Environ Biol Fish (2020) 103:389–410
https://doi.org/10.1007/s10641-019-00918-y

Relating survival of fall-run Chinook Salmon through the San Joaquin Delta to river flow

Rebecca A. Buchanan · John R. Skalski

Received: 20 November 2018 / Accepted: 29 September 2019 / Published online: 29 October 2019

Abstract Survival of juvenile fall-run Chinook Salmon *Oncorhynchus tshawytscha* from the San Joaquin River (SJR) during their migration through the Sacramento-San Joaquin Delta of California has been low in recent years, and there is uncertainty about the role of river flow on survival. Five years (2010–2014) of acoustic telemetry data from juvenile hatchery-reared salmon offer spatially detailed survival information through this region. Multinomial regression and generalized linear models were used to relate survival to river flow in the SJR and its distributary, Old River (OR), on various spatial and temporal scales. Higher survival to Delta exit (rkm 77 from Golden Gate Bridge) was associated with higher root mean square of OR flow in the strongly tidal interior Delta (rkm 123; $P < 0.0001$), but not with higher SJR flow either entering the Delta from upstream (rkm 196; $P = 0.2795$) or measured in the Delta near the riverine/tidal interface (rkm 150; $P = 0.3845$). Survival in the upstream, more riverine region of the Delta was positively associated with SJR flow measured at rkm 150 and average net flow in the interior Delta ($P \leq 0.0001$ for each), suggesting different mechanisms driving survival in the upstream versus downstream reaches of the Delta. The spatial complexity of the survival-flow relationship suggests that efforts to maximize total Delta survival should focus on a sequence of smaller regions, tailoring management strategies to each region rather than a single strategy for the Delta as a whole. Highly variable environmental conditions in this region combined with very low survival require more data to fully address the complex survival-flow relationship, both more years of data on various spatial scales and larger sample sizes of acoustic-tagged fish.

Keywords Juvenile salmonids · Migration · River discharge · Salinity · Estuary

R. A. Buchanan (✉) · J. R. Skalski
School of Aquatic and Fishery Sciences, University of Washington, 1325 Fourth Ave, Suite 1515, Seattle, WA 98101-2540, USA
e-mail: rabuchan@uw.edu

Introduction

The Central Valley of California historically supported a large population of Chinook Salmon *Oncorhynchus tshawytscha*, consisting of runs returning from the ocean during all seasons of the year (Yoshiyama et al. 1998). Estimated to have had spawning populations nearing 2 million individuals in the 1800s, population levels have declined considerably, and adult escapement in 2007–2016 averaged only about 200,000 fish (Fisher 1994; CDFW 2019). The majority of the adult salmon returning from the ocean are from the fall-run component of the population, which forms the basis of the California-Southern Oregon ocean salmon fishery. Despite their relative abundance compared to other Central Valley salmon runs, the combined fall-run population from the Sacramento and San Joaquin river basins has also shown reduced adult returns in recent years; this resulted in the closure of the ocean salmon fishery in 2008 and 2009, when escapement was as low as 53,129 adults (Williams 2006; NOAA 2008, 2009a; CDFW 2019). Representing the southern-most portion of the Chinook Salmon range, fall-run Chinook Salmon from the San Joaquin River basin in particular face increasing challenges during their freshwater life history as river conditions have been altered due to climate change, resource (e.g., water) demand from human populations, and contaminants from agriculture and industry. One factor thought to contribute to the low adult returns is juvenile passage through the Sacramento-San Joaquin River delta.

All Central Valley Chinook Salmon migrate as juveniles to the Pacific Ocean through the Sacramento-San Joaquin River delta ("Delta") and the San Francisco Bay (Fig. 1). The Delta is a complex network of natural and manmade interconnected channels, providing multiple passage routes for both fish and water. The Delta provides water for agricultural and municipal use for the Central Valley and southern California via large state and federal extraction ("pumping") facilities and aqueducts as part of a water "export" system. Water managers in the Central Valley face the complex task of meeting the resource needs of California residents without jeopardizing the salmonids listed in the Endangered Species Act (ESA; winter-run and spring-run Chinook Salmon, and Central Valley steelhead *O. mykiss*). Although not ESA-listed, fall-run Chinook Salmon from the San Joaquin River basin largely share Delta migration pathways and timing with ESA-listed steelhead originating in the San Joaquin basin, and so they share the effects of management actions designed to protect steelhead. Nevertheless, more than two decades of coded-wire tag and acoustic-tag studies have found especially low survival of juvenile fall-run Chinook

