 2). Sampling occasion was defined based

89   on the jth telemetry station within the mainstem Sacramento River, with the upstream release site

90   defined as occasion one. Migrating juvenile salmon first arrive at Sutter and Steamboat Slough

91   (B_3), which diverges from the Sacramento River at the first river junction and converges again

92   with the Sacramento River upstream of A_5 (Figs. 1 and 2). Fish remaining in the Sacramento

93   River then pass the Delta Cross Channel (C_4), a man-made gated canal that diverts fish, when its

94   gates are open, into reach 6 and subsequently into the interior Delta (reach 8). The Delta Cross

95   Channel is used to control salinity at the water pumping stations, undergoes mandatory closures

96   for fisheries protection in mid-December each year, and also closes when Sacramento River flow

97   exceeds 708 $m^3 \cdot s^{-1}$ (25,000 $ft^3 \cdot s^{-1}$). Fish then pass Georgiana Slough (D_4), a natural channel

98   (reach 5) that also leads to the interior Delta (reach 8). All routes then converge at Chipps Island

99   (A_6), the terminus of the Delta. With this configuration, survival to site A_6 is confounded with

100   detection probability at the last telemetry station. Therefore, to estimate survival to A_6, we

101   pooled detections from numerous tag detecting monitors downstream of A_6 in San Francisco Bay

102   for estimating detection probability at Chipps Island.

103   Although there are numerous possible migration pathways, we focused on these four

104   routes because management actions likely have the largest influence on movement and survival

105   among these routes. For example, fish may enter the interior Delta from the Sacramento River

106   through either Georgiana Slough or the Delta Cross Channel, where they subsequently become

6

107 vulnerable to migration delays and entrainment at the water pumping projects (Perry et al. 2010;

108 Newman and Brandes 2010). Steamboat and Sutter Slough is an important migration route

109 because fish using this route bypass the Delta Cross Channel and Georgiana Slough (Fig. 1)

110 thereby avoiding the interior Delta. Thus, monitoring these primary migration routes provides

111 information about the likely ultimate fate of individuals.

112

113 *Fish tagging and release*

114   All juvenile late fall Chinook salmon were obtained from the Coleman National Fish

115 Hatchery in Anderson, California. Release groups were defined based on release timing and data

116 source, with the exception of release group 3, which was pooled over a longer period of release

117 times owing to small sample size (Table 1). All fish other than release group 1 were tagged with

118 a 69 kHz acoustic tag weighing 1.58 g (Vemco Model V7-2L-R64K, Amirix Systems, Inc.,

119 Halifax, Nova Scotia, Canada) transmitting either every 30–90 s (release groups 1–3) or 15–60 s

120 (release groups 4–17). Battery life of these transmitters ranged from 98–749 d based on tests

121 conducted by Michel et al. (2015). Fish from release group 1 were tagged with an acoustic tag

122 weighing 1.44 g, which had an expected battery life of 70 d (Vemco Model V7-2L-R64K).

123   Most juvenile salmon were surgically tagged at the hatchery and then transported to

124 release sites, but fish from release groups 8 and 11 were tagged at release sites. Fish were

125 randomly selected and those ≥140 mm fork length were retained for tagging to maintain tag

126 burden below 6% of the fish weight. Fish tagged by Michel et al. (2015) were held at the

127 hatchery for 24 h following surgery, transported to release sites, and held in-river for 1–3 h prior

128 to release. Fish tagged by Perry et al. (2010, 2012, 2013) fish were transported to release sites,

129 held in-river at release sites for 24 h, and then released into either the Sacramento River near

7

130   Sacramento, CA (n_{A1}) or Georgiana Slough (n_{D4} ; Fig. 1 and 2). Fish were released into

131   Georgiana Slough to increase the number of fish entering the interior Delta (reach 8) and

132   improve precision of survival estimates for that region. For the Michel et al. (2015) study, fish

133   were released well upstream of the Delta, at four locations in the Sacramento River (Table 1). In

134   most migration years, two releases were made; one in December and another in January.

135   Releases in December occurred prior to seasonal closure of the Delta Cross Channel gates, which

136   typically occurs on December 15; whereas the Delta Cross Channel gates were closed for all

137   January releases. Further details of tagging and release protocols can be found in the citations

138   listed in Table 1.

139

140   *Screening for false positive detections and predators*

141   Telemetry data were screened for false positive detections by first summarizing data into

142   detection events defined by the number of consecutive detections from an individual tag within a

143   30-minute period at a given telemetry station. Any detection event with at least two detections at

144   a given location was considered as valid. Detection events with a single detection were

145   considered valid if the detection was consistent with the entire spatiotemporal detection history

146   of the individual's tag (e.g., a single detection was preceded by an upstream detection and

147   proceeded by a downstream detection). Otherwise, single detections were considered false

148   positives and removed from analysis.

149   Tags that may have been consumed by predators were identified by adapting the methods

150   of Gibson et al. (2015), which consisted of several steps. First we calculated five movement

151   metrics from tag detections that quantified differences in behavioral patterns between live tagged

152   smolts and tagged smolts that had been consumed by predators such as striped bass (*Morone*

153   *saxatilis*), smallmouth bass (*Micropterus dolomieu*), largemouth bass (*Micropterus salmoides*),

154   and spotted bass (*Micropterus punctulatus*). The metrics included: 1) the mean rate of

155   downstream movement calculated as the shortest channel distance between consecutive

156   detections of downstream movements divided by the elapsed time between detections, 2) the

157   number of consecutive detection events occurring at the same location, 3) the cumulative

158   distance travelled divided by the total number of days spent in the study area, 4) the number of

159   transitions between telemetry stations that were deemed to be only possible by a predator (i.e.,

160   movement upstream against the flow), and the total time in the array from the time of release to

161   the time of last detection.

162   Next we used hierarchical cluster analysis to group each tag by the multivariate

163   characteristics of the five metrics. We used the hclust package in R (R Core Team 2015) and

164   divided the tags in three groups based on the dendrogram resulting from hierarchical clustering

165   using Ward's minimum variance method (Ward 1963; Gibson et al. 2015). We then selected the

166   group whose movement characteristics were most consistent with that of predator-like behavior

167   (i.e., upstream movement against flow, long residence times near receivers, and low average

168   distance travelled per day). We examined each tag's time series of movement metrics to identify

169   if and when the tag transitioned from smolt-like to predator-like behavior.   The detection history

170   was then truncated at this point in the detection history. Overall, 17% percent of tags were

171   flagged for review based on the movement metrics, and 11% percent exhibited predator-like

172   behavior that required truncation of their capture history.

173

174   *Structure of the mark-recapture model*

175   The multistate mark-recapture model estimates three types of parameters from detections

176   of acoustic-tagged juvenile Chinook Salmon: $S_{r,j}$ is the probability of surviving from a

177   telemetry station within route r at sampling occasion j to the next downstream telemetry station;

178    $\Psi_{r,s,j}$ is the probability of entering route s from route r at sampling occasion j, conditional on

179   surviving to occasion j (henceforth, routing probability); and $P_{r,j}$ is the probability of detecting a

180   tagged fish at a telemetry station on sampling occasion j within route r, conditional on fish

181   surviving to occasion j (Fig. 2). In the parlance of multistate mark-recapture models, the routes

182   constitute the states, the routing probabilities represent the state transition probabilities, and

183   survival and detection probabilities are conditioned on migration route (i.e., conditioned on

184   state).

185   In addition, our modeling framework includes an auxiliary model for travel times, which

186   we used to impute arrival times of undetected individuals in each reach for the purposes of

187   assigning daily covariate values. This model estimates two travel time parameters associated

188   with lognormally distributed travel times: $\mu_{r,j}$ is the mean of log-travel times from a telemetry

189   station in route r at sampling occasion j to the next downstream telemetry station, and $\sigma^2_{r,j}$ is the

190   variance of the travel times. Because reaches 1–8 are associated with a unique r, j combination

191   (route, sampling occasion) we generally refer to travel time and survival parameters as being

192   reach-specific (Fig. 1 and 2).

193   To understand how both migration routing and reach-specific survival contribute to

194   overall survival through the Delta, we model the underlying parameters as functions of

195   covariates and then reconstruct the overall relationship from these component parts. Overall

196   survival through the Delta was reconstructed from the individual components as:

197   (1)

$$S_{\text{Delta}} = \sum_{r \in \{A,B,C,D\}} \Psi_r S_r$$

198   where S_r is the survival from telemetry stations A_2 to A_6 (i.e., from the entrance to the exit of the

199   Delta) for fish taking migration route r, and Ψ_r is the total probability of a fish taking route r.

200   Thus, S_r is the product of reach-specific survival probabilities that trace a unique migration

201   route through the Delta (e.g., $S_D = S_{A2}S_{A3}S_{D4}S_{D5}$), and Ψ_r is the product of routing probabilities

202   along that route (e.g., $\Psi_D = \Psi_{AA3}\Psi_{AD4}$, Perry et al., 2010).

203

204   *Time-varying individual covariates*

205   We hypothesized that river discharge affected migration routing, travel times, survival,

206   and detection probabilities. Mean daily discharge varies among the nine reaches owing to the

207   distribution of total discharge among the Delta's channel network. However, tidally averaged

208   net discharge in most reaches is a direct function of 1) river flows entering the Delta (as

209   measured in the Sacramento River at Freeport located near telemetry station A_2 in Fig. 1), and 2)

210   whether the Delta Cross Channel Gate is open or closed (Fig. A1[1]). Furthermore, as river inflow

211   increases, tidal fluctuations are dampened in all but reaches 7 and 8 (Fig. 3). Therefore, we used

212   river discharge at Freeport (Q) and the position of the Delta Cross Channel gate ($G = 1$ or 0 for

213   gates open or gates closed, respectively) as an index of variation in reach-specific mean

214   discharge affecting migration routing, travel times, survival, and detection probabilities.

215   Specifically, time-varying individual covariates Q_d and G_d were assigned based on the day d

216   when the ith individual passed a telemetry station in route r at sampling occasion j.

---

[1] Supplementary data are available with the article through the journal Web site at
http://nrcresearchpress.com/doi/supp/...

217   We modeled μ, the log-mean of the travel time distribution, as a linear function of

218   individual time-varying covariates:

219   (2) $\mu_{i,r,j} = \alpha_{0,r,j} + \alpha_{1,r,j}Q_d + \alpha_{2,r,j}G_d + z_{\mu,n,r,j}\xi_{\mu,r,j}$

220   where r, j indexes the route and occasion where individuals entered reaches 0, …, 8 (Fig. 1 and

221   2), $\mu_{i,r,j}$ is the log-mean travel time for individual i in each reach, $\alpha_{0,r,j}$ is the intercept, $\alpha_{1,r,j}$ is

222   the slope for the effect of discharge on μ, and $\alpha_{2,r,j}$ is the effect of Delta Cross Channel gate

223   position on μ. We modeled $\sigma_{r,j}$, the variance parameter of the log-normal travel time

224   distribution, as a constant for all individuals within a reach. In addition, $\alpha_{2,r,j}$ was set to zero for

225   reaches located upstream of the of the Delta Cross Channel (i.e., for reaches 0, 1, 2, 3, and 6).

226   Given that discrete groups of fish were released in different months, years, and locations,

227   we expected considerable variation in release-specific travel time, survival, and routing over and

228   above variation that could be accounted for by covariates in the model. Extra variation among

229   release groups was structured as a non-centered random effect where $z_{\mu,n,r,j}$ in Eq. 2 is a

230   standard normal deviate for the nth release group entering each reach, $\xi_{\mu,r,j}$ is the standard

231   deviation of the random effect in each reach, and their product is the deviation of each release

232   group from the mean, conditional on the covariates. We used a non-centered random effect to

233   reduce autocorrelation and speed convergence of the model fitting routine (Papaspiliopoulos et

234   al. 2007; Monnahan et al. 2017).

235   Reach-specific survival was modeled as a logistic function using the same linear structure

236   as travel time:

237   (3) $\text{logit}(S_{i,r,j}) = \beta_{0,r,j} + \beta_{1,r,j}Q_d + \beta_{2,r,j}G_d + \beta_3\ell_i + z_{S,n,r,j}\xi_{S,r,j}$

12

238   where logit(·) is the logit link function, ℓ_i is the fork length of individual i, β_3 is the slope for the

239   effect of fork length on survival, and all other coefficients are defined as in Eq. 2 except with

240   respect to survival. In this model, survival is constant among individuals that enter a given reach

241   on a particular day. Travel time influences survival only through its effect on arrival times to a

242   given telemetry station, which determines the discharge that individuals experienced when they

243   entered a given reach.

244   We modeled three routing probabilities as a function of covariates: Ψ_{AB3}, Ψ_{AC4}, and

245    $\Psi_{AD4|C'}$. Here, Ψ_{AB3} is the probability of entering Sutter and Steamboat Slough (route B) from

246   the Sacramento River (route A) at sampling occasion 3, Ψ_{AC4} is the probability of entering the

247   Delta Cross Channel (route C) from the Sacramento River at sampling occasion 4, and $\Psi_{AD4|C'}$

248   is the probability of entering Georgiana Slough (route D) from the Sacramento River, conditional

249   on not having entered the Delta Cross Channel (C'). Since routing probabilities must sum to one

250   at each of the two river junctions, the unconditional probability of entering Georgiana Slough (

251   Ψ_{AD4}) at sampling occasion 4 is $\left(1-\Psi_{AC4}\right)\Psi_{AD4|C'}$.

252   We model routing probabilities using a generalized logistic function:

253   (4)
$$\Psi_i = L + \frac{U-L}{1+\exp\left(-\left(\gamma_0 + \gamma_1 Q_d + \gamma_2 G_d + z_{\gamma,n}\xi_\Psi\right)\right)}$$

254   where Ψ_i is one of the three routing probabilities described above for individual i, L is the lower

255   limit of Ψ_i, U is the upper limit of Ψ_i, and all other parameters are described as in Eq. 2 except

256   with respect to routing. The parameters U and L allow the logistic function to take on values

257   other than one or zero for upper and lower limits, respectively. This equation reduces to the

258   standard inverse logit function by setting $U=1$ and $L=0$. We used the generalized logistic

259   function because we expected routing probabilities to follow a relationship similar to that

260   between total discharge (Q) and the fraction of discharge entering each route. As these channels

261   transition from bidirectional tidal flows to unidirectional flows with increasing total discharge,

262   the fraction of discharge entering a route either increases (Sutter and Steamboat sloughs) or

263   decreases (Georgiana Slough) with discharge before leveling off at a constant fraction of

264   discharge (Fig. A2). Therefore, for Sutter and Steamboat Slough (Ψ_{AB3}) we set $L = 0$ and $\gamma_2 = 0$;

265   for the Delta Cross Channel (Ψ_{AC4}) we set $L = 0$, $U = 1$, and $\gamma_2 = 0$; and for Georgiana Slough (

266    $\Psi_{AD4|C'}$) we set $U = 1$.

267   We hypothesized that increases in discharge could reduce detection probabilities by

268   increasing acoustic noise and by increasing the speed at which juvenile salmon pass telemetry

269   stations. In addition, many telemetry stations were monitored each year with different

270   hydrophones, varying numbers of hydrophones, and different spatial configurations that could

271   have influenced detection probability. Therefore, we modeled these effects on detection

272   probability as linear on the logit scale:

273   (5)
$$\text{logit}\left(P_{i,r,j}\right) = \theta_{0,r,j,y} + \theta_{1,r,j}Q_d$$

274   where $\theta_{0,r,j,y}$ is an intercept for year y at occasion j within route r, and $\theta_{1,r,j}$ is the slope for the

275   effect of river discharge on detection probability at occasion j in route r.

276

277   *Complete data likelihood*

278   To estimate model parameters as a function of time-varying individual covariates, we

279   used the complete data likelihood of the multistate model within a Bayesian framework. The

280   complete data likelihood proceeds as if there were no missing values by augmenting the

281   observed data with the unobserved missing data and treating the missing data as additional model

282   parameters to be estimated (King et al. 2010; Link and Barker 2010). This approach relies on

283   using an appropriate probability model for imputing missing covariate values and then

284   constructing the joint likelihood of the mark-recapture model parameters, the covariate model

285   parameters, and the missing data (Bonner and Schwarz 2004). To impute missing covariate

286   values for non-detected individuals whose arrival times are unknown, we model arrival times by

287   estimating parameters of the distribution of travel times through each reach.

288   The observed data for each individual required to estimate model parameters include 1)

289   the detection history, 2) cumulative travel times, 3) reach-specific travel times, and 4) covariates

290   linked to the fish's arrival time in each reach. A "detection history" is the alpha-numeric vector

291   h_i indicating whether individual i was detected in route r at occasion j ($h_{i,j}$ = A, B, C, or D) or

292   not detected at occasion j ($h_{i,j}$ = 0). The detection history compactly represents each fish's

293   detection and movement history through the telemetry network. For example, the detection

294   history A0ADD00 indicates a fish that was released into the Sacramento River ($h_{i,1}$ = A) and was

295   not detected at A$_2$ but was detected at A$_3$ ($h_{i,2:3}$ = 0A), indicating it remained in the Sacramento

296   River at its junction with Sutter and Steamboat sloughs. This fish was then detected entering

297   Georgiana Slough at D$_4$ and once more at D$_5$ before never being detected again ($h_{i,4:7}$ = DD00).

298   Associated with the observed detection history of each individual is the vector of observed

299   cumulative travel times T_i. For example, if h_i = A0ADD00 then T_i = ($T_{i,1}$, NA, $T_{i,3}$, $T_{i,4}$, $T_{i,5}$,

300   NA, NA) where $T_{i,1} = 0$, $T_{i,j}$ is the time from release to detection at a telemetry station at

301   sampling occasion j, and $T_{i,j}$ is missing (NA) when an individual is not detected. Time-varying

302   covariate values $x_{i,j}$ defined based on arrival date in each reach are missing (NA) whenever an

303   individual is not detected. Thus, for A0ADD00, $_i$ = ($x_{i,1}$, NA, $x_{i,3}$, $x_{i,4}$, $x_{i,5}$, NA, NA).

304 Observed reach-specific travel times $t_{i,r,j}$ for individual i in route r at occasion j are obtained by

305 taking the consecutive differences of the cumulative travel times. For A0ADD00, $t_i = $ (NA, NA,

306 $t_{i,A3}$, $t_{i,D4}$, NA, NA). Note that $t_{i,r,j}$ is observed only when fish are detected at consecutive

307 telemetry stations whereas $T_{i,j}$ is defined whenever a fish is detected.

308   Adapting the notation of the King et al. (2010), the complete data likelihood augments

309 the observed detection history, h_i, by imputing the latent (unobserved) states when individuals

310 are not detected:

311 (6)
$$z_{i,j} = \begin{cases} h_{i,j} & \text{if } h_{i,j} \neq 0 \\ g_{i,j} & \text{if } h_{i,j} = 0 \end{cases}$$

312 where $g_{i,j}$ is the latent state of unobserved individual i at detection occasion j, $z_{i,j}$ is the state of

313 individual i at detection occasion j (whether detected or non-detected), and z_i is the complete

314 state history for individual i. Although death can never be directly observed in detection history

315 h_i, death is included as a latent state such that $g_{i,j} \in (A,B,C,D,\dagger)$ where $\dagger$ is the death state.

316   The complete data likelihood is the product of three conditional likelihoods: 1) a

317 Bernoulli distribution for detection at occasion j given survival to occasion j in state r, 2) a

318 Bernoulli distribution for survival from occasion j to j+1 in state r given survival to occasion j,

319 and 3) a generalized Bernoulli distribution (i.e., a multinomial distribution for a single

320 observation) for the probability of moving from state r at occasion j to state s at occasion j+1

321 given survival to occasion j+1:

322 (7) $$L[S,\Psi,P \mid h,g] = \prod_{i=1}^{N} \prod_{j=F_i}^{J-1} \prod_{r \in R_j} \left[P_{i,r,j+1}^{u_{i,j+1,r}} \left(1 - P_{i,r,j+1}\right)^{v_{i,j+1,r}} \right] \left[S_{i,r,j}^{w_{i,j,r,\cdot}} \left(1 - S_{i,r,j}\right)^{w_{i,j,r,\dagger}} \right] \prod_{s \in R_{j+1}} \Psi_{i,r,s,j}^{w_{i,j,r,s}}$$

323 where

324   F_i is the occasion of release for individual i,

325   R_j is the set of states, excluding the death state, available to an individual in state r at occasion j

326   (Fig. 2),

327      $u_{i,j,r} = I\left(h_{i,j} = r\right)$ and $I(\cdot)$ is an indicator function resolving to one if individual i is detected in

328   state r at occasion j and zero otherwise,

329      $v_{i,j,r} = I\left(g_{i,j} = r\right)$ is one if individual i is imputed to be in state r at detection occasion j and zero

330   otherwise,

331      $w_{i,j,r,s} = I\left(z_{i,j} = r, z_{i,j+1} = s\right)$ is one if individual i is in state r at detection occasion j and in state s

332   at detection occasion $j+1$ and zero otherwise.

333   Note that $w_{i,j,r,\dagger}$ is one if individual i dies between j and $j+1$, $w_{i,j,r,\cdot} = \sum\limits_{s \in R_{j+1}} w_{i,j,r,s}$ is one if the

334   individual survives, and the dot represents any state but the death state.

335   We modeled reach-specific travel times using a lognormal distribution because travel

336   times of migrating juvenile salmon are typically right-skewed, and the lognormal distribution

337   often fits travel time data well (Muthukumarana et al. 2008). Missing travel times (i.e., $t_{i,r,j} = $

338   NA) are imputed from a lognormal distribution subject to the constraint

339   (8) $$T_{i,j+K} = T_{i,j} + \sum_{k=0}^{K-1} t_{i,r,j+k}^{\text{mis}}$$

340   where $T_{i,j}$ and $T_{i,j+K}$ are observed cumulative travel times, $t_{i,r,j}^{\text{mis}}$ are missing reach-specific travel

341   times between occasions j and $j+K$, and the K is the number of missing reach-specific travel

342   times between $T_{i,j}$ and $T_{i,j+K}$ ($K = 2, \ldots, J\text{-}1$). Since the sum of missing travel times are

343   constrained to be equal to $T_{i,j+K} - T_{i,j}$, this constraint on imputed travel times imposes a form of

344   left censoring, thereby providing additional information to the parameter estimation.

345   Given observed and imputed travel times, the complete data likelihood for the travel time

346   data is:

347   (9) $$L\left[\mu, \sigma \mid t^{\text{obs}}, t^{\text{mis}}\right] \propto \prod_{i=1}^{N} \prod_{j=F_i}^{J-1} \prod_{r \in R_j} \frac{1}{\sigma_{i,r,j} t_{i,r,j}} \exp\left(\frac{-\left(\ln\left(t_{i,r,j}\right) - \mu_{i,r,j}\right)^2}{2\sigma_{i,r,j}^2}\right)$$

348   where $t_{i,r,j}$ is the observed (t^{obs}) or imputed (t^{mis}) travel time for individual i in state r at

349   detection occasion j and $\sigma_{i,r,j}^2$ is the variance of the lognormal travel time distribution for

350   individual i in state r at occasion j. We estimated $\sigma_{i,r,j}^2$ as a constant over all individuals for each

351   reach.

352

353   *Other parameter constraints*

354   In addition to constraining parameters as a function of covariates, a number of other

355   constraints were imposed owing to telemetry station outages, multiple release locations, and

356   parameter identifiability issues.

357   For reach 0, individuals were either released at Sacramento (rkm 172), at rkm 191, or

358   well upstream of these locations (>rkm 191, Table 1). For fish released well upstream of

359   Sacramento, we included in the analysis only those that were detected by telemetry stations in

360   the vicinity of Sacramento or at a telemetry station located near the Feather River at rkm 204

361   (see "number analyzed" in Table 1). To account for the effect of detection or release upstream of

362   Sacramento on travel times through reach 0, we included coefficients that estimated the

363   difference in intercepts for fish detected at rkm 204 or released at rkm 191 relative to those

364   detected or released at Sacramento (rkm 172).

365   We treated the first reach after release as an "acclimation" reach to allow fish to recover

366   from handling and release procedures before drawing inferences about travel time and survival

367   (reach 0 for releases at Sacramento and reach 5 for releases in Georgiana Slough). Therefore,

368   fish released directly into Georgiana Slough (rkm 115, Table 1) were modeled with unique

369   coefficient values in reach 5 relative to fish that entered reach 5 volitionally from upstream

370   locations. Coefficients based only on fish that entered reach 5 volitionally were then used for

371   inference about travel time and survival in reach 5.

372   Telemetry station A_3 was not deployed until January 2007, affecting release 1, and was

373   not deployed between December 2007 and March 2008, affecting releases 4–7. To incorporate

374   the effect of these receiver outages, detection probability was set to zero for fish that were

375   imputed to arrive at site A_3 during these time periods. In preliminary analysis, we found

376   coefficients associated with survival in reach 2 were weakly identifiable (i.e., large credible

377   intervals), and we identified undue influence of the prior distribution on U, the upper limit of the

378   logistic function for routing into Sutter and Steamboat Slough (Ψ_{AB3}). Both issues were likely

379   driven by the extended receiver outages at telemetry station A_3. Therefore, we set all survival

380   coefficients for reach 2 equal to those for reach 1 and estimated common slopes, intercepts, and

381   random-effects parameters. This constraint was supported by previous analyses showing similar

382   survival between reaches 1 and 2 (Perry 2010; Perry et al. 2010).

383   For routing into Sutter and Steamboat Slough, we included auxiliary data from an

384   independent telemetry study to bolster parameter estimates associated with Ψ_{AB3} (California

385   Department of Water Resources 2016, Romine et al. 2017). Of 4,528 acoustically tagged

19

386   juvenile late-fall Chinook salmon released at Sacramento between 1 March and 15 April 2014,

387   3,548 fish were detected at the junction of the Sacramento River and Sutter and Steamboat

388   Slough. We modeled this binary data (1 = Sutter and Steamboat Slough, 0 = Sacramento River)

389   using a Bernoulli likelihood with probability Ψ_{AB3} and jointly estimated the parameters of Eq. 4

390   for Ψ_{AB3} over both data sets.

391   Last, unique detection probabilities could not be estimated at the entrance to the Delta

392   Cross Channel (telemetry station C_4) and Georgiana Slough (telemetry station D_4) owing to a

393   single downstream detection site common to both reaches (telemetry station D_5). Therefore, a

394   common set of coefficients for detection probability were estimated for sites D_4 and C_4.

395

396   *Prior distributions, parameter estimation, and goodness of fit*

397   Prior distributions for parameters associated with routing, survival, and detection were

398   based on the default priors for logistic regression recommended by Gelman et al. (2013). First,

399   all continuous covariates were scaled to have mean zero and standard deviation 0.5 (for

400   discharge, Q, mean = 610.1 $m^3 \cdot s^{-1}$, SD = 407.1 $m^3 \cdot s^{-1}$; for fork length, ℓ, mean = 155.1 mm, SD

401   = 10.8 mm). Next, slope parameters associated with routing, survival, and detection were drawn

402   from a Student's t distribution with a mean of zero, standard deviation of 2.5, and 7 degrees of

403   freedom. Intercepts associated with routing, survival, and detection were drawn from a

404   Cauchy(0, 10) distribution. We used a Normal(0, 1) distribution truncated at zero as the prior

405   distribution for ξ_S and ξ_Ψ (Gelman et al. 2013). Last, a Uniform(0, 1) prior was used for L and

406   U. For travel time parameters, slopes and intercepts for μ were drawn from a Normal(0, 10)

407   prior distribution, and ξ_μ and σ were drawn from a Uniform(0, 10) prior.

408   We coded the model in the Markov Chain Monte Carlo (MCMC) software package

409   JAGS (http://mcmc-jags.sourceforge.net/) as called from R (Denwood 2016), which allowed us

410   to simultaneously estimate all model parameters and impute missing data (see Supplement B[1]).

411   JAGS uses Gibbs sampling and Metropolis-Hastings methods to sequentially update each

412   parameter value, conditional on the current value for all other parameters. We ran three MCMC

413   chains in JAGS each for 50,000 iterations that consisted of a 1000-iteration adaptation phase and

414   an additional 30,000-iteration burn-in phase. The final 20,000 iterations were thinned at a rate of

415   1 in 20 resulting in 1,000 iterations from each chain that were used to form the joint posterior

416   distribution of the parameters. With these MCMC settings, the model took five days to run

417   (10,000 iterations per day) on desktop computer with a 3.5 GHz processer and 64 GB of RAM.