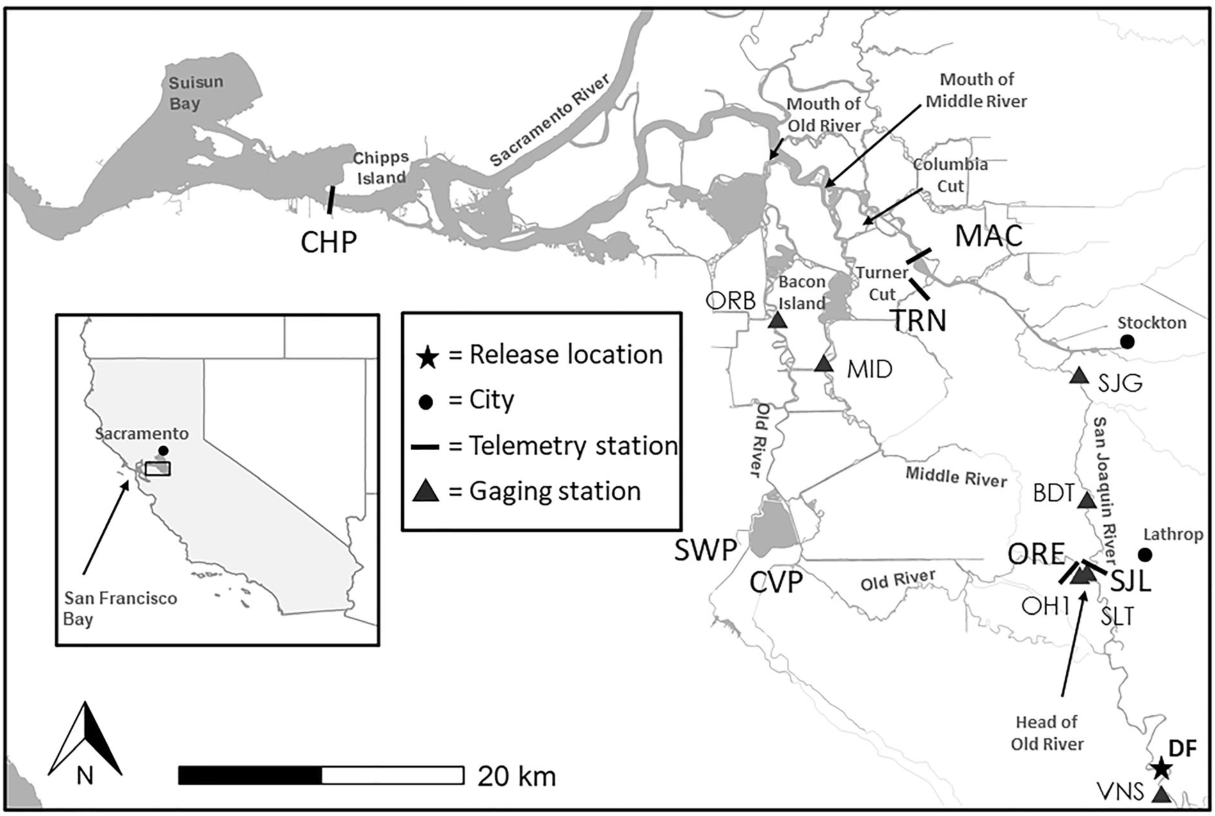

Fig. 1 The portion of the Sacramento-San Joaquin River delta that was studied, including acoustic telemetry stations (bars; bold labels), river gaging stations (triangles), Durham Ferry (DF) release site (star), and key cities (dots). Inset map shows state of California, USA, (light shading) and the Delta and San Francisco Bay (dark shading); detailed area is marked with rectangle. Telemetry stations are: SJL = San Joaquin River route (Lathrop), ORE = Old River route, MAC = MacDonald Island, TRN = Turner Cut, and CHP = Chipps Island. River gaging stations are: VNS = Vernalis, SLT = Lathrop, OH1 = Old River head, BDT = Brandt Bridge, SJG = Garwood Bridge, ORB = Old River at Bacon Island, and MID = Middle River. Water export facilities are CVP = Central Valley Project and SWP = State Water Project

Salmon outmigrating through the Delta (e.g., ≤0.10; Buchanan et al. 2018b), raising questions about the adequacy of current management practices.

Management efforts to promote juvenile salmon survival through the Delta have focused on impacts of water volume entering the Delta, rates of water extraction (diversion and pumping), temporary barriers to affect fish routing through the Delta, and infrastructure changes to improve survival at the water pumping facilities (NOAA 2009b). These strategies are largely based on conceptual models of juvenile salmonid survival in the Delta that hold that, among other things, (1) more water leads to higher survival, and (2) higher export rates result in lower survival through the Delta by drawing fish to the water export facilities where they may be delayed, predated upon, or entrained in the pumps (NOAA 2009b; SST 2017). It is generally accepted that the amount of river discharge ("flow"), reflecting both water volume and velocity, has a strong influence on fish migration (e.g., timing and speed; Jonsson 1991). In the Delta, the survival benefit of higher river flows has been hypothesized to arise partially from faster travel times through areas of lower survival (Anderson et al. 2005; Perry et al. 2018). Additionally, higher river flows expand the amount of habitat available to migrating or rearing salmon, and are associated with lower water temperature, improved dissolved oxygen level, lower concentration of contaminants, and possibly lower predator densities.

The amount of water present in the Delta depends on the rate of water entering the Delta from upstream ("Delta inflow"), primarily from the San Joaquin and Sacramento rivers, and the amount of water removed at the pumping facilities or by private water users. Delta inflow is measured as the flow volume per second (in units of ft^3/s; cfs) at river gaging stations near Vernalis on the San Joaquin River (Fig. 1), and at Freeport, CA, on the Sacramento River, located approximately 20 km downstream from Sacramento, CA. Inflow is partially managed by reservoir releases upstream, but is also affected by annual precipitation and snow melt patterns. Hydrodynamic conditions throughout the Delta are variably affected by Delta inflow, tidal action, and water pumping operations, and the direction of river flow can reverse due to semidiurnal tidal dynamics and the influence of pumping (Cavallo et al. 2013; SST 2017). The extent and velocity of reverse flows vary spatially throughout the Delta and are affected by Delta inflow and export rates, as well as by temporary or operable manmade barriers installed in Delta channels to influence flow and fish pathways. The San Joaquin River in Delta regions farthest from the ocean are more affected by patterns of Delta inflow from upstream in the San Joaquin River, whereas regions in the interior Delta (i.e., west or south of the San Joaquin River) are more affected by export rates and tidal actions; regions in the downstream reaches are affected primarily by tides and, to a lesser extent, export rates and Delta inflow from the Sacramento River (Cavallo et al. 2013; SST 2017). Salmonids migrating through these regions experience both instantaneous and cumulative effects of hydrodynamic conditions over multiple days, influenced by the travel time and movement patterns of both water and fish.

Evidence for a positive relationship between Delta inflow and juvenile salmon survival has been based primarily on estuary and ocean recovery rates of salmon implanted with coded wire tags (CWTs; Brandes and McLain 2001). Several investigations (Newman and Rice 2002; Newman 2003; and Perry 2010) found support for a positive inflow-survival relationship for Sacramento River salmon. The San Joaquin River Group Authority (SJRGA 2007) and Newman (2008) found support for a positive inflow-survival relationship for San Joaquin River basin salmon as well, but the relationship depended on the presence of a temporary rock barrier at the head of Old River that was designed to prevent migrating salmonids from entering the interior Delta via Old River, a distributary of the San Joaquin River in the Delta (Fig. 1). SJRGA (2007) also found a positive association between Delta inflow at Vernalis in the spring and adult escapement 2½ years later. Despite previous evidence that higher Delta inflow improves juvenile salmonid survival through the Delta, and management policies to boost inflow and limit exports during the juvenile outmigration from the San Joaquin River, survival through the Delta has remained low. Additionally, recent annual estimates of Delta survival have been very low (≤0.05) even in high flow years such as 2011 (Buchanan et al. 2018b), raising questions about the strength of the inflow-survival relationship.

To date, there has been little investigation into how flow conditions at locations throughout the Delta may be related to either total Delta survival or survival through particular regions of the Delta. The previous assessments of the Delta inflow-survival relationship for San Joaquin River basin salmon depend on CWT data or adult escapement rates, and thus are unable to account for variability in the experience of individual fish. Starting in 2007, the large CWT survival studies of South Delta fall-run Chinook Salmon have been replaced with annual acoustic telemetry (AT) studies, in which hundreds to thousands of hatchery-reared juvenile salmon have been surgically implanted with microacoustic transmitters, released to the river, and then monitored as they migrate past fixed-site acoustic hydrophones located throughout the Delta (SJRGA 2013; Buchanan et al. 2018b). The AT studies require smaller annual sample sizes than the CWT studies and provide detailed individual-based spatial and temporal information on within-Delta survival, route selection, and migration timing. Now that multiple years of AT data are available, there is an opportunity to update the decade-old CWT assessment of the conceptual model component that higher Delta inflow results in higher survival, as well as to address related questions: Are there identifiable flow conditions at locations within the Delta that are associated with higher survival? What spatial and temporal scales are appropriate for relating survival to environmental conditions such as flow? This paper synthesizes five years of AT data for which annual analyses are completed to address these questions, highlights the challenges of definitively answering such questions for a complex environment such as the Delta, and provides study recommendations for both managers and future investigations.