418   We inspected trace plots of each MCMC chain and used the $\hat{R}$ statistic to assess

419   convergence of the posterior for each parameter, where $\hat{R} < 1.1$ indicates convergence (Gelman

420   et al. 2013). We then performed posterior predictive checks to assess goodness of fit by

421   simulating replicated data from the joint posterior distribution. We used the joint log-likelihood

422   of the capture histories (Eq. 7) and travel times (Eq. 9) as a goodness of fit statistic, which was

423   calculated for both observed and replicated data for each draw in the joint posterior distribution.

424   We calculated the probability that the observed data could have been generated by the model by

425   calculating the proportion of times that the likelihood of the observed data was greater than that

426   for replicated data. Often referred to as a Bayesian *p*-value, a probability >0.95 or <0.05 is

427   typically taken as evidence of lack of fit (Gelman et al. 2013).

428

429   **Results**

430   The $\hat{R}$ statistics indicated that the Markov Chains converged to a stable stationary

431   distribution. Of the 155 estimated parameters, $\hat{R}$ was less than 1.1 for all but one parameter (

432    $\theta_{0,D4,4}$, the intercept for P at telemetry station D_4 in year 4), and its $\hat{R}$ was 1.115, just slightly

433   higher than the standard cutoff value. In addition, we found no evidence of lack of fit; 54.4% of

434   log-likelihood values for the observed data were greater than those for replicated data, indicating

435   that the observed data were just as likely to have been generated by the model compared to

436   replicated data that was known to have been generated by the model.

437   Daily inflow to the Delta varied widely over the study period, ranging from 193 $m^3 \cdot s^{-1}$ to

438   2,180 $m^3 \cdot s^{-1}$ (Fig. 3), which encompassed the 1st to 95th percentile of daily discharge in the 69-

439   year flow record for the December through March migration period. Inflows influenced

440   detection probabilities, travel time, survival, and routing. We found that discharge had a

441   negative effect on detection probabilities at most telemetry stations, but the magnitude of the

442   effect declined from the upper to lower Delta as tidal influence increased (Fig. A3[1]). In general,

443   detection probabilities were greater than 0.8 at most telemetry stations when flows were below

444   1,000 $m^3 \cdot s^{-1}$, but decreased at higher flows with the rate of decrease varying among years and

445   telemetry stations (Fig. A4[1]).

446   Most survival and travel time parameters associated with reach 6 (the Delta Cross

447   Channel) exhibited wide credible intervals because only 6 release groups were released prior to

448   mid-December when the Delta Cross Channel undergoes mandatory closures for fish protection

449   (Fig. 4). Consequently, there was relatively little data from which to estimate the effects of river

450   discharge on travel time and survival for reach 6.

451   For all other reaches, we found that median travel time was influenced by river flow.

452   Posterior distributions for the effect of flow on travel time (α_1) were negative and credible

22

453   intervals excluded zero, indicating that increases in river flow reduced median travel times (Figs.

454   4 and 5). Credible intervals for the effect of the Delta Cross Channel on median travel time (α_2)

455   overlapped zero, with the exception of reach 7, indicating little evidence for an effect of an open

456   gate on travel time (Fig. 4). Credible intervals for the standard deviation of the release-group

457   random effects (ξ_μ) were well above zero, providing evidence that median travel times varied

458   among release groups after accounting for other effects in the model. At low inflows, median

459   travel times for tidal reaches (reaches 7 and 8) were considerably longer than other reaches (Fig.

460   5). Furthermore, at low flows, median travel times for reach 8 were about four times that of

461   reach 7.

462   In contrast to travel time, survival was strongly related to river flow in just three of eight

463   reaches. In the upper two reaches, which exhibit the least tidal influence, the effect of flow (β_1)

464   was positive (Fig. 4) but the relative change in survival was small because survival was >0.90

465   over the range of observed discharge (Fig. 6). However, we estimated strong positive effects of

466   river flow in reaches 3-5 (Fig. 4); these reaches transition from bidirectional to unidirectional

467   flow as river discharge increases (Fig. 3 middle panel). Although discharge affected travel time

468   in the tidal reaches (reaches 7 and 8), the posterior distributions of β_1 were centered on zero for

469   these reaches and credible intervals were narrow, providing strong evidence of little relationship

470   between survival and discharge. We also found evidence that operation of the Delta Cross

471   Channel, which removes water from the Sacramento River, was associated with lower survival in

472   reaches of the Sacramento River downstream of the Delta Cross Channel (reaches 4 and 7). For

473   these reaches, posterior medians of β_2 were negative, and 75–90% of the posterior distribution

474   was less than zero (Fig. 4). Similar to findings with travel time, the posterior distributions for

475   standard deviations of random effects associated with survival were positive, indicating

476   additional release-to-release variation in survival over and above the effects of covariates

477   included in the model. Last, we also found a positive effect of fork length on survival (β_3,

478   median = 0.152, 90% credible interval = 0.062–0.243, Fig. A5[1]).

479   Reach-specific flow-survival relationships revealed that survival increased sharply with

480   river flow in transitional reaches but not riverine or tidal reaches (Fig. 6). Survival in riverine

481   reaches (reaches 1 and 2) were high regardless of discharge, approaching 1 as flow increased. In

482   transitional reaches, median survival at the lowest flows was about 0.75 for reach 4 (Sacramento

483   River) and 0.5 for reach 3 (Sutter and Steamboat Slough) and reach 5 (Georgiana Slough). In

484   these reaches, survival increased sharply with river flow, approaching 1 as river flow exceeded

485   1,000 $m^3 \cdot s^{-1}$, which coincides with the transition from bidirectional to unidirectional flow (Fig. 3

486   middle panel). In tidal reaches, survival was not related to discharge, but median survival in

487   reach 7 (Sacramento River) was about twice that observed in reach 8 (interior Delta).

488   We found that routing probabilities (Fig. 7) followed a relationship similar to that

489   between total discharge (Q) and the fraction of discharge entering each route (Fig. A2),

490   indicating that the distribution of mean daily flow among channels is a key driver of migration

491   routing (see also Cavallo et al. 2015). As discharge increases, the probability of entering Sutter

492   and Steamboat Slough increased by 12 percentage points from about 0.23 to an estimated upper

493   limit (U) of 0.35 (Table 2, Fig. 7). In contrast, as flow increases, the probability of entering

494   Georgiana Slough (when the Delta Cross Channel gate is closed) decreased by 16 percentage

495   points from 0.43 to an estimated lower limit (L) of 0.27 (Table 2, Fig. 7). For these routes,

496   routing probabilities approach upper and lower limits at an inflow of about 1,000 $m^3 \cdot s^{-1}$ (Fig. 7),

497   the point at which transitional reaches switch from bidirectional to unidirectional flows (Fig. 3

498   middle panel). We found little variation in routing probability among release groups for Sutter

499   and Steamboat Sloughs and the Delta Cross Channel, but considerable variation for Georgiana

500   Slough, particularly at low discharge (Fig. 7).

501   We found that operation of the Delta Cross Channel increased the proportion of fish

502   migrating through interior Delta (reach 8) where survival is low. Routing into the Delta Cross

503   Channel decreased as flow increased, although credible intervals were wide (Table 2, Fig. 7).

504   We found evidence that an open Delta Cross gate reduced the probability of entering Georgiana

505   Slough (Table 2, Fig. 7 lower right panel). However, the combined probability of entering

506   Georgiana Slough and Delta Cross Channel, both of which lead fish to the interior Delta (reach

507   8), was 15 percentage points higher than the probability of entering Georgiana Slough alone

508   when the gates are closed (Fig. 7 lower right panel).

509   The reach-specific survival relationships with flow dictate the composite survival of

510   juvenile salmon migrating through the Delta via alternative migration routes. At low flows, fish

511   migrating through the Sacramento River exhibit the highest through-Delta survival, followed by

512   Sutter and Steamboat Slough, but as river discharge increases, survival for Sutter and Steamboat

513   Slough approaches that of the Sacramento River, leveling off at a survival of about 0.75 (Fig. 8).

514   Survival of fish migrating through Georgiana Slough also increases with inflow but approaches a

515   maximum of about 0.4. Since survival in all reaches except 7 and 8 approach 1 as discharge

516   increases, survival in the tidal reaches imposes an upper limit on the overall through-Delta flow-

517   survival relationship for each route.

518   Since routing probabilities determine the fraction of the population experiencing a given

519   route-specific survival, both factors contribute to the shape of the relationship between overall

520   survival and discharge. Mean overall survival increases with discharge from about 0.32 to 0.70

521   and falls in between the route-specific survival relationships (Fig. 8 lower right panel).

522   However, at low flows, overall survival is pulled more towards the low survival of Georgiana

523   Slough (Fig. 8 lower right panel) because the proportion of fish entering Georgiana Slough is

524   highest at low flows (Fig. 7). By contrast, as the proportion of fish entering Georgiana Slough

525   decreases with increasing flow, overall survival not only increases owing to the flow-survival

526   relationships, but is weighted more towards the higher-survival migration routes owing to the

527   flow-routing relationships.

528   Route-specific travel time distributions also vary considerably with river flow, and fish

529   traveling through the interior Delta (reach 8) via Georgiana Slough or the Delta Cross Chanel

530   exhibit longer travel times than those that migrate through the north Delta via the Sacramento

531   River and Sutter and Steamboat Slough (Fig. 9). For example, at inflows of 235 $m^3 \cdot s^{-1}$, the

532   median travel time for Georgiana Slough is 18.0 d, with some travel times as long as 40 d. By

533   comparison, for north Delta routes, median travel times are 12.2–12.6 d, with the tail of the

534   distribution extending to 30 d. In contrast, at inflows of 1,357 $m^3 \cdot s^{-1}$, expected median travel

535   times are 2.7–3.1 d for north Delta routes compared to 6.4 d for Georgiana Slough, with a 10-d

536   difference between the tails of the distributions.

537

538   **Discussion**

539   Understanding spatiotemporal variation in survival of migrating populations is critical for

540   identifying underlying mechanisms driving survival, particularly in a highly dynamic and

541   spatially complex environment such as the Sacramento-San Joaquin River Delta. Although

542   variation in survival of juvenile salmon migrating through the Delta has long been linked to

543   freshwater inflows (Kjelson and Brandes 1989; Newman and Rice 2002; Newman 2003), we

544   lacked understanding of how spatial variation in survival gave rise to this overall relationship.

545 Our analysis has revealed that the overall flow-survival relationship is driven by three key

546 reaches that transition from unidirectional flow at high inflows to tidally driven bidirectional

547 flow at low inflows. In contrast, riverine reaches exhibited high survival at all levels of inflow

548 and tidal reaches had lower but constant survival with respect to inflow. Thus, the flow-survival

549 relationship captures the gradient that occurs as transitional reaches shift from tidal to riverine

550 environments as inflow increases.

551   In addition to being the hub of California's water delivery system, the Delta forms a

552 critical nexus between freshwater and ocean environments. Juvenile salmon emigrating from

553 natal tributaries first experience a tidal environment during their migration through the Delta.

554 Juvenile salmon are particularly vulnerable during this transition because they must modify their

555 migration tactics to progress seaward while undergoing physiological changes in preparation for

556 seawater entry. Although some researchers have found high survival rates in estuaries (Clark et

557 al. 2016), others have found that migration through estuaries is associated with high mortality

558 rates relative to riverine or early marine phases (Thorstad et al. 2012 and references therein). For

559 example, in a study of juvenile Atlantic salmon (*Salmo salar*) in riverine, estuarine, and early

560 ocean environments, Halfyard et al. (2013) found that survival was most impacted in estuarine

561 habitats near the head of tide. Our study is consistent with these findings and highlights how

562 river inflows can interact with tides to influence survival by shifting the location at which the

563 hydrodynamics switch from unidirectional to bidirectional flow.

564   Many studies (ours included) have correlated travel time and survival to river flow

565 because these relationships provide a direct linkage between a key management variable and the

566 subsequent response of migrating juvenile salmon populations (Connor et al. 2003; Smith et al.

567 2003; Courter et al. 2016). However, it is important to recognize that river flow affects travel

27

568   time and survival through both direct and indirect mechanisms. River flow directly influences

569   migration rates of juvenile salmon by dictating water velocity, which is a function of channel

570   geometry (Zabel and Anderson 1997; Zabel 2002; Tiffan et al. 2009). In turn, migration rates

571   dictate arrival timing at ocean entry, which can influence early ocean survival (Satterthwaite et

572   al. 2014). In contrast, river flow affects survival indirectly through a number of possible

573   mechanisms. River flow can affect the proportion of fish using alternative routes at

574   hydroelectric projects (Coutant and Whitney 2000) and in channel network systems such as the

575   Delta (Cavallo et al. 2015; Perry et al. 2015). If survival differs among routes, which is often the

576   case, then river discharge affects population survival by influencing the proportion of fish using

577   high- or low-survival routes (Perry et al. 2013, 2016). In addition, river flow is often correlated

578   with other environmental variables that influence survival such as turbidity and water

579   temperature (Baker et al. 1995; Connor et al. 2003; Smith et al. 2003), which in turn may

580   influence predation rates (Vogel and Beauchamp 1999; Ferrari et al. 2013).

581   Reducing travel time and exposure to predators is a key mechanism by which river flow

582   has been hypothesized to affect survival of migrating juvenile salmonids, but establishing this

583   linkage has proven elusive. Although travel time has been consistently linked with discharge via

584   water velocity, some studies in the Snake and Columbia Rivers found no significant relationship

585   between travel time and survival, but a significant relation between migration distance and

586   survival (Bickford and Skalski 2000; Smith et al. 2002). To explain these counterintuitive

587   findings, Anderson et al. (2005) developed a predator-prey model that expressed survival as a

588   function of both travel time and travel distance. Their analysis revealed that the dependence of

589   survival on travel time is dictated by the nature of predator-prey interactions. When prey migrate

590   in a directed fashion through a field of stationary predators, survival is independent of travel time

28

591   and depends only on travel distance. In contrast, survival depends on travel time when random

592   movement dominates directed migration or when predators adopt prey searching tactics. These

593   findings illustrate how the relationship between flow and survival is context dependent, arising

594   from a combination of mechanisms that may directly affect survival (e.g., temperature) or

595   indirectly affect survival by modifying predator encounter rates (temperature, turbidity, predator

596   and prey behavior). Although our analysis here focused on estimating the association between

597   discharge and survival, our modeling framework allows exploration of alternative model

598   structures for linking flow to survival via travel time. For example, the XT model can be

599   incorporated into our analytical framework and compared against the current model structure to

600   assess the strength of evidence for the dependence of survival on travel time.