Methods

Study area

The region of focus for this paper is the southern portion of the Sacramento-San Joaquin River delta from Old River in the south to Chipps Island in the northwest ("South Delta"; Fig. 1). This southern portion of the delta is bounded to the south by the head (i.e., source) of Old River; to the east and north by the San Joaquin River; and to the west by Old River. The river delta feeds into San Pablo, Suisun, and San Francisco bays to the west, and then to the Pacific Ocean. Unless otherwise noted, this paper uses the term "Delta" to refer to the southern portion of the overall Sacramento-San Joaquin delta that is bounded by the San Joaquin and Old rivers.

There are two major migration routes through the Delta, determined by route selection at the head of Old River: the San Joaquin River route and the Old River route (Fig. 1). In addition to migrating entirely within the San Joaquin River to Chipps Island, the San Joaquin River route includes the possibility of entering the interior Delta downstream of Stockton, CA, via Turner Cut, Columbia Cut, or the mouths of Old and Middle rivers. Although the entire Delta is affected by tidal action, the San Joaquin River upstream of Turner Cut is often more riverine, while the region downstream of Turner Cut and in the interior Delta is more tidally influenced (Cavallo et al. 2013). The Old River route through the Delta includes both Old River and Middle River, which branches off Old River approximately 6.7 km downstream of Old River's distributary point from the San Joaquin; the Old River route also includes salvage and trucking from the federal water export facility (Central Valley Project, CVP) or the state water export facility (State Water Project, SWP). The CVP and SWP pumping facilities are both located off Old River in the southwestern corner of the Delta. Fish that are salvaged and trucked from the export facilities are returned to the river in the San Joaquin River or Sacramento River approximately 20 km upstream of Chipps Island. Fish in the San Joaquin River route that enter the interior Delta may also be salvaged and trucked from the water export facilities.

A temporary rock barrier was installed in Old River near its head in spring of 2012 and 2014, to prevent salmonid access to Old River. The barrier included culverts that allowed for limited water and fish passage. In 2010, an experimental non-physical barrier (NPB) was installed at the head of Old River, also designed to prevent entry to Old River. The NPB used a bioacoustic fish fence, which consisted of lights and a bubble curtain (Bowen and Bark 2012). The NPB was operational for approximately half of the 2010 study.

Field study methods

In the spring of each year from 2010 to 2014, from 504 to 1895 juvenile, hatchery-reared, fall-run Chinook salmon were surgically implanted with microacoustic transmitters and released in the San Joaquin River at Durham Ferry, located approximately 25 river km upstream of the head of Old River (Fig. 1; Table 1). The release site was located upstream of the Delta to allow tagged fish to recover from handling and to distribute naturally in the river before entering the study area. Study fish were provided by the Merced River Fish

Table 1 Release dates, number released at Durham Ferry (N), and mean (range) fork length at tagging (mm), estimates (SE in parentheses) of the probability of survival (S) and conditional detection probability (P) for release groups of acoustic-tagged juvenile Chinook Salmon smolts used in the 2010–2014 South Delta tagging studies (SJRGA 2011, 2013; Buchanan et al. 2015, 2016, 2018a)

Year	Release Dates	N	Fork length	$\hat{S}_{SJL-CHP}$	$\hat{S}_{ORE-CHP}$	$\hat{S}_{SJL-TCJ}$	$\hat{P}_{CHP}$	$\hat{P}_{MAC}$	$\hat{P}_{TRN}$
2010	April 27–29	74	108.0 (100–117)	0.07 (0.03)	0.00 (0.00)	0.50 (0.07)	1.00	1.00	1.00
	April 30 – May 2	74	108.8 (100–115)	0.01 (0.01)	0.03 (0.02)	0.42 (0.07)	1.00	1.00	1.00
	May 4–6	73	109.4 (100–118)	0.01 (0.01)	0.01 (0.01)	0.17 (0.05)	1.00	1.00	1.00
	May 7–9	70	110.5 (101–119)	0.04 (0.02)	0.11 (0.04)	0.29 (0.06)	1.00	1.00	1.00
	May 11–13	70	111.8 (99–121)	0.06 (0.03)	0.14 (0.04)	0.51 (0.06)	1.00	0.98 (0.03)	1.00
	May 14–16	73	112.8 (101–119)	0.02 (0.02)	0.08 (0.03)	0.12 (0.04)	1.00	1.00	1.00
	May 18–20	70	112.5 (101–119)	0.08 (0.03)	0.16 (0.05)	0.39 (0.07)	1.00	0.99 (0.02)	1.00
	2010 Total	504	110.5 (99–121)	0.04 (0.01)	0.07 (0.01)	0.34 (0.02)	1.00	1.00 (0.00)	1.00
2011	May 17–21	475	106.0 (95–116)	0.01 (0.01)	0.00 (0.00)	0.55 (0.03)	0.75 (0.31)	1.00	1.00
	May 22–26	473	108.2 (99–122)	0.00 (0.00)	0.02 (0.01)	0.53 (0.03)	1.00	1.00	1.00
	June 7–11	473	114.0 (104–130)	0.01 (0.01)	0.07 (0.02)	0.41 (0.03)	1.00	0.99 (0.00)	1.00
	June 15–19	474	114.8 (94–140)	0.00 (0.00)	0.07 (0.02)	0.43 (0.03)	1.00	1.00	0.98 (0.03)
	2011 Total	1895	110.8 (94–140)	0.01 (0.00)	0.04 (0.01)	0.49 (0.02)	0.99 (0.01)	0.99 (0.01)	1.00 (0.00)
2012	May 2–7	480	109.9 (100–126)	0.05 (0.01)	0.17 (0.15)	0.34 (0.03)	1.00	1.00	0.97 (0.03)
	May 17–22	479	115.5 (100–135)	0.00[a] (0.00)	0.00[a] (0.00)	0.08 (0.02)	$n = 0$	0.97 (0.03)	1.00
	2012 Total	959	112.7 (100–135)	0.03 (0.01)	0.11 (0.11)	0.24 (0.02)	1.00	0.99 (0.00)	0.98 (0.02)
2013	May 1–5	477	113.5 (101–132)	0.01 (0.01)	0.03 (0.01)	0.02 (0.02)	1.00	1.00	$n = 0$
	May 15–19	473	117.1 (104–135)	0.00[a] (0.00)	0.00[a] (0.00)	0.00[a] (0.00)	$n = 0$	$n = 0$	$n = 0$
	2013 Total	950	115.3 (101–135)	0.01 (0.01)	0.01 (0.01)	0.02 (0.01)	1.00	1.00	$n = 0$
2014	April 30 – May 4	646	100.3 (89–119)	0.00[a] (0.00)	0.00[a] (0.00)	0.02 (0.01)	$n = 0$	1.00	1.00
	May 15–19	629	97.4 (88–117)	0.00[a] (0.00)	0.00[a] (0.00)	0.00 (0.00)	$n = 0$	1.00	1.00
	2014 Total	1275	98.9 (88–119)	0.00[a] (0.00)	0.00[a] (0.00)	0.01 (0.01)	$n = 0$	1.00	1.00