601   Predation by a host of non-native piscivorous fishes is thought to be the primary

602   proximate cause of juvenile salmon mortality in the Delta (Cavallo et al. 2013; Grossman 2016;

603   Sabal et al. 2016). Variation in survival among reaches observed in our study is consistent with

604   expectations based on predator-prey models. Juvenile salmon migrate downstream through

605   riverine reaches in a directed fashion and survival was high regardless of inflows and variation in

606   travel time. We observed a similar pattern at high flows when transitional reaches exhibit

607   unidirectional flows similar to riverine reaches. As inflow declines and tidal influence moves

608   upstream into transitional reaches, not only does travel time increase but travel distance increases

609   because juvenile salmon may be advected upstream on flood tides (Moser et al. 1991).

610   Simultaneously increasing both travel time and cumulative travel distance will act to increase

611   predator encounter rates. Thus, the flow-survival relationship that we observed in transitional

612   reaches likely arises from the transition from directed downstream movement at high flows to

613   less directed, bidirectional movement during low flows. In tidal reaches, our *a priori* expectation

614   was that neither travel time nor survival would be related to inflow because the magnitude of

615   tidal flows (on the order of $\pm 3{,}500$ m^3·s^{-1}) swamps the signal of net inflow (Fig. 3 bottom panel).

616   Although we observed no relation between survival and inflow in tidal reaches, we were

617   surprised to find a strong effect of inflow on travel time, suggesting that survival may be

618   decoupled from travel time in tidal reaches.

619   We included only inflow, DCC gate position, and fork length as covariates on reach-

620   specific survival, but numerous other factors drive variation in survival. By casting our mark-

621   recapture model in a hierarchical Bayesian framework and including a random effect on release

622   group, we were able to quantify the magnitude of this variation but not its source. Seasonal and

623   annual variation in reach-specific predator densities, environmental drivers (e.g., water

624   temperature, turbidity), and spring-neap tidal cycles will act to modulate how travel time and

625   survival respond to changes in inflow, thereby propagating variation among cohorts of juvenile

626   salmon that experience a common set of flow conditions. Specifically, variation in survival

627   among release groups was highest in tidal reaches and in transition reaches during low inflows,

628   further suggesting that tidal cycles play an important role in driving variation in survival. For

629   example, at a given inflow, cohorts migrating through the Delta during neap tides will experience

630   lower-magnitude flood tides and first encounter bidirectional flows further downstream relative

631   to cohorts migrating during spring tides. The high release-to-release variation in our study

632   provides opportunity for future work to quantify how factors other than inflow influence survival

633   in the Delta.

634   Our Bayesian mark-recapture model makes two important advances in the development

635   of statistical mark-recapture models used to estimate survival of migrating juvenile salmonids.

636   First, modeling individual covariates that vary through time is challenging owing to missing

637   covariate values for undetected individuals. Consequently, most approaches have ignored

638   within- and among-individual variation by averaging covariates over individuals within release

639   groups (Conner et al. 2003; Smith et al. 2003) or averaging covariates over space and time for

640   each individual (Stitch et al. 2015). In contrast, our model allows for individual covariates that

641   vary through space and time by incorporating an auxiliary model for travel times to impute

642   missing travel time, reach entry times, and covariates at the time of reach entry. Given the

643   considerable capital expense associated with conducting telemetry studies, our framework allows

644   the maximum amount of information to be extracted from telemetry data sets that typically have

645   small sample sizes. Second, our joint travel time and mark-recapture model explicitly considers

646   both migration and demographic processes under a single analytical framework. Thus, our

647   modeling framework opens the door to a number of useful extensions such as modeling survival

648   directly as a function of an individual's travel time (Muthukumarana et al. 2008) or by using an

649   event-time framework (e.g., Sparling et al. 2006; Zabel et al. 2014) where survival can be

650   modeled as a function of temporal variation in covariates during an individual's residence time

651   within a reach.

652   Our analysis provides insight into how water management decisions that influence inflow

653   and water routing are likely to affect travel time, routing, and survival of migrating juvenile

654   salmonids. First, survival decreases sharply and routing into the interior Delta (where survival is

655   low) increases sharply as Delta inflows decline below approximately 1,000 $m^3 \cdot s^{-1}$, the point at

656   which transitional reaches shift from bidirectional to unidirectional flow (Figs 7 and 8). In

657   contrast, at inflows greater than 1,000 $m^3 \cdot s^{-1}$, survival is maximized and changes relatively little

658   with flow while routing into the interior Delta via Georgiana Slough is minimized and insensitive

659   to inflow. These findings indicate that water management actions that reduce inflows to the Delta

660   will have relatively little effect on survival at high flows, but potentially considerable negative

661   effects at low flows. Furthermore, operation of the Delta Cross Channel not only increases the

662   fraction of the population that enters the interior Delta where survival is low (Fig. 7), but is

663   associated with lower survival for the Sacramento River (Fig. 4). These compounding effects of

664   opening the Delta Cross Channel act to further reduce overall survival relative to inflows alone

665   (Fig. A6[1]). Our findings illustrate how tradeoffs between juvenile salmon survival and water

666   management for human use vary with the amount of flow entering the Delta. Thus, our

667   modeling framework can be used as a management tool to explore the consequences of such

668   tradeoffs and to quantitatively assess the effect of alternative management scenarios on travel

669   time, routing, and survival.

670   Water flow has been dubbed the "master" variable in the Delta because of its economic

671   importance and its pervasive effect on all components of this complex and dynamic aquatic

672   ecosystem (Mount et al. 2012; Lund et al. 2015). Indeed, our work is beginning to shed light on

673   the multiple ways in which river flows differentially affect survival in different reaches of the

674   Delta and interact with water and fish routing to affect overall survival. In turn, these insights

675   will aid managers in devising strategies to balance consumptive water use with management

676   actions that aim to recover threatened and endangered salmon populations in the Sacramento

677   River.

678

683 Fish Hatchery for logistical support and for providing the juvenile salmon used in our analysis.

684 Amy Hansen, Ken Tiffan, and Josh Korman provided many insightful comments that improved

685 the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and

686 does not imply endorsement by the U.S. Government

687

688 **References**

689 Anderson, J.J., Gurarie, E. and Zabel, R.W. 2005. Mean free-path length theory of predator–prey

690   interactions: application to juvenile salmon migration. Ecol. Modell. **186**(2): 196–211.

691   doi: 10.1016/j.ecolmodel.2005.01.014.

692 Baker, P.F., Ligon, F.K. and Speed, T.P. 1995. Estimating the influence of temperature on the

693   survival of Chinook salmon smolts (Oncorhynchus tshawytscha) migrating through the

694   Sacramento–San Joaquin River Delta of California. Can. J. Fish. Aquat. Sci. **52**(4): 855–

695   863. doi: 10.1139/f95-085.

696 Bickford, S.A. and Skalski, J.R. 2000. Reanalysis and interpretation of 25 years of Snake–

697   Columbia River juvenile salmonid survival studies. N. Am. J. Fish. Manage. **20**(1): 53–

698   68. doi: 10.1577/1548-8675(2000)020<0053:RAIOYO>2.0.CO;2.

699 Bonner, S.J. and Schwarz, C.J. 2004. Continuous time–dependent individual covariates and the

700   Cormack–Jolly–Seber model. Anim. Biodiversity Conserv. **27**(1): 49–155.

701 Brandes, P.L., and McLain, J.S. 2001. Juvenile Chinook salmon abundance, distribution, and

702   survival in the Sacramento–San Joaquin Estuary. *In* Contributions to the Biology of the

703   Central Valley Salmonids, Fish Bulletin 179, vol. 2. *Edited by* R.L. Brown. California

704   Department of Fish and Game, Sacramento, C.A. pp 39–138.

705   California Department of Water Resources. 2016. 2014 Georgiana Slough Floating Fish

706   Guidance Structure Performance Evaluation Project Report. Bay-Delta Office,

707   Sacramento, California. Available from

708   http://baydeltaoffice.water.ca.gov/sdb/GS/docs/Final%20Report%20October%202016%2

709   0Edition%20103116-signed.pdf [accessed 22 November 2017].

710   Catchpole, E.A., Morgan, B.J. and Tavecchia, G. 2008. A new method for analysing discrete life

711   history data with missing covariate values. J. R. Stat. Soc. B. **70**(2): 445–460. doi:

712   10.1111/j.1467-9868.2007.00644.x.

713   Cavallo, B., Merz, J. and Setka, J. 2013. Effects of predator and flow manipulation on Chinook

714   salmon (*Oncorhynchus tshawytscha*) survival in an imperiled estuary. Environ. Biol.

715   Fishes, **96**(2-3): 393–403. doi: 10.1007/s10641-012-9993-5.

716   Cavallo, B., Gaskill, P., Melgo, J. and Zeug, S.C. 2015. Predicting juvenile Chinook Salmon

717   routing in riverine and tidal channels of a freshwater estuary. Environ. Biol. Fishes,

718   **98**(6): 1571–1582. doi: 10.1007/s10641-015-0383-7.

719   Clark, T.D., Furey, N.B., Rechisky, E.L., Gale, M.K., Jeffries, K.M., Porter, A.D., Casselman,

720   M.T., Lotto, A.G., Patterson, D.A., Cooke, S.J. and Farrell, A.P. 2016. Tracking wild

721   sockeye salmon smolts to the ocean reveals distinct regions of nocturnal movement and

722   high mortality. Ecol. App. **26**(4): 959–978. doi: 10.1890/15-0632.

723   Connor, W.P., Burge, H.L., Yearsley, J.R. and Bjornn, T.C. 2003. Influence of flow and

724   temperature on survival of wild subyearling fall Chinook salmon in the Snake River. N.

725 Am. J. Fish. Manage. **23**(2): 362–375. doi: 10.1577/1548-

726 8675(2003)023<0362:IOFATO>2.0.CO;2.

727 Courter, I.I., Garrison, T.M., Kock, T.J., Perry, R.W., Child, D.B. and Hubble, J.D. 2016.

728 Benefits of prescribed flows for salmon smolt survival enhancement vary longitudinally

729 in a highly managed river system. River Res. Appl. **32**(10): 1999–2008. doi:

730 10.1002/rra.3066.

731 Coutant, C.C. and Whitney, R.R. 2000. Fish behavior in relation to passage through hydropower

732 turbines: a review. Trans. Am. Fish. Soc. **129**(2): 351–380. doi: 10.1577/1548-

733 8659(2000)129<0351:FBIRTP>2.0.CO;2.

734 Denwood, M.J. 2016. runjags: An R package providing interface utilities, model templates,

735 parallel computing methods and additional distributions for MCMC models in JAGS. J.

736 Stat. Software, **71**(9): 1–25. doi: 10.18637/jss.v071.i09.

737 Ferrari, M.C., Ranåker, L., Weinersmith, K.L., Young, M.J., Sih, A. and Conrad, J.L. 2013.

738 Effects of turbidity and an invasive waterweed on predation by introduced largemouth

739 bass. Environ. Biol. Fishes, **97**(1): 79–90. doi: 10.1007/s10641-013-0125-7.

740 Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A. and Rubin, D.B. 2013. Bayesian

741 data analysis. CRC Press, Boca Raton, F.L.

742 Gibson, A.J.F., Halfyard, E.A., Bradford, R.G., Stokesbury, M.J. and Redden, A.M. 2015.

743 Effects of predation on telemetry-based survival estimates: insights from a study on

744 endangered Atlantic salmon smolts. Can. J. Fish. Aquat. Sci. **72**(5): 728–741. doi:

745 10.1139/cjfas-2014-0245.

746   Grossman, G.D. 2016. Predation on fishes in the Sacramento–San Joaquin Delta: current

747   knowledge and future directions. San Francisco Estuary and Watershed Science, **14**(2).

748   Available from http://escholarship.org/uc/item/9rw9b5tj [accessed 12 July 2017].

749   Halfyard, E.A., Gibson, A.J.F., Stokesbury, M.J., Ruzzante, D.E. and Whoriskey, F.G. 2013.

750   Correlates of estuarine survival of Atlantic salmon postsmolts from the Southern Upland,

751   Nova Scotia, Canada. Can. J. Fish. Aquat. Sci. **70**(3): 452–460. doi: 10.1139/cjfas-2012-

752   0287.

753   Healey, M., Goodwin, P., Dettinger, M., and Norgaard, R. 2016. The State of Bay–Delta Science

754   2016: An Introduction. San Francisco Estuary and Watershed Science, **14**(2). Available

755   from http://escholarship.org/uc/item/9k43h252. doi:

756   http://dx.doi.org/10.15447/sfews.2016v14iss2art5 [accessed 12 July 2017].

757   King, R., Morgan, B., Gimenez, O. and Brooks, S. 2010. Bayesian analysis for population

758   ecology. CRC press, Boca Raton, F.L.

759   Kjelson, M.A., Raquel, P.F., and Fisher, F.W. 1982. Life history of fall-run juvenile Chinook

760   salmon, *Oncorhynchus tshawytscha*, in the Sacramento–San Joaquin Estuary, California.

761   *In* Estuarine Comparisons. *Edited by* V.S. Kennedy. Academic Press, New York, N.Y.

762   pp. 393–411.

763   Kjelson, M.A. and Brandes, P.L. 1989. The use of smolt survival estimates to quantify the effects

764   of habitat changes on salmonid stocks in the Sacramento-San Joaquin rivers, California.

765   *In* Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid

766   Stocks, Nanaimo, B.C., 6–8 May 1987. Canadian special publication of fisheries and

767   aquatic sciences 105, Department of Fisheries and Oceans, Ottowa, Canada. pp. 100–115.

768   Link, W.A. and Barker, R.J. 2010. Bayesian inference: with ecological applications. Academic

769   Press, San Diego, C.A.

770   Lund, B., Brandt, S., Collier, T., Atwater, B., Canuel, E., Fernando, H.J.S., Meyer, J., Norgaard,

771   R., Resh, V., Wiens, J., and Zedler, J. 2015. Flows and fishes in the Sacramento-San

772   Joaquin Delta: Research needs in support of adaptive management. Delta Stewardship

773   Council, Sacramento, C.A. Available from

774   http://deltacouncil.ca.gov/sites/default/files/2015/09/2015-9-29-15-0929-Final-Fishes-

775   and-Flows-in-the-Delta.pdf [accessed 12 July 2017].

776   Michel, C.J., Ammann, A.J., Lindley, S.T., Sandstrom, P.T., Chapman, E.D., Thomas, M.J.,

777   Singer, G.P., Klimley, A.P. and MacFarlane, R.B. 2015. Chinook salmon outmigration

778   survival in wet and dry years in California's Sacramento River. Can. J. Fish. Aquat. Sci.

779   **72**(11): 1749–1759. doi: 10.1139/cjfas-2014-0528.

780   Monnahan, C.C., Thorson, J.T. and Branch, T.A. 2017. Faster estimation of Bayesian models in

781   ecology using Hamiltonian Monte Carlo. Methods Ecol. Evol. **8**(3): 339–348. doi:

782   10.1111/2041-210X.12681.

783   Moser, M.L., Olson, A.F. and Quinn, T.P. 1991. Riverine and estuarine migratory behavior of

784   coho salmon (*Oncorhynchus kisutch*) smolts. Can. J. Fish. Aquat. Sci. **48**(9): 1670-1678.

785   doi: 10.1139/f91-198.

786   Mount, J., Bennett, W., Durand, J., Fleenor, W., Hanak, E., Lund, J. and Moyle, P. 2012. Aquatic

787   Ecosystem Stressors in the Sacramento-San Joaquin Delta. Public Policy Institute of

788   California, San Francisco, C.A. Available from

789   http://www.ppic.org/content/pubs/report/R_612JMR.pdf [accessed 12 July 2017].

790   Muthukumarana, S., Schwarz, C.J. and Swartz, T.B. 2008. Bayesian analysis of mark-recapture

791   data with travel time-dependent survival probabilities. Can. J. Stat. **36**(1): 5–21. doi:

792   10.1002/cjs.5550360103.

793   Newman, K.B. 2003. Modelling paired release-recovery data in the presence of survival and

794   capture heterogeneity with application to marked juvenile salmon. Stat. Modell. **3**(3):

795   157–177. doi: https://doi.org/10.1191/1471082X03st055oa.

796   Newman, K.B. and Rice, J. 2002. Modeling the survival of Chinook salmon smolts outmigrating

797   through the lower Sacramento River system. J. Am. Stat. Assoc. **97**(460): 983-993. doi:

798   10.1198/016214502388618771.

799   Newman, K.B. and Brandes, P.L. 2010. Hierarchical modeling of juvenile Chinook salmon

800   survival as a function of Sacramento–San Joaquin Delta water exports. N. Am. J. Fish.

801   Manage. **30**(1): 157–169. doi: 10.1577/M07-188.1.

802   Papaspiliopoulos, O., Roberts, G.O. and Sköld, M. 2007. A general framework for the

803   parametrization of hierarchical models. Stat. Sci. **22**(1): 59–73.

804   doi:10.1214/088342307000000014.

805   Perry, R.W. 2010. Survival and migration dynamics of juvenile Chinook salmon (*Oncorhynchus*

806   *tshawytscha*) in the Sacramento-San Joaquin River Delta. Ph.D. dissertation, School of

807   Aquatic and Fishery Sciences, University of Washington, Seattle, W.A.

808   Perry, R.W., Skalski, J.R., Brandes, P.L., Sandstrom, P.T., Klimley, A.P., Ammann, A. and

809   MacFarlane, B. 2010. Estimating survival and migration route probabilities of juvenile

810   Chinook salmon in the Sacramento–San Joaquin River Delta. N. Am. J. Fish. Manage.

811   **30**(1): 142–156. doi: 10.1577/M08-200.1.

812   Perry, R.W., Romine, J.G., Brewer, S.J., LaCivita, P.E., Brostoff, W.N. and Chapman, E.D.

813   2012. Survival and migration route probabilities of juvenile Chinook salmon in the

814   Sacramento-San Joaquin River Delta during the winter of 2009-10. US Geological

815   Survey Open File Report No. 2012-1200. Available from

816   https://pubs.usgs.gov/of/2012/1200/ [accessed 12 July 2017].

817   Perry, R.W., Brandes, P.L., Burau, J.R., Klimley, A.P., MacFarlane, B., Michel, C. and Skalski,

818   J.R. 2013. Sensitivity of survival to migration routes used by juvenile Chinook salmon to

819   negotiate the Sacramento-San Joaquin River Delta. Environ. Biol. Fishes, **96**(2-3): 381–

820   392. doi: 10.1007/s10641-012-9984-6.

821   Perry, R.W., Brandes, P.L., Burau, J.R., Sandstrom, P.T. and Skalski, J.R. 2015. Effect of tides,

822   river flow, and gate operations on entrainment of juvenile salmon into the Interior

823   Sacramento–San Joaquin River delta. Trans. Am. Fish. Soc. **144**(3): 445–455. doi:

824   10.1080/00028487.2014.1001038 .

825   Perry, R.W., Buchanan, R.A., Brandes, P.L., Burau, J.R. and Israel, J.A. 2016. Anadromous

826   salmonids in the Delta: new science 2006–2016. San Francisco Estuary and Watershed

827   Science, **14**(2). Available from http://escholarship.org/uc/item/27f0s5kh [accessed 12

828   July 2017].

829   R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for

830   Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/

831   [accessed 20 October 2017].

832   Raymond, H.L. 1988. Effects of hydroelectric development and fisheries enhancement on spring

833   and summer chinook salmon and steelhead in the Columbia River basin. N. Am. J. Fish.

834   Manage. **8**(1): 1–24. doi: 10.1577/1548-8675(1988)008<0001:EOHDAF>2.3.CO;2.

835   Romine, J.G., Perry, R.W., Pope, A.C., Stumpner, P., Liedtke, T.L., Kumagai, K.K. and Reeves,

836   R.L. 2017. Evaluation of a floating fish guidance structure at a hydrodynamically

837   complex river junction in the Sacramento–San Joaquin River Delta, California, USA.

838   Marine and Freshwater Research, **68**(5): 878–888. doi: 10.1071/MF15285.

839   Sabal, M., Hayes, S., Merz, J. and Setka, J. 2016. Habitat alterations and a nonnative predator,

840   the Striped Bass, increase native Chinook Salmon mortality in the Central Valley,

841   California. N. Am. J. Fish. Manage. **36**(2): 309–320. doi:

842   10.1080/02755947.2015.1121938.

843   Satterthwaite, W.H., Carlson, S.M., Allen-Moran, S.D., Vincenzi, S., Bograd, S.J. and Wells,

844   B.K. 2014. Match-mismatch dynamics and the relationship between ocean-entry timing

845   and relative ocean recoveries of Central Valley fall run Chinook salmon. Mar. Ecol. Prog.

846   Series. **511**: 237–248. doi. 10.3354/meps10934.

847 Skalski, J.R., Townsend, R., Lady, J., Giorgi, A.E., Stevenson, J.R., and McDonald, R.D. 2002.

848   Estimating route-specific passage and survival probabilities at a hydroelectric project

849   from smolt radiotelemetry studies. Can. J. Fish. Aquat. Sci. **59**(8): 1385–1393. doi:

850   10.1139/f02-094.

851 Smith, S.G., Muir, W.D., Williams, J.G. and Skalski, J.R. 2002. Factors associated with travel

852   time and survival of migrant yearling Chinook salmon and steelhead in the lower Snake

853   River. N. Am. J. Fish. Manage. **22**(2): 385–405. doi: 10.1577/1548-

854   8675(2002)022<0385:FAWTTA>2.0.CO;2.

855 Smith, S.G., Muir, W.D., Hockersmith, E.E., Zabel, R.W., Graves, R.J., Ross, C.V., Connor,

856   W.P. and Arnsberg, B.D. 2003. Influence of river conditions on survival and travel time

857   of Snake River subyearling fall Chinook salmon. N. Am. J. Fish. Manage. **23**(3): 939–

858   961. doi: 10.1577/M02-039.

859 Sparling, Y.H., Younes, N., Lachin, J.M. and Bautista, O.M. 2006. Parametric survival models

860   for interval-censored data with time-dependent covariates. Biostatistics, **7**(4): 599–614.

861   doi: https://doi.org/10.1093/biostatistics/kxj028.

862 Stich, D.S., Bailey, M.M., Holbrook, C.M., Kinnison, M.T. and Zydlewski, J.D. 2015.

863   Catchment-wide survival of wild-and hatchery-reared Atlantic salmon smolts in a

864   changing system. Can. J. Fish. Aquat. Sci. **72**(9): 1352–1365. doi: 10.1139/cjfas-2014-

865   0573.

866 Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H. and Finstad, B. 2012. A

867   critical life stage of the Atlantic salmon Salmo salar: behaviour and survival during the

868   smolt and initial post-smolt migration. J. Fish Biol. **81**(2): 500–542. doi: 10.1111/j.1095-

869   8649.2012.03370.x.

870 Tiffan, K.F., Kock, T.J., Haskell, C.A., Connor, W.P. and Steinhorst, R.K. 2009. Water velocity,

871   turbulence, and migration rate of subyearling fall Chinook salmon in the free-flowing and

872   impounded Snake River. Trans. Am. Fish. Soc. **138**(2): 373–384. doi: 10.1577/T08-

873   051.1.

874 Vogel, J.L. and Beauchamp, D.A. 1999. Effects of light, prey size, and turbidity on reaction

875   distances of lake trout (*Salvelinus namaycush*) to salmonid prey. Can. J. Fish. Aquat. Sci.

876   **56**(7): 1293–1297. doi: 10.1139/f99-071.

877 Ward Jr, J.H. 1963. Hierarchical grouping to optimize an objective function. J. Am. Stat. Assoc.

878   **58**(301): 236–244. doi: 10.1080/01621459.1963.10500845.

879 White, G.C. and Burnham, K.P. 1999. Program MARK: survival estimation from populations of

880   marked animals. Bird Study, **46**(sup1): S120–S139. doi: 10.1080/00063659909477239.

881 Zabel, R.W. 2002. Using "travel time" data to characterize the behavior of migrating animals.

882   Am. Nat. **159**(4): 372–387. doi: 10.1086/338993.

883 Zabel, R.W. and Anderson, J.J. 1997. A model of the travel time of migrating juvenile salmon,

884   with an application to Snake River spring chinook salmon. N. Am. J. Fish. Manage.

885   **17**(1): 93–100. doi: 10.1577/1548-8675(1997)017<0093:AMOTTT>2.3.CO;2.

886   Zabel, R.W., Burke, B.J., Moser, M.L. and Caudill, C.C. 2014. Modeling temporal phenomena in

887   variable environments with parametric models: an application to migrating salmon. Ecol.

888   Modell. **273**: 23–30.

Tables

Table 1. Description of release groups and data sources.

Release group	Source	Year	Release dates	Number released	Number analyzed	Release sites (rkm)
1	Perry et al. (2010, 2013)	2006	Dec 5-6	64	64	172
2	Perry et al. (2010, 2013)	2007	Jan 17-18	80	80	172
3	Michel et al. (2015)		Jan 15-Feb 2	200	11	517
4	Perry et al. (2013)		Dec 4-7	208	208	115, 172
5	Michel et al. (2015)		Dec 7	150	60	345, 398, 500
6	Perry et al. (2013)	2008	Jan 15-18	211	211	115, 172
7	Michel et al. (2015)		Jan 17	154	65	345, 398, 500
8	Perry et al. (2013)		Nov 30-Dec 6	292	292	115, 172
9	Michel et al. (2015)		Dec 13	149	82	345, 398, 500
10	Michel et al.	2009	Jan 11	151	63	345, 398, 500

	(2015)					
11	Perry et al. (2013)		Jan 13-19	292	292	115, 172
12	Perry et al. (2012)		Dec 2-5	239	239	115, 191
13	Michel et al. (2015)		Dec 15	153	63	345, 398, 500
14	Perry et al. (2012)		Dec 16-19	240	240	115, 191
15	Michel et al. (2015)	2010	Jan 6	153	42	345, 398, 500
16	Michel et al. (2015)		Dec 17	120	79	500
17	Michel et al. (2015)	2011	Jan 5	120	79	500
All groups				2,976	2,170	

891 **Note**: Release sites are indicated by river kilometer (rkm) measured from the distance to the

892 Pacific Ocean. For fish release upstream of the Delta (> rkm 208), the number analyzed

893 indicates fish that were included in the analysis based on detections at telemetry stations near the

894 entrance to the Delta at rkm 189 or rkm 226.

895

896 **Table 2.** Posterior medians (90% credible intervals) for routing probabilities expressed as a
897 function of time-varying individual covariates. Parameter values without associated credible
898 intervals were set to the given value.

Parameter	Sutter and Steamboat Slough (Ψ_{AB3})	Delta Cross Channel (Ψ_{AC4})	Georgiana Slough ($\Psi_{AD4|C'}$)
U	0.35 (0.31 – 0.43)	1	1
L	0	0	0.27 (0.20 – 0.32)
γ_0	1.89 (0.91 – 3.30)	-1.49 (-2.40 – -0.67)	-2.95 (-4.57 – -1.83)
γ_1	2.17 (1.10 – 4.15)	-1.25 (-3.47 – 0.90)	-6.53 (-5.46 – -1.24)
γ_2	0	0	-0.55 (-2.76 – 0.33)
ξ_Ψ	0.19 (0.04 – 0.50)	0.31 (0.06 – 0.87)	0.89 (0.46 – 1.58)

899 **Note**: U = upper limit of logistic function, L = lower limit of logistic function, γ_0 = intercept, γ_1

900 = slope for effect of discharge on routing, γ_2 = slope for effect of open Delta Cross Channel

901 gates on routing, ξ_Ψ = standard deviation of the release group random effect.

902

903

Figure Captions

Fig. 1. Map of the Sacramento-San Joaquin River Delta showing the location of acoustic telemetry receiving stations (filled black circles) used to detect acoustic tagged juvenile salmon as they migrated through the Delta. Telemetry stations are labeled by migration route (A-D) and sampling occasion (1-7; see Fig. 2). These telemetry stations divide the Delta into eight discrete reaches (shown by numbered shaded regions), with an additional reach upstream of telemetry station A_2 (Reach 0) used as acclimation reach to allow fish to recover from post-release handling. The location of water pumping stations in the southern interior Delta is indicated by the pink diamonds.

Fig. 2. Schematic of the multistate mark-recapture model with parameters indexed by state (migration route) and sampling occasion. Parameters include reach-specific survival probabilities (S), site-specific detection probabilities (P), routing probabilities (Ψ), and λ, the joint probability of surviving and being detected at telemetry stations downstream of site A_6. Release locations are indicated by the nth release in route r at occasion j: n_{A1} (at Sacramento or upstream – see Table 1) and n_{D4} in Georgiana Slough.