TCJ = Turner Cut Junction, denoted by the MAC and TRN telemetry stations. See Fig. 1 for location of stations. Detection probabilities without standard errors were estimated at exactly 1.00; $n = 0$ indicates 0 detections

[a] under assumption of 100% conditional detection probability

Hatchery (2010–2013) and the Mokelumne River Fish Hatchery (2014), located approximately 100 km and 80 km from Durham Ferry by truck, respectively. The 2010 and 2011 studies used the Hydroacoustic Technology, Inc. (HTI) Model 795 microacoustic tag. The VEMCO V5–180 kHz tag was used in 2012 and 2013, and the VEMCO V4–180 kHz tag was used in 2014. Fish fork length at the time of tagging ranged from 80 mm to 140 mm, and averaged 98.9 mm (2014) to 115.3 mm (2013) over years (Table 1). Tag burden (i.e., the ratio of tag weight in air to body weight) averaged between 3.7% and 4.2% each year. Tagging was performed at the Tracy Fish Collection Facility in 2010–2012, located at the CVP approximately 40 km by truck from Durham Ferry, and at the hatchery in 2013–2014. After tagging, fish were trucked to the release site and held 24 h before release. Fish tagging and handling procedures were based on those outlined in Adams et al. (1998) and Martinelli et al. (1998) in 2010–2012, and were updated to the Standard Operating Protocol developed by the U.S. Geological Survey (USGS)-Columbia River Research Laboratory (Liedtke et al. 2012) for 2013–2014. More details on fish surgery and handling methods are available in Buchanan et al. (2018b).

Tagged salmon were monitored during their migration through the Delta as they passed fixed-site acoustic hydrophones and receivers ("telemetry stations"; Fig. 1). Of primary importance were the receivers that marked the upstream and downstream boundaries of the study area. The upstream boundary was marked by receivers located within 0.6–3.0 km downstream of the head of Old River in the San Joaquin River near

Lathrop, CA, (SJL) and in Old River (ORE) (Fig. 1). The downstream boundary was monitored by receivers at Chipps Island (CHP), 77 rkm from the Golden Gate Bridge (exit of the San Francisco Bay to the Pacific Ocean) (Fig. 1). The station at Chipps Island consisted of two parallel lines of acoustic receivers that spanned the river channel; the two lines were spaced 0.2–0.6 km apart, depending on the year. The primary migration routes through the Delta were monitored by the SJL (San Joaquin River route) and ORE (Old River route) receivers near the head of Old River. In the San Joaquin River route, receivers were also located at MacDonald Island (MAC) and in Turner Cut (TRN) off the San Joaquin River and denoted survival to the "Turner Cut Junction". Additional telemetry stations were deployed each year and used in computing estimates of migration route selection and reach-specific survival probabilities (Buchanan et al. 2018b), but were not used for the analyses presented in this article.

The receiver network was implemented and maintained by the USGS-Sacramento office; detection data were downloaded from the receivers, processed by the USGS, and transferred to the University of Washington for further analysis. More details on the annual salmon survival studies from 2010 to 2014 are available in Buchanan et al. (2018b) and in the annual technical reports (SJRGA 2011, 2013; Buchanan et al. 2015, 2016, 2018a).

Survival analysis was initiated at the SJL and ORE telemetry stations using the tags that were detected at those stations ("virtual release"). Tag detections were used from the SJL and ORE stations as well as the stations located in the San Joaquin River route near the Turner Cut Junction (MAC and TRN) and at Chipps Island (CHP) (Fig. 1). The 2014 tagging study was complicated by a manufacturing error in the tags used in the mid-April release group, resulting in tag failure during the time when fish were still moving through the study area. Rather than risking misestimation of survival by attempting to adjust for this high degree of tag failure (Holbrook et al. 2013), the mid-April release group from 2014 was omitted from analysis.

Covariate data

Hydrological and environmental data from various river gaging stations (Fig. 1) were downloaded from the California Data Exchange Center (CDEC) website (cdec.water.ca.gov/queryTools.html), the California Water Data Library (CDWL; water.ca.gov/waterdatalibrary/), and the USGS National Water Information System (NWIS) database (waterdata.usgs.gov/nwis). Gaging station data were reviewed for quality, and obvious errors were omitted. More details are available in the annual technical reports (SJRGA 2011, 2013; Buchanan et al. 2015, 2016, 2018a). Additional hydrological data were downloaded from the California Department of Water Resources' Dayflow database (water.ca.gov) and the NWIS database. Data on export rates were downloaded from the Dayflow database.

The primary covariates considered were measures of river discharge ("river flow") from several locations in the San Joaquin River and throughout the Delta: Vernalis (Delta inflow; VNS), Lathrop (SLT, station number B95765 in CWDL), Old River head (OH1), Brandt Bridge (BDT), Garwood Bridge (SJG), Old River at Bacon Island (ORB, station number 11313405 in NWIS), Middle River (MID), and the sum of the ORB and MID measures, which is hereafter referred to as OMT (Table 2, Fig. 1). Data from ORB, MID, and OMT represented interior Delta flow. Flow data were downloaded as 15-min event data from all Delta locations. Mean daily flow values at Vernalis (VNS) were downloaded from the CDEC website. Estimates of total daily Delta outflow at Chipps Island (QOUT) were downloaded from the Dayflow database.

Covariates other than flow measures were also considered to represent possible additional influences on salmon survival through the Delta, including fish size, water project operations, and non-flow environmental conditions. Fish size was represented as fish length at the time of tagging. Operational covariates included the presence of the rock barrier at the head of Old River, measures of exports at the CVP and SWP, and the ratio of Delta inflow at Vernalis to combined CVP and SWP exports (I:E). Exports were measured on a daily basis, and were represented as the total from either CVP, SWP, or combined, and the proportion of combined exports that were from the CVP. Non-flow environmental covariates consisted of measures of temperature, time of day of fish detection at the SJL or ORE telemetry station (day or night, omitting crepuscular period), and the daily salinity measure X2, which is defined as the distance in km upstream from the Golden Gate Bridge to the location where the salinity concentration at the river bottom reached 2 ppt.