Fig. 3. Daily inflow into the Sacramento-San Joaquin River Delta (top panel) and tidal influence on discharge at three locations in the Sacramento River during 2010 (middle and bottom panels). The top panel shows mean daily discharge of the Sacramento River at Freeport (A_2 in Fig. 1). In the two lower panels, lines show mean daily discharge and the shaded regions encompass the daily minimum and maximum discharge with values less than zero indicating reverse flows

926   caused by tidal forcing. The middle panel shows the Sacramento River at Freeport (black line,

927   gray shading) and the Sacramento River just downstream of Georgiana Slough (pink link and

928   shading; A_4 in Fig. 1). The bottom panel shows the Sacramento River at Rio Vista (A_5 in Fig. 1).

929

930   **Fig. 4.** Summary of posterior distributions of parameters estimating the effects of river flow and

931   Delta Cross Channel (DCC) gate position on travel time and survival. Points show the median of

932   the posterior distribution, heavy lines show the 25th to 75th percentile, and thin lines show the 5th

933   to 95th percentile. Green bars are density strips with darker regions illustrating higher posterior

934   density. Parameter definitions as follows: α_1 = slope for effect of discharge on mean of log-

935   travel time, α_2 = slope for effect of an open DCC gate on mean of log-travel time, ξ_μ =

936   standard deviation of release group random effect on μ, σ = variance parameter of the lognormal

937   travel time distribution, β_1 = slope for effect of discharge on survival, β_2 = slope for effect of an

938   open DCC gate on survival, ξ_S = standard deviation of release group random effect on survival.

939

940   **Fig. 5.** Reach-specific relationships between median travel time and inflow to the Delta as

941   measured at the Sacramento River at Freeport (shown for closed Delta Cross Channel gates and

942   plotted at the mean fork length). The heavy magenta line shows the mean relationship and the

943   dotted lines show the random effects estimates for each release group based on medians of the

944   joint posterior distribution. The dark gray region shows 95% credible intervals about the mean

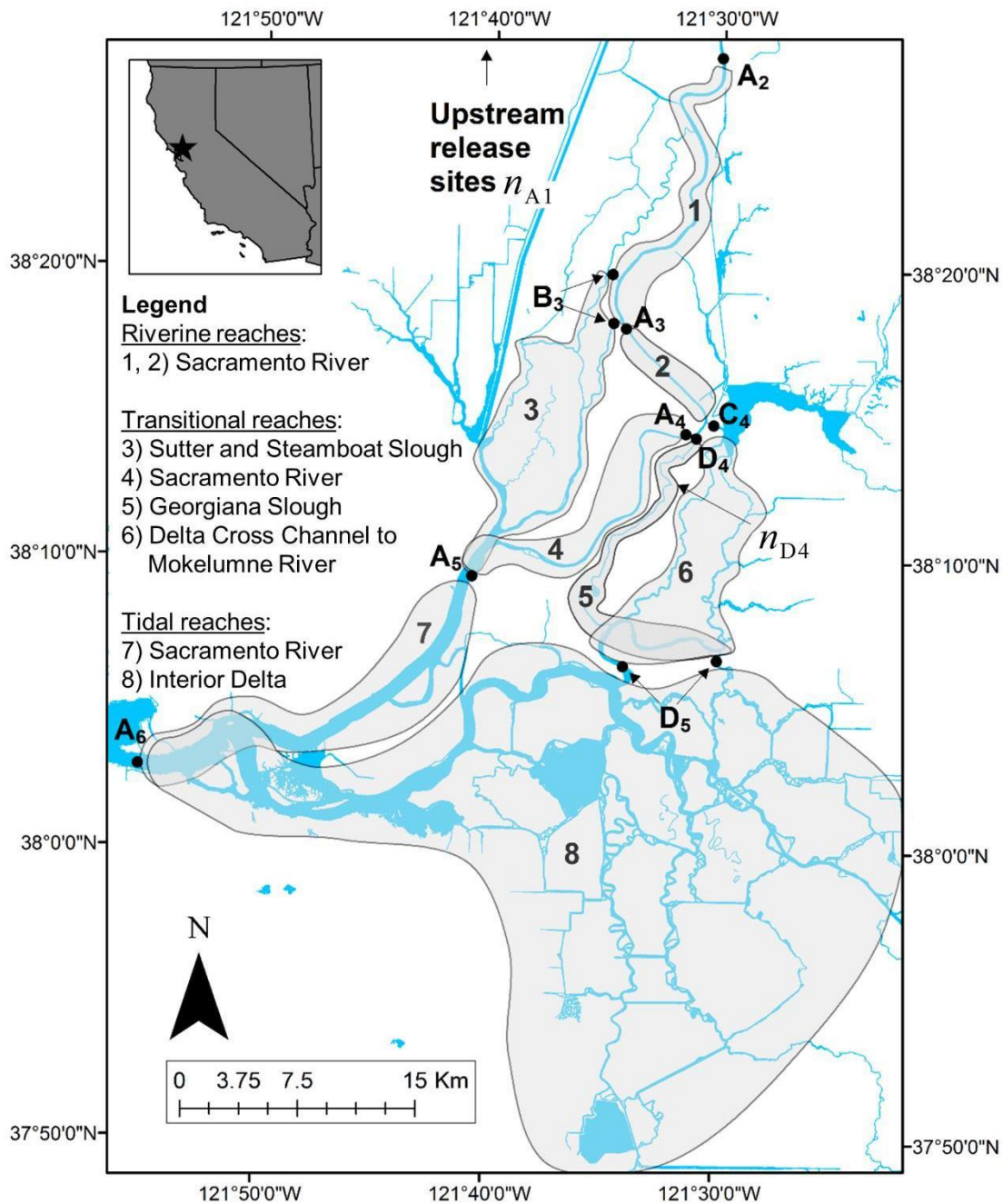945   relationship. The light gray region shows the 95% confidence interval among release groups.

946

947   **Fig. 6.** Reach-specific relationships between survival and inflow to the Delta as measured at the

948   Sacramento River at Freeport (shown for closed Delta Cross Channel gates and plotted at the

949   mean fork length). The heavy magenta line shows the mean relationship and dotted lines show

950   the random effects estimates for each release group based on medians of the joint posterior

951   distribution. The dark gray region shows 95% credible intervals about the mean relationship.

952   The light gray region shows the 95% confidence interval among release groups.

953

954   **Fig. 7.** Relationships between routing probability and inflow to the Delta as measured at the

955   Sacramento River at Freeport (A_2 in Fig. 1). The lower right panel shows the effect of Delta

956   Cross Channel (DCC) gate position on routing probabilities at the junction of the Sacramento

957   River, Delta Cross Channel, and Georgiana Slough (A_4, C_4, and D_4 in Fig. 1), plotted at the

958   posterior median of the parameters. Other panels show mean routing relationships (heavy

959   magenta line), random effects estimates for each release group (dotted lines), 95% credible

960   interval about the mean relationship (dark gray region), and 95% confidence interval among

961   release groups (light gray region).

962

963   **Fig. 8.** Route-specific survival through the Sacramento-San Joaquin River Delta between

964   Freeport (A_2 in Fig. 1) and Chipps Island (A_6 in Fig. 1). Route-specific survival based on

965   posterior median parameter values was calculated as the product of reach-specific survival for

966   reaches that trace each unique migration route through the Delta (shown for closed Delta Cross

967   Channel gates). The first three panels show the mean relationship for each route with thin gray

968   lines showing the random effects estimates for each release group. The last panel shows overall

969   survival through Delta for all routes (with random effects estimates as thin gray lines) along with

970   route-specific survival relationships. Overall survival was calculated as the average of route-

971   specific survival weighted by routing probabilities (see Eq. 1).

972

973 **Fig. 9.** Route-specific travel time distributions between Freeport (A_2 in Fig. 1) and Chipps Island

974 (A_6 in Fig. 1) at the 5th (top panel) and 95th (bottom panel) percentiles of discharge based on the

975 historical flow record (235 $m^3 \cdot s^{-1}$ and 1357 $m^3 \cdot s^{-1}$, respectively). Arrows show the median travel

976 times for each route. Travel time distributions were based on posterior medians of parameters

977 for reach-specific travel time distributions assuming closed Delta Cross Channel gates.

Fig. 1. Map of the Sacramento-San Joaquin River Delta showing the location of acoustic telemetry receiving stations (filled black circles) used to detect acoustic tagged juvenile salmon as they migrated through the Delta. Telemetry stations are labeled by migration route (A-D) and sampling occasion (1-7; see Fig. 2). These telemetry stations divide the Delta into eight discrete reaches (shown by numbered shaded regions), with an additional reach upstream of telemetry station A_2 (Reach 0) used as acclimation reach to allow fish to recover from post-release handling. The location of water pumping stations in the southern interior Delta is indicated by the pink diamonds.

51

Migration route (State)

Steamboat and Sutter Slough (B)   Sacramento River (A)   Georgiana Slough (D)   Delta Cross Channel (C)

Sampling occasion

1 — n_{A1}

Reach 0: S_{A1}

2 — P_{A2}

Reach 1: S_{A2}

Ψ_{AB3} Ψ_{AA3}

3 — P_{B3} P_{A3}

Reach 3: S_{B3} Reach 2: S_{A3}

Ψ_{AA4} Ψ_{AD4} Ψ_{AC4}

4 — P_{A4} P_{D4} P_{C4}

Reach 4: S_{A4} Reach 5: S_{D4} Reach 6: S_{C4}

n_{D4}

$S_{D4,D}$

5 — P_{A5} P_{D5}

Reach 7: S_{A5} Reach 8: S_{D5}

6 — P_{A6}

λ

7 —

Fig. 2. Schematic of the multistate mark-recapture model with parameters indexed by state (migration route) and sampling occasion. Parameters include reach-specific survival probabilities (S), site-specific detection probabilities (P), routing probabilities (Ψ), and λ, the joint probability of surviving and being detected at telemetry stations downstream of site A_6. Release locations are indicated by the nth release in route r at occasion j: n_{A1} (at Sacramento or upstream – see Table 1) and n_{D4} in Georgiana Slough.

Fig. 3. Daily inflow into the Sacramento-San Joaquin River Delta (top panel) and tidal influence on discharge at three locations in the Sacramento River during 2010 (middle and bottom panels). The top panel shows mean daily discharge of the Sacramento River at Freeport (A_2 in Fig. 1). In the two lower panels, lines show mean daily discharge and the shaded regions encompass the daily minimum and maximum discharge with values less than zero indicating reverse flows caused by tidal forcing. The middle panel shows the Sacramento River at Freeport (black line, gray shading) and the Sacramento River just downstream of Georgiana Slough (pink link and shading; A_4 in Fig. 1). The bottom panel shows the Sacramento River at Rio Vista (A_5 in Fig. 1).