Table 2 Covariates evaluated in individual-based models

Name	Type	Station	Duration	Metric	Units
VNS.2	Flow (Delta inflow)	VNS	2	Daily	cfs
SLT.1net, SLT.2net, SLT.3net	Flow	SLT	1, 2, 3	Net	cfs
SLT.1rms, SLT.2rms, SLT.3rms	Flow	SLT	1, 2, 3	RMS	cfs
BDT.1net, BDT.2net, BDT.3net	Flow	BDT	1, 2, 3	Net	cfs
BDT.1rms, BDT.2rms, BDT.3rms	Flow	BDT	1, 2, 3	RMS	cfs
SJG.1net, SJG.2net, SJG.3net	Flow	SJG	1, 2, 3	Net	cfs
SJG.1rms, SJG.2rms, SJG.3rms	Flow	SJG	1, 2, 3	RMS	cfs
OH1.1net, OH1.2net, OH1.3net	Flow	OH1	1, 2, 3	Net	cfs
OH1.1rms, OH1.2rms, OH1.3rms	Flow	OH1	1, 2, 3	RMS	cfs
ORB.1net, ORB.2net, ORB.3net	Flow	ORB	1, 2, 3	Net	cfs
ORB.1rms, ORB.2rms, ORB.3rms	Flow	ORB	1, 2, 3	RMS	cfs
MID.1net, MID.2net, MID.3net	Flow	MID	1, 2, 3	Net	cfs
MID.1rms, MID.2rms, MID.3rms	Flow	MID	1, 2, 3	RMS	cfs
OMT.1net, OMT.2net, OMT.3net	Flow	OMT	1, 2, 3	Net	cfs
OMT.1rms, OMT.2rms, OMT.3rms	Flow	OMT	1, 2, 3	RMS	cfs
QOUT	Delta outflow	Chipps Island[a]	1	Daily	cfs
Tslt.2	Temperature	SLT	2	Average	°C
Toh1.2	Temperature	OH1	2	Average	°C
CVP.2	Exports	CVP	2	Daily	cfs
SWP.2	Exports	SWP	2	Daily	cfs
CVPSWP.2	Exports	CVP, SWP	2	Daily	cfs
pCVP.2	Proportion CVP exports	CVP, SWP	2	Daily	
IE.2	Inflow:Export Ratio	VNS, CVP, SWP	2	Daily	
X2.2	Distance from Golden Gate Bridge to 2 ppt salinity		2	Daily	km
Fork length at tagging	Fish size				mm
Physical Barrier	Barrier				T/F
Day, Night	Departure time from SJL/ORE				T/F

Station = gaging station or water export facility; see Fig. 1 for station locations (OMT = ORB + MID). Summary period (duration in days) started at detection at SJL or ORE unless otherwise noted. Daily = daily measure or average daily mean; Net = average net flow; RMS = root mean square; Average = average of 15-min event data

[a] as reported in CDWR Dayflow database (water.ca.gov); measured on observed date of tag detection at the CHP telemetry station, or 6 days after detection at SJL and 3 days after detection at ORE if tag was not detected at CHP

Environmental and operational covariates were defined as summaries of measures of Delta inflow, river flow, temperature, salinity, exports, and I:E conditions over summary periods selected to represent the majority of the fish movement in the Delta. Each summary period began at the time of tag detection at either the SJL or ORE telemetry stations. The duration of the summary period was selected based on observed travel times through the Delta during the five years of study. Median travel time from detection at SJL or ORE to Chipps Island was approximately 3.5 days over all years, although it was considerably longer for the San Joaquin River route (5.7 days) than for the Old River route (2.6 days). For fish in the Old River route that were salvaged at the water export facilities, the upstream portion of their transit time to Chipps Island represented the largest proportion of their total transit time. Fish in the San Joaquin River route had a longer distance to swim, and observed travel times varied from 2.5 days to 12 days. Three candidate summarization periods lasting 1 day (24 h), 2 days, or 3 days were selected for both routes in order to reflect flow conditions in both the upstream, more riverine sections of the Delta and in the intermediate regions of the Delta, as well as to ensure that the conditions represented were experienced by the majority of the fish, i.e., before most mortalities occurred. All other environmental and operational conditions were summarized over a period of 2 days from detection at SJL and ORE: Delta inflow at Vernalis (VNS), temperature at the SLT and OH1 gaging stations, export measures, the salinity measure (X2), and I:E. For each Delta gaging station (i.e., not VNS), river flow was represented both as the average net flow during the selected time period, and as the root mean square (RMS; square root of the average of the squared values) of flow during that time period; both measures were computed using 15-min event data. The average net flow represented both water volume and velocity and the proportion of time flow was directed downstream versus upstream (reverse flow). The RMS was used to reflect the average volume of flow (magnitude) without effects of reverse flows or short-term cyclic fluctuations such as tidal and diurnal effects. In tidally influenced regions, the average net flow varies about 0, whereas the RMS flow tends to be considerably greater; in less tidally influenced regions, the RMS and average net flow values are similar.

Estimated Delta outflow was measured on the observed date of tag detection at the CHP telemetry station, or on the expected day of arrival to that station for tags not detected there. The expected day of arrival was based on the median travel time to Chipps Island within the route selected by the tag, rounded to the nearest day: 6 days after detection at SJL, and 3 days after detection at ORE.

Statistical methods

The relationship between salmon migration survival in the Delta and potential influential variables was evaluated on two spatial scales. Overall interest was in survival from the head of Old River to Chipps Island in the two possible routes:

S_{SJL} = of surviving from SJL to CHP (San Joaquin River route);

S_{ORE} = of surviving from ORE to CHP (Old River route).

Also investigated was the relationship between survival and covariates through the upstream portion of the San Joaquin River route, in particular to the receivers at MacDonald Island (MAC) and in Turner Cut (TRN), located just downstream of the Turner Cut Junction:

$S_{SJL-TCJ}$ = of surviving from SJL to MAC or TRN at the Turner Cut Junction.

The probability of survival from the head of Old River receivers at SJL and ORE to Chipps Island, S_{SJL} and S_{ORE}, and the conditional probability of detection at Chipps Island, P_{CHP}, were jointly modeled using an individual-based regression model. Tag detection at Chipps Island required both survival to Chipps Island and reading of the acoustic tag signal by one or both receiver lines there. A regression model using multinomial errors and a logit link function was used to separately model the probabilities of survival to and detection at the Chipps Island receivers. The possibility of tag failure was accommodated by using the release group-specific estimates of tag survival to Chipps Island as a group-level offset. The Chipps Island detection probability model was developed first, using unique survival effects for each release group in 2010 and 2011; release groups from 2012, 2013, and 2014 were pooled to achieve sufficient degrees of freedom to fit the model. The detection probability at each of the two lines of receivers composing the CHP station was modeled as a function of estimated Delta outflow (QOUT). The Akaike Information Criterion (AIC; Burnham and Anderson 2002) was used to select among models that used either unique or common outflow coefficients and intercepts for the two telemetry lines.