Fig. 4. Summary of posterior distributions of parameters estimating the effects of river flow and Delta Cross Channel (DCC) gate position on travel time and survival. Points show the median of the posterior distribution, heavy lines show the 25th to 75th percentile, and thin lines show the 5th to 95th percentile. Green bars are density strips with darker regions illustrating higher posterior density. Parameter definitions as follows: α_1 = slope for effect of discharge on mean of log-travel time, α_2 = slope for effect of an open DCC gate on mean of log-travel time, ξ_μ = standard deviation of release group random effect on μ, σ = variance parameter of the lognormal travel time distribution, β_1 = slope for effect of discharge on survival, β_2 = slope for effect of an open DCC gate on survival, ξ_S = standard deviation of release group random effect on survival.
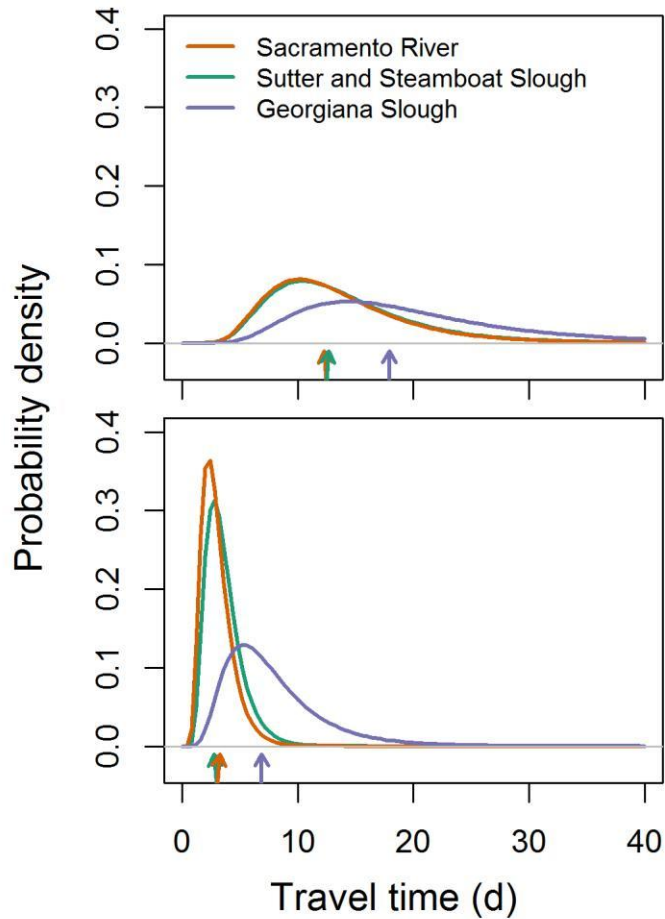
Fig. 5. Reach-specific relationships between median travel time and inflow to the Delta as measured at the Sacramento River at Freeport (A_2 in Fig. 1; shown for closed Delta Cross Channel gates and plotted at the mean fork length). The heavy magenta line shows the mean relationship and the dotted lines show the random effects estimates for each release group based on medians of the joint posterior distribution. The dark gray region shows 95% credible intervals about the mean relationship. The light gray region shows the 95% confidence interval among release groups.
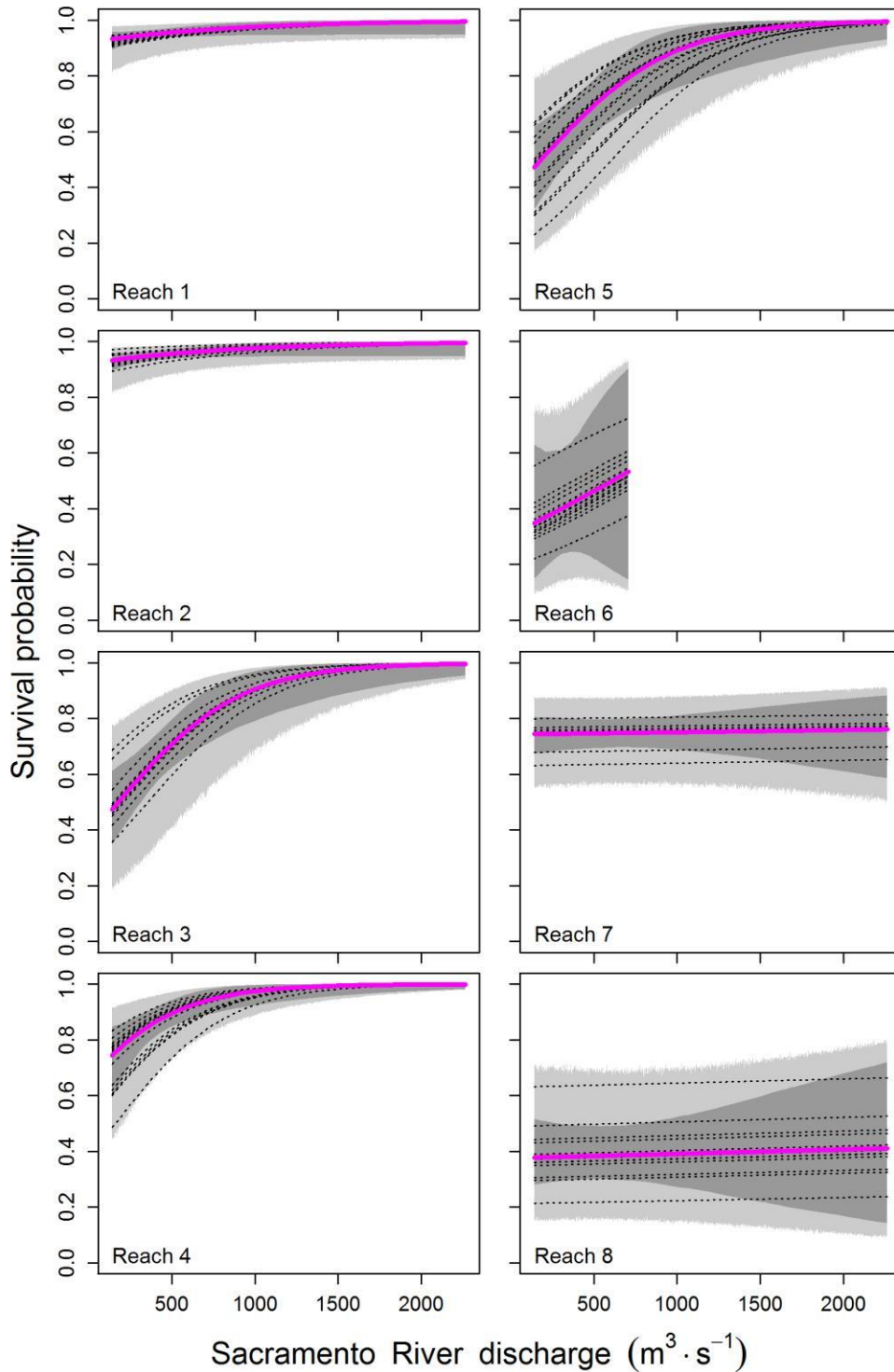
1019   **Fig. 6.** Reach-specific relationships between survival and inflow to the Delta as measured at the
1020   Sacramento River at Freeport (A_2 in Fig. 1; shown for closed Delta Cross Channel gates and
1021   plotted at the mean fork length). The heavy magenta line shows the mean relationship and
1022   dotted lines show the random effects estimates for each release group based on medians of the
1023   joint posterior distribution. The dark gray region shows 95% credible intervals about the mean
1024   relationship. The light gray region shows the 95% confidence interval among release groups.

Fig. 7. Relationships between routing probability and inflow to the Delta as measured at the Sacramento River at Freeport (A_2 in Fig. 1). The lower right panel shows the effect of Delta Cross Channel (DCC) gate position on routing probabilities at the junction of the Sacramento River, Delta Cross Channel, and Georgiana Slough (A_4, C_4, and D_4 in Fig. 1), plotted at the posterior median of the parameters. Other panels show mean routing relationships (heavy magenta line), random effects estimates for each release group (dotted lines), 95% credible interval about the mean relationship (dark gray region), and 95% confidence interval among release groups (light gray region).

Fig. 8. Route-specific survival through the Sacramento-San Joaquin River Delta between Freeport (A_2 in Fig. 1) and Chipps Island (A_6 in Fig. 1). Route-specific survival based on posterior median parameter values was calculated as the product of reach-specific survival for reaches that trace each unique migration route through the Delta (shown for closed Delta Cross Channel gates). The first three panels show the mean relationship for each route with thin gray lines showing the random effects estimates for each release group. The last panel shows overall survival through Delta for all routes (with random effects estimates as thin gray lines) along with route-specific survival relationships. Overall survival was calculated as the average of route-specific survival weighted by routing probabilities (see Eq. 1).

Fig. 9. Route-specific travel time distributions between Freeport (A_2 in Fig. 1) and Chipps Island (A_6 in Fig. 1) at the 5th (top panel) and 95th (bottom panel) percentiles of discharge based on the historical flow record (235 $m^3 \cdot s^{-1}$ and 1357 $m^3 \cdot s^{-1}$, respectively). Arrows show the median travel times for each route. Travel time distributions were based on posterior medians of parameters for reach-specific travel time distributions assuming closed Delta Cross Channel gates.