For survival from Lathrop (SJL) to the Turner Cut Junction, an individual-based generalized linear model with binomial errors and logit link function was used to relate detections at the MAC and TRN telemetry stations to covariates. Drawing inferences to survival separately from detection depended on 100% conditional detection probabilities at TRN and MAC (i.e., all tags that were present were detected).

Both group-level and individual-level covariates were considered in modeling survival to Chipps Island and to the Turner Cut Junction. Fixed effects of the group-level covariates year and barrier were accounted for before modeling effects of other covariates. Year was included in all models in order to account for annual differences in the average survival probability that were unrelated to flow, and to examine the relationships between flow and survival within seasons. After accounting for group-level effects, individual-level covariates such as Delta inflow, flow, exports, I:E, water temperature, salinity, fish size, and time of day of departure were considered. For models without barrier effects, the survival component of the competing models had the form:

$$logit\left(S_{yi}\right) = \beta_{0y} + \beta_X X_i,$$

where $logit(\cdot)$ is the logit link function, S_{yi} is the probability of survival for individual fish i from year y, β_{0y} is the intercept for year y, β_X is the slope (regression coefficient) for covariate X, and X_i is the value of covariate X for individual i. Single-variate models were used to identify the covariates associated with survival for two reasons. First, the high degree of correlation among many flow and non-flow covariates complicated interpretation of multiple regression models. Second, the sparse detection data at CHP in some years limited the degrees of freedom available for fitting and testing more complex models. The best flow models were identified, as were the best single-variate models among all covariates. For modeling survival from the head of Old River to Chipps Island, the potential for different relationships between flow and survival in the two major migration routes was also of interest. Detection data at CHP were too sparse to accommodate both year effects and route effects in the same model. Thus, the top flow models were also fit using route effects in place of year effects to explore differential relationships between flow and survival in the two routes.

Model selection was performed using a combination of hypothesis testing and AIC. The statistical significance of the association between single covariates and survival, after adjusting for year, barrier, and/or route effects, used an experimentwise Type I error rate of $\alpha = 0.05$, using Bonferroni corrections to account for the number of tests being performed (Sokal and Rohlf 1995). Model selection used analysis of deviance with F-tests for group-level covariates, and likelihood ratio tests (χ^2 tests) for individual-level covariates (McCullagh and Nelder 1989; Skalski et al. 1993). Non-nested models or those with common significance levels were compared using AIC. Selected models were those that were significant at the experimentwise 0.05 level and with ΔAIC<2 compared to the basic flow model with the smallest AIC.

Goodness-of-fit was assessed by computing the area under the curve (AUC) of the Receiver Operating Characteristic (ROC) curve (Nam and D'Agostino 2002); the joint probability of survival and detection at the downstream receivers was used for this purpose. Values of AUC can range from 0 to 1.0; a value of 0.5 indicates no discrimination, and values >0.7 are considered "acceptable" (Hosmer and Lemeshow 2000). For the selected models, goodness-of-fit was additionally assessed visually by comparing the predicted joint probability of survival and downstream detection to the observed frequencies of survival and detection at the downstream receivers for each survival model selected, computed for groups of individual records ordered by predictions from the selected model. Fifteen approximately equal-sized groups were used for this purpose.

Results

Delta conditions

From the perspective of water project operations, 2010 was classified as an above normal year, 2011 as wet, 2012 as dry, and 2013 and 2014 as critically dry (California Department of Water Resources, cdec.water.ca.gov/cgi-progs/iodir/WSIHIST). Delta inflow at Vernalis (measured at the VNS gaging station) was considerably higher before and during the study period in 2011 than in the other years (Fig. 2). Mean daily Delta inflow was consistently <4500 cfs from April through May for 2012, 2013, and 2014. Average combined (i.e., CVP + SWP) daily export rates during the release days of each year ranged from 1517 cfs in 2010 to 6041 cfs in 2011. Export rates tended to be <5000 cfs throughout the study periods, and were held stable at approximately 1530 cfs for the entirety of the 2010 study; the exception was for the final two release groups in 2011, which occurred later than releases in all other years and had considerably higher export rates (>7500 cfs). Average water temperature measured at the SLT gaging station during the release days each year was 16.3 °C to 16.6 °C in 2010 and 2011, and 18.8 °C to 19.1 °C in 2012, 2013, and 2014.

The magnitude and variability of covariate observations used in the analysis reflected the prevailing conditions during the study periods and the timing of fish arrival at the SJL and ORE telemetry stations. The 2-day summary of Delta inflow at Vernalis (VNS.2) tended to be considerably higher in 2011, and consistently low in 2012, 2013, and 2014 (Fig. 3). Old River flow measured near the head of Old River (OH1) and San Joaquin River flow measured at Garwood Bridge (SJG) followed

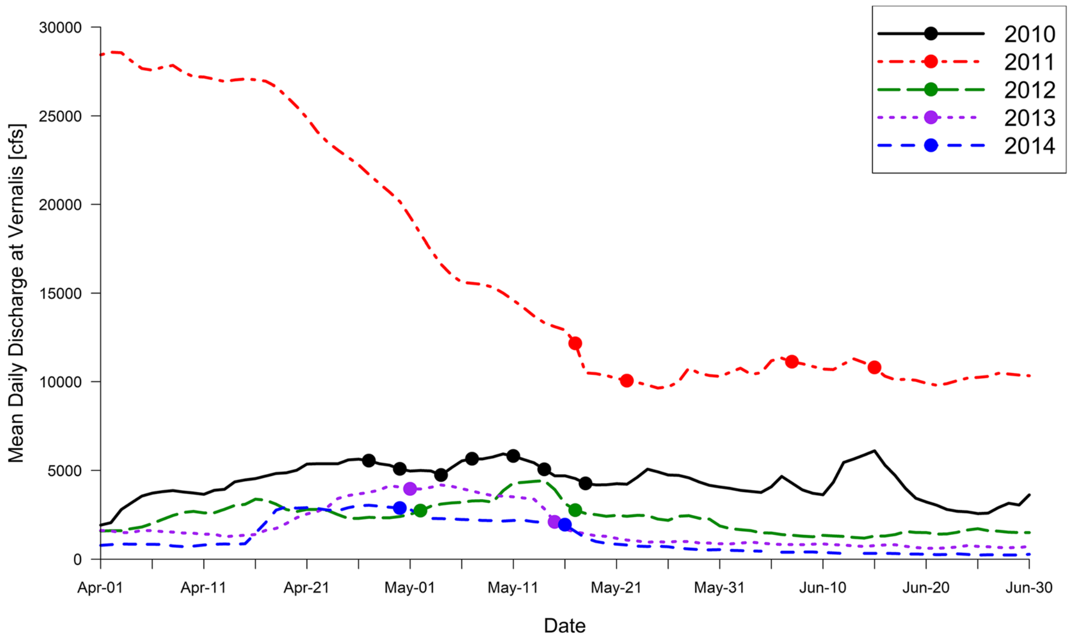

Fig. 2 Mean daily San Joaquin River discharge (flow) at the VNS gaging station near Vernalis (Delta inflow) throughout the study period for each year. Points indicate the observed mean daily discharge on the first day of each release group; second release day is shown for mid-May 2014 group to offset it from 2013

similar patterns. For each of the flow metrics at VNS, OH1, and SJG, there was no overlap in observations between 2011 and the other years, and only limited overlap between 2010 and 2012–2014 (Fig. 3). At the Old River gaging station near Bacon Island (ORB), the median 2-day average net flow was again highest in 2011, but there was a high amount of variability in 2011 and more overlap between years than at the previous sites (Fig. 3). The 2-day root mean square (RMS) of flow at ORB was generally highest in 2012 and lowest in 2014 (Fig. 3). Middle River flow at MID and the combined Old and Middle River flows ("OMT") followed similar patterns as the ORB flow metrics. Flow data were unavailable from the SLT and SJG gaging stations in 2014, and at the BDT station for 8 to 82 observations (depending on flow metric summary period) in 2014.

The similarity in conditions during the studies in 2012, 2013, and 2014, combined with differences in survival, suggested that there were factors acting on survival on an annual basis other than the measured covariates, especially from SJL to Turner Cut. On the other hand, the much higher Delta inflow in 2011 was not accompanied by commensurately higher (or lower) average survival to Chipps Island (Table 1), suggesting that any discernable relationships between flow and survival would be found within individual years rather than primarily between years. For these reasons, fixed year effects were retained in the model regardless of their statistical significance.

As expected from a network of river and delta flow monitoring stations, there was high correlation among various flow covariates, both spatially and temporally (Fig. 4). Correlation was highest among flow metrics from the same region, e.g., among the interior Delta metrics (ORB, MID, OMT) and separately among the San Joaquin River stations (SLT, BDT, SJG). Delta inflow measured at Vernalis (VNS.2) and Old River flow at OH1 were both strongly associated with the San Joaquin River flow metrics. There was lower correlation between the interior Delta flow metrics and flow measured at OH1 or at the San Joaquin River stations (Fig. 4). Within the San Joaquin River and OH1 flow metrics, there was high correlation among the flow metrics of different type (average net flow vs. RMS flow) and duration (1, 2, or 3 days). Among the interior Delta metrics, there was high correlation between different durations within the same metric type, although

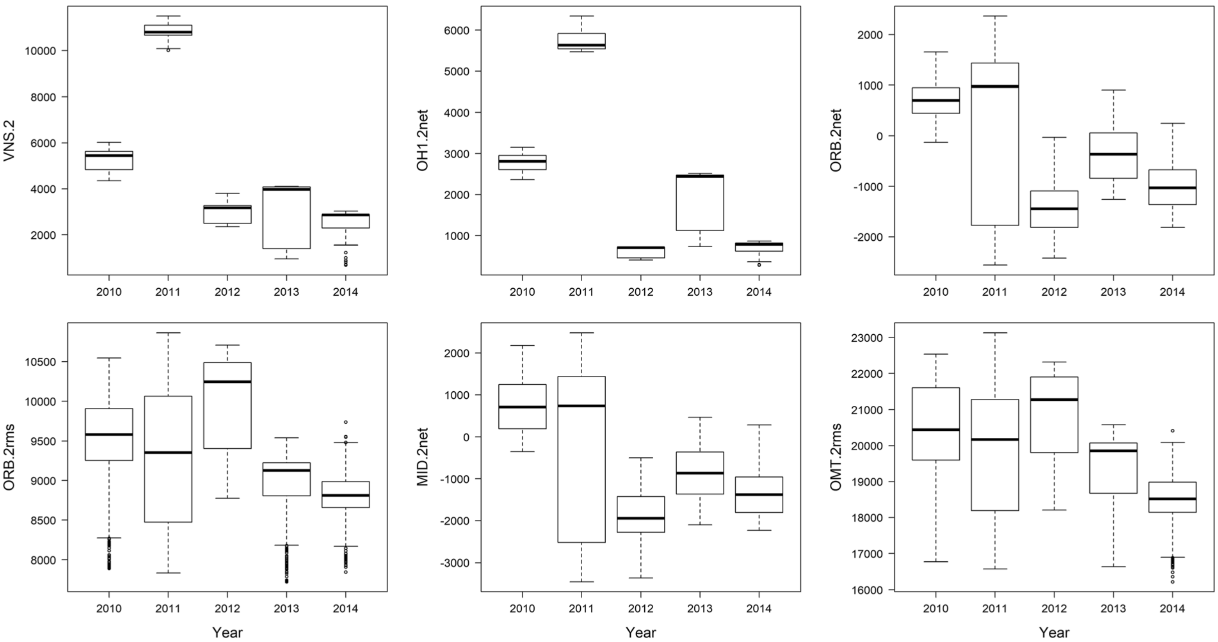

Fig. 3 Box plots of Delta inflow and flow covariates by study year. Box represents interquartile range, and the thick horizontal line is median. Covariates are the 2-day average daily mean Delta inflow at Vernalis (VNS.2) and measures of river flow at the OH1, ORB, and MID gaging stations (OMT = ORB + MID), summarized using the Root Mean Square ("rms") or average net ("net") flow over a period of 2 days. Flow is measured in cfs

the relationship was more variable among the RMS flow metrics (r = 0.83 to 0.98) than among the average net flow metrics (r = 0.96 to 0.99). There was considerably lower correlation between flow metrics of different types at the interior Delta stations. For example, there was a distinct positive relationship between the 2-day RMS of Middle River flow at MID and the 3-day RMS of Old River flow at ORB, but no obvious linear or monotonic relationship between either of those metrics and the 2-day average net flow at ORB (Fig. 4). This was expected in a tidal environment where reverse flows may yield negative values of average net flows, but RMS flow remains >0. The salinity measure X2 was highly negatively correlated with the flow metrics from the San Joaquin River and OH1 (r = −0.86 to −0.97).