Supplement A.
Perry et al. Flow-mediated effects on travel time, survival, and routing of juvenile Chinook salmon in a spatially complex, tidally forced river delta
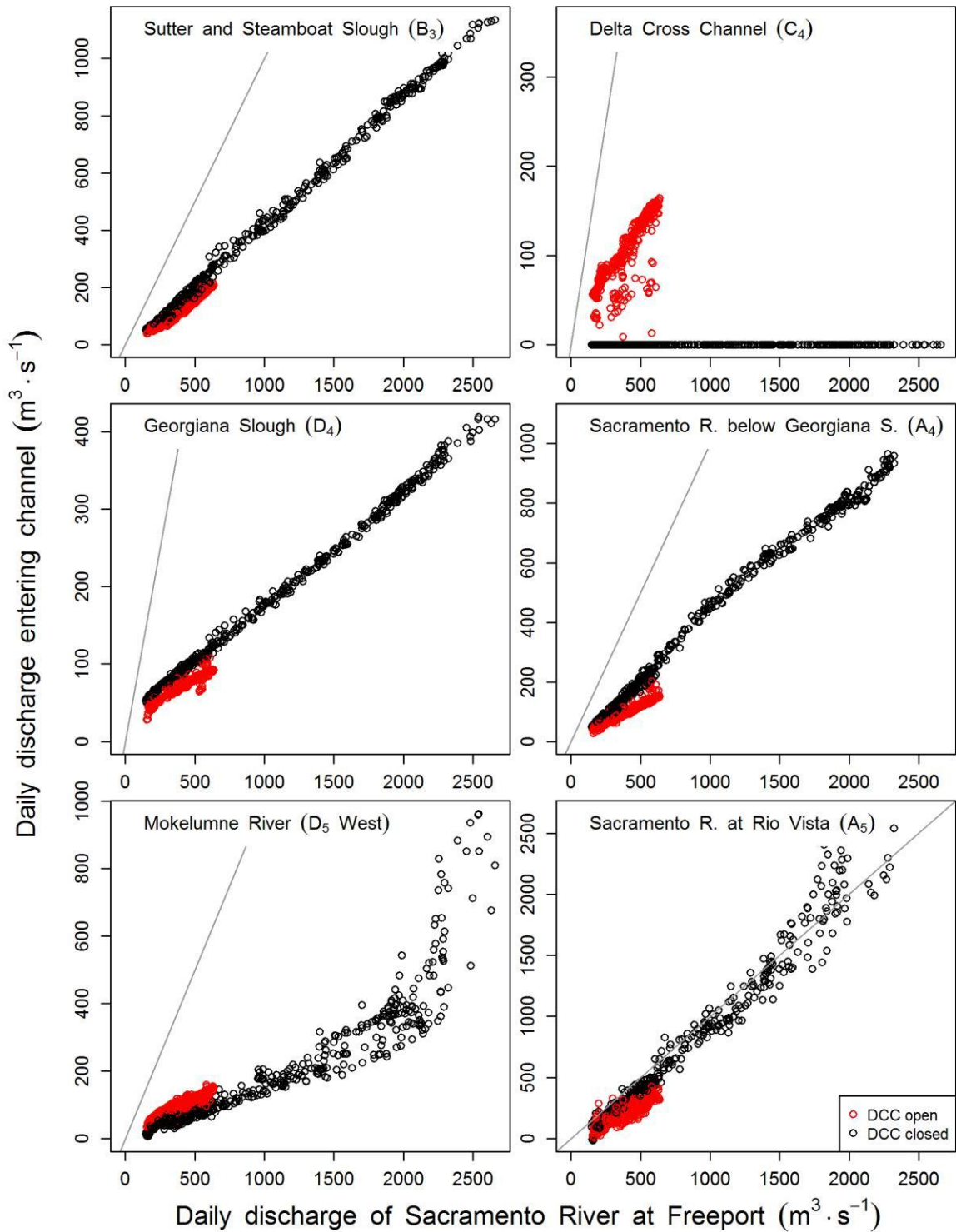
Fig. A1. Scatter plots showing the relationship between daily discharge of the Sacraemento River at Freeport and discharge entering other channels downstream of Freeport. The grey reference line shows where discharge in a given channel is equal to discharge at Freeport. Subscripted letters in parentheses refer to the location of USGS gauging stations near telemetry stations shown in Fig. 1.
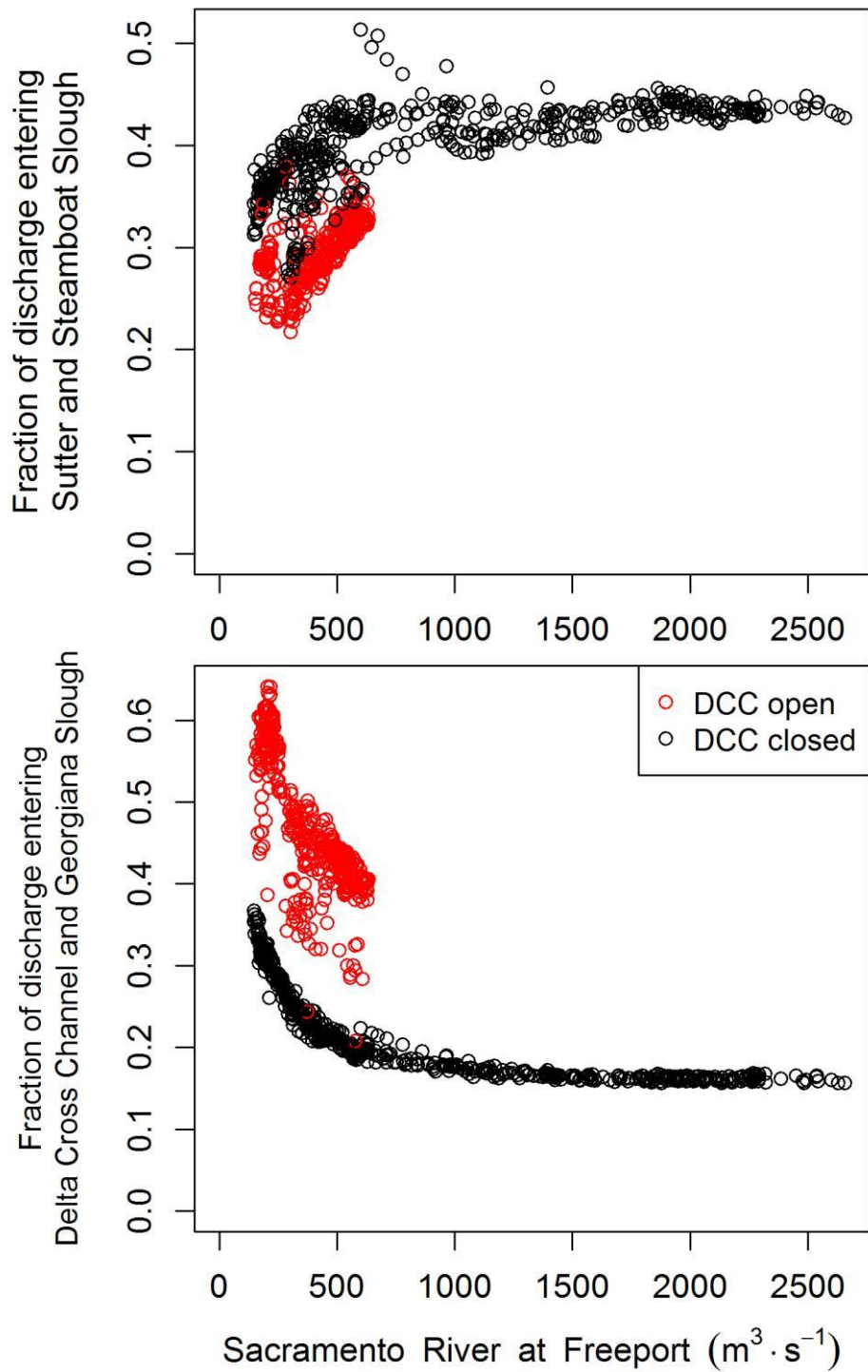
Fig. A2. Fraction of dishcharge entering Sutter and Steamboat Slough (top) and Delta Cross Channel and Georgiana Slough (bottom) calculated as the proportion of total inflow relative to Sacramento River discharge at Freeport.
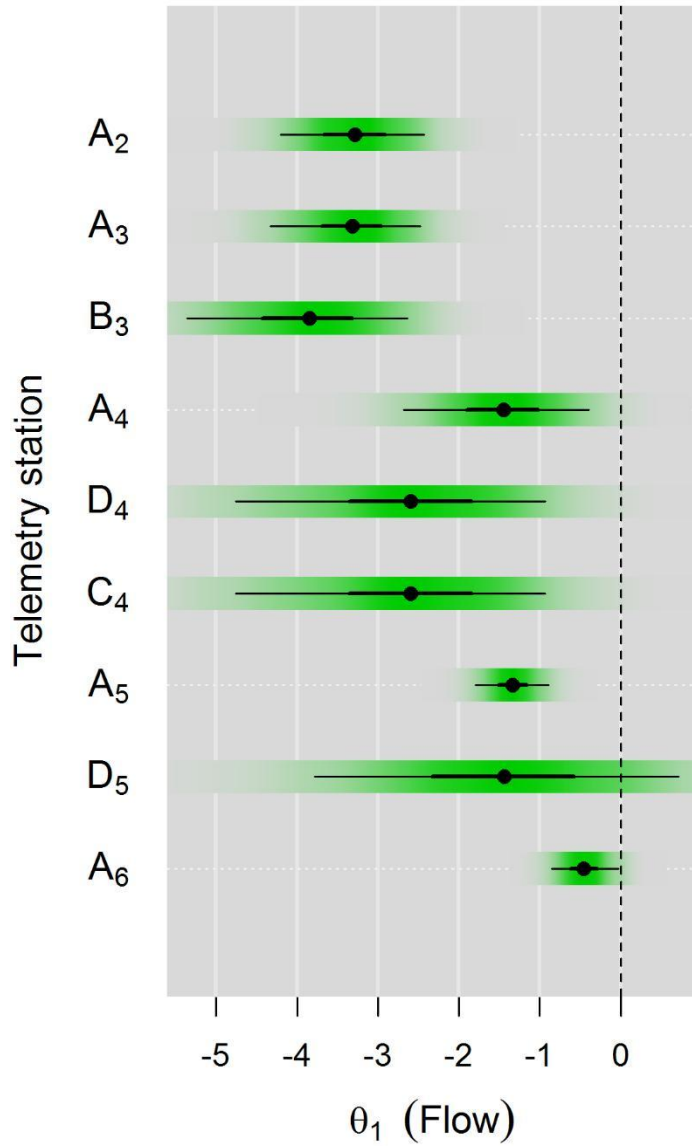
Fig. A3. Posterior distributions for θ_1, the coefficient measuring the effect of flow on detection probability at each telemetry station. Points show the median of the posterior distribution, heavy lines show the 25th to 75th percentile, and thin lines show the 5th to 95th percentile. Green bars are density strips with darker regions illustrating higher posterior density. See Fig. 1 for locations of telemetry stations.
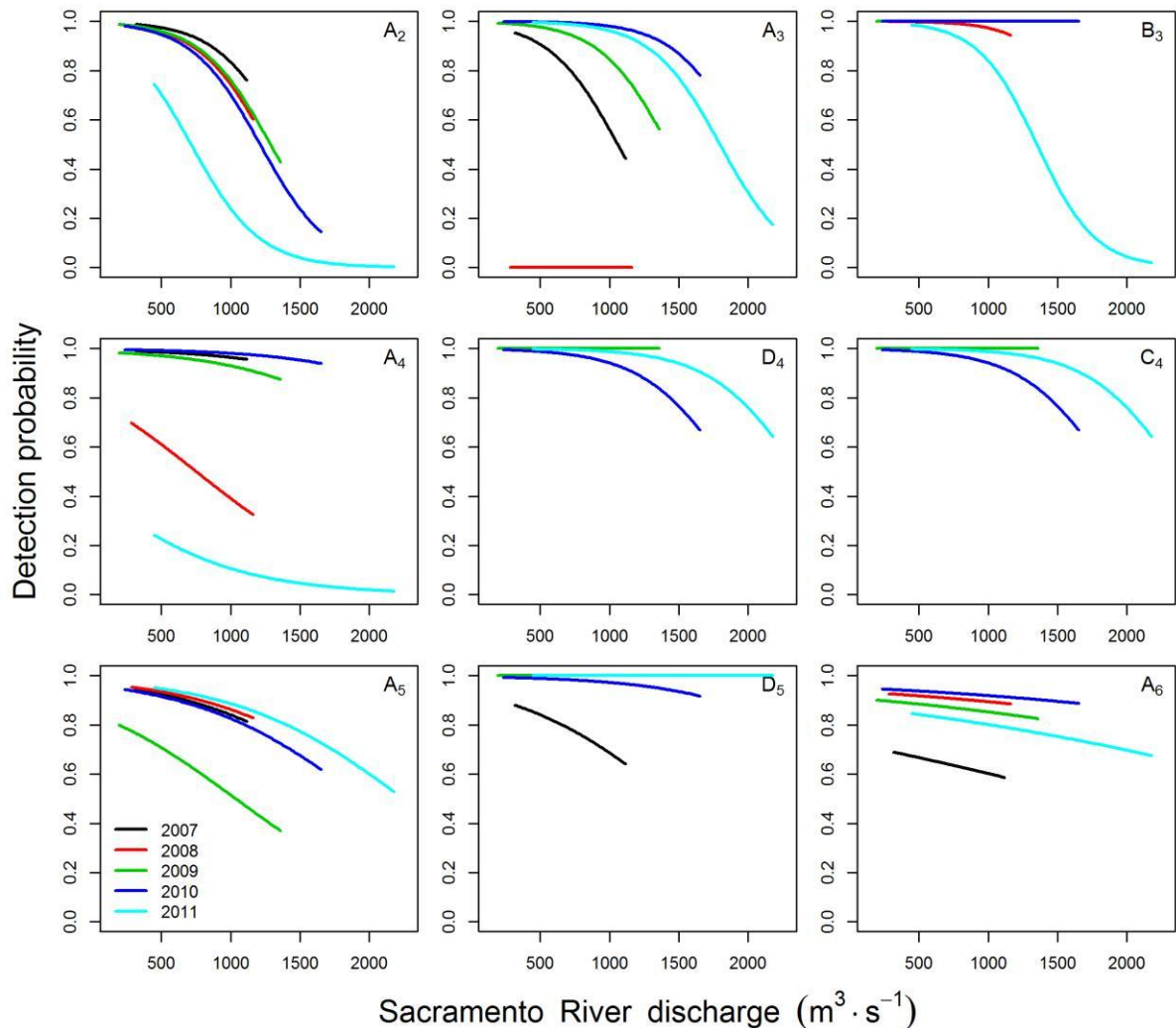
Fig. A4. Year-specific effects of discharge on detection probability of each telemetry station based on posterior medians of the parameters. Lines are plotted over the range of discharge observed in each year. See Fig. 1 for locations of telemetry stations.
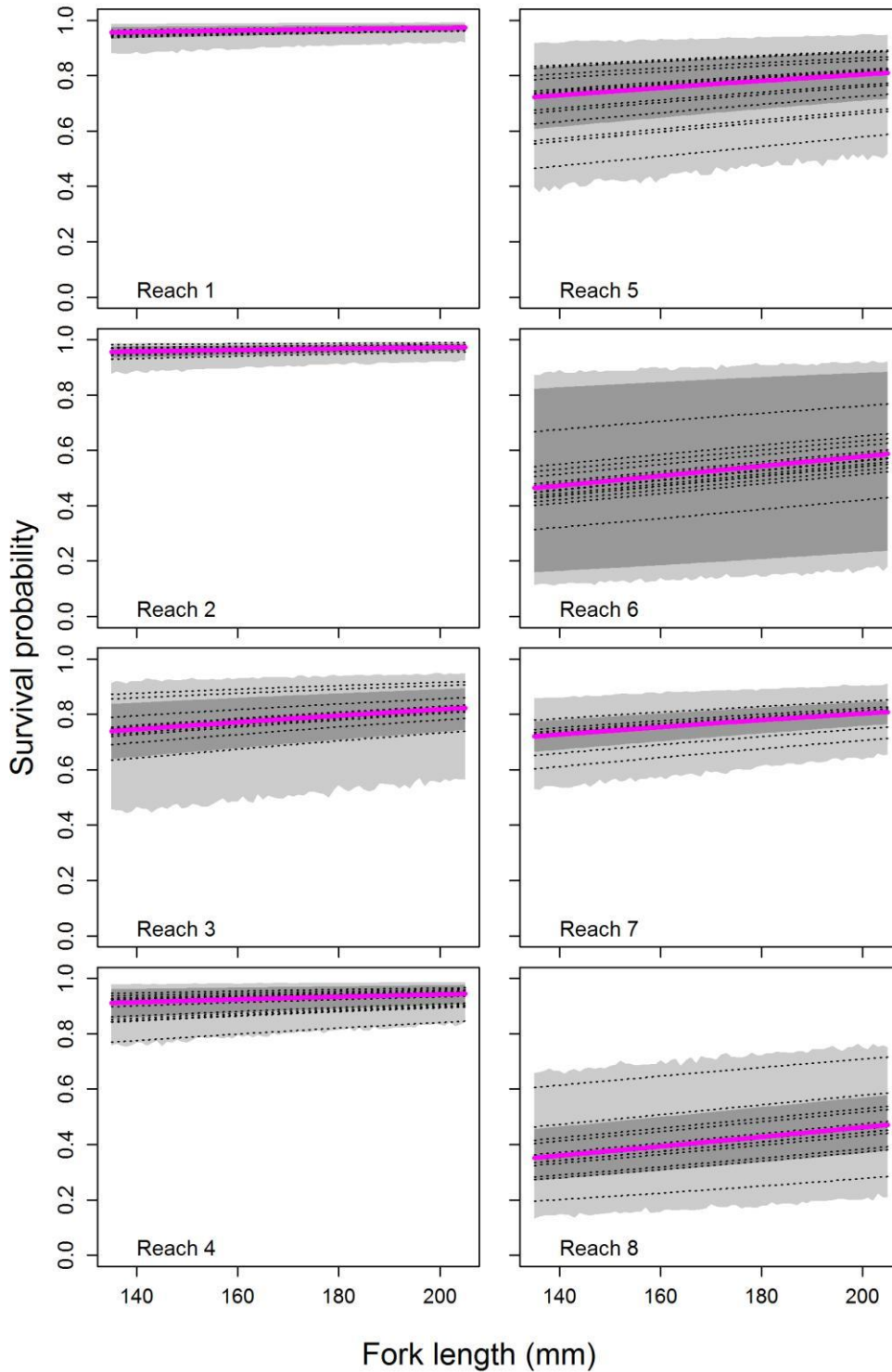
Fig. A5. Reach-specific relationships between survival and fork length (shown for closed Delta Cross Channel gates and plotted at the mean discharge). The heavy magenta line shows the mean relationship and dotted lines show the random effects estimates for each release group based on medians of the joint posterior distribution. The dark gray region shows 95% credible intervals about the mean relationship. The light gray region shows the 95% confidence interval among release groups.
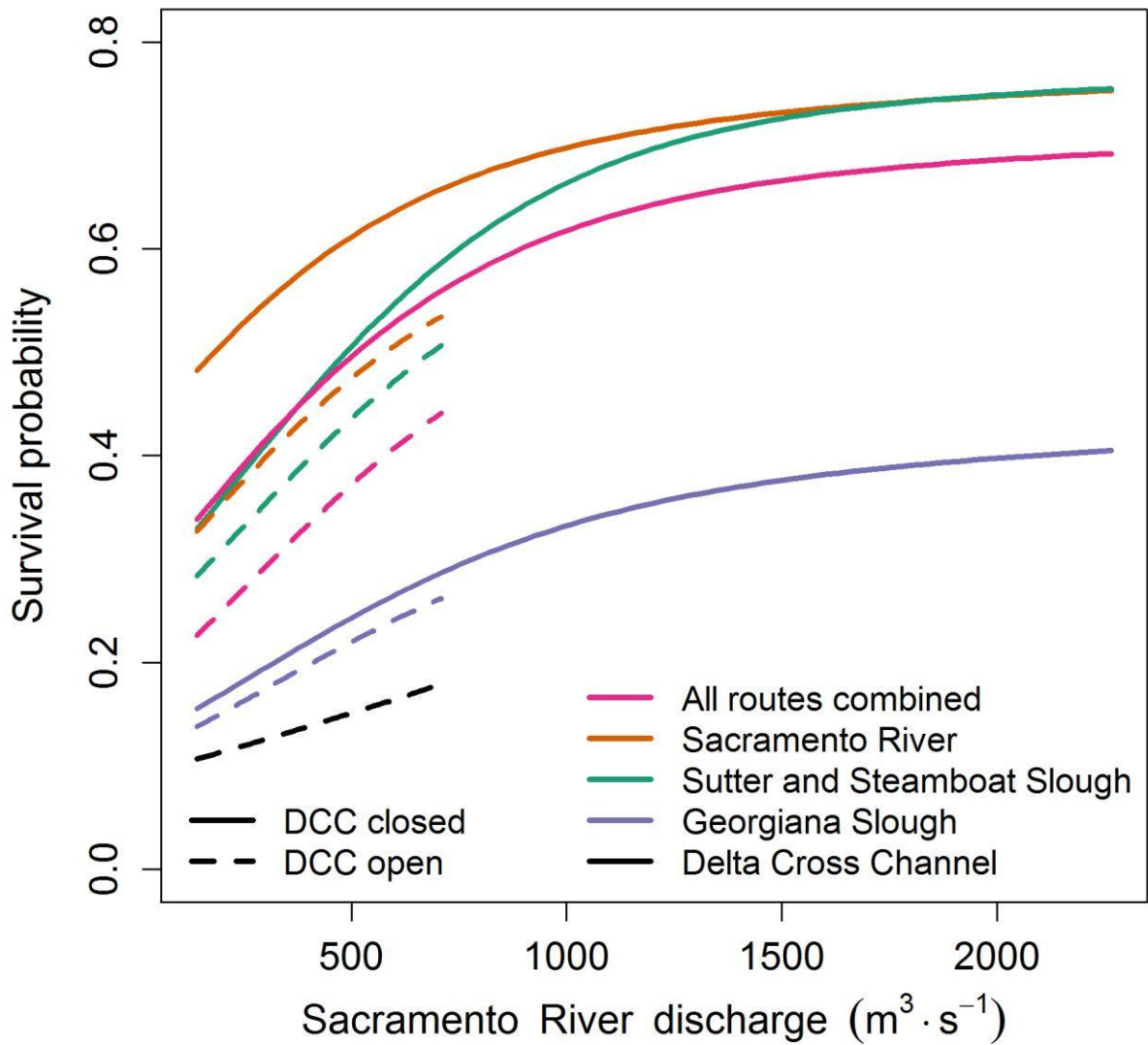
Fig. A6. Route-specific flow-survival relationships for Delta Cross Channel (DCC) open and closed. Relationships are plotted at the posterior medians of parameter distributions.