Salmon detection and survival data

The size of the virtual release groups (i.e., number detected) at the SJL telemetry station each year ranged from 102 in 2014 to 919 in 2011; at ORE, the virtual release group sizes varied from 9 in both 2012 and 2014 to 656 in 2011 (Table 3). The presence of the rock barrier at the head of Old River in 2012 and 2014 restricted the number of tagged salmon detected at the ORE station in those years. The number of tags detected at the CHP station at Chipps Island annually ranged from 0 in 2014 and 3 in 2013 to 31 in 2011, for a total of 30 CHP detections from the 1773 tags detected at SJL over the five years, and 47 CHP detections from the 1243 tags detected at ORE (Table 3). For the telemetry stations at the Turner Cut Junction, MAC detections ranged from 1 in 2014 to 348 in 2011, and TRN detections varied from 0 in 2013 to 95 in 2011 (Table 3). Annual detection probability estimates at all five sites were 1.00 $S\hat{E}$≤0.01) for most cases, and were ≥ 0.98 $S\hat{E}$ =0.02) in all cases (Table 1). The CHP detection probability estimates were unavailable in 2014 because no tags were detected there. Survival estimates for the San Joaquin River route (i.e., from SJL to CHP) for each release group ranged from 0 $S\hat{E}$ =0) for individual groups in 2011–2014, to 0.08 $S\hat{E}$ =0.03) for the final release in 2010, and averaged 0.02 $S\hat{E}$ =0.01) over all releases (Table 1). In the Old River route, survival estimates from ORE to CHP ranged from 0 for individual release groups in every year, to 0.17 $S\hat{E}$ =0.15) for the first release in 2012, and averaged 0.05 $S\hat{E}$ =0.01;

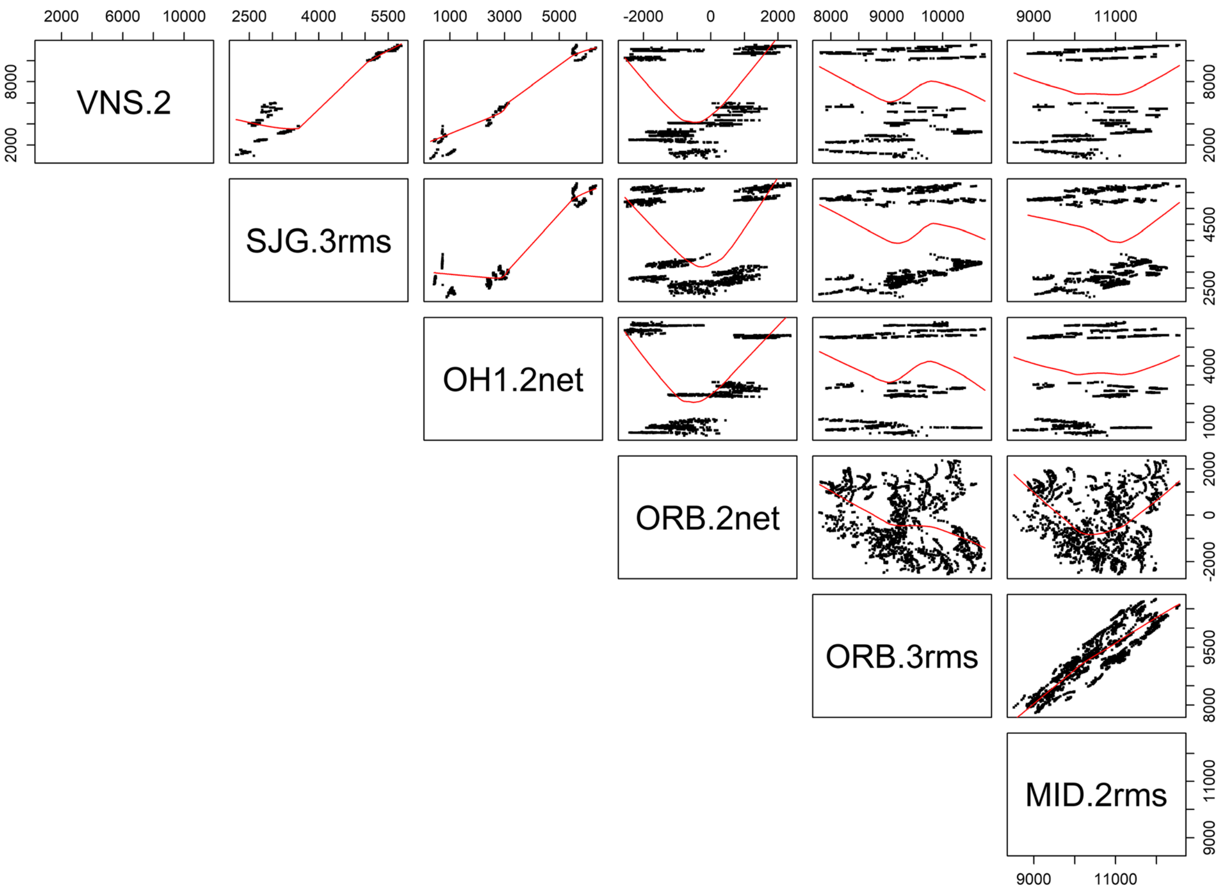

Fig. 4 Pairwise correlation plots with LOWESS smoother for 2-day average daily mean Delta inflow at Vernalis (VNS.2) and measures of river discharge (flow) at the SJG, OH1, ORB, and MID gaging stations, summarized using the Root Mean Square ("rms") or average net ("net") flow over a period of two or three days since tag detection at SJL or ORE. Flow is measured in cfs

Table 1). Estimates of survival from the SJL station to the Turner Cut Junction ranged from 0 for the mid-May release groups in 2013 and 2014, to 0.55 $\widehat{SE}$ =0.03) for the first release in 2011 (Table 1).

Survival models: Head of Old River to Chipps Island

A total of 77 tags were detected at Chipps Island in the 2010–2014 studies, out of the 3016 tags defining the virtual release groups at the SJL and ORE telemetry stations (Table 3). There was little difference in the fit of the Chipps Island detection probability model whether unique or common intercepts and Delta outflow coefficients were used for the two telemetry receiver lines (ΔAIC = 1.92). Thus, the detection probability model used both common intercepts and common outflow effects for the two lines.

Neither year ($F_{4,37} = 0.51$, $P = 0.7252$) nor route ($F_{1,41} = 0.77$, $P = 0.3853$) accounted for a sizeable proportion of the variability in survival from the head of Old River to Chipps Island. The effect of the barrier was not significant ($F_{1,41} = 0.001$, $P = 0.9705$). As addressed above, year-based models were nevertheless used as the foundation of further modeling efforts in order to focus on within-year variation in conditions rather than between-year survival differences that were unrelated to flow or other covariates. However, no tags from 2014 were detected at Chipps Island, so 2014 contributed no degrees of freedom to the detection data. For this reason, 2014 was omitted from year-based models with individual-level covariates.

Using fixed year effects and omitting 2014, the top flow model selected by AIC used the 3-day RMS of Old River flow at Bacon Island (ORB.3rms; Table 4).

Table 3 Counts of tag detections at SJL and ORE and subsequent detections at Chipps Island (CHP), MacDonald Island (MAC), and Turner Cut (TRN)

Year	Upstream Site		CHP			MAC	TRN
	Station	Count	*11*	*10*	*01*		
2010	SJL	202	9	0	0	75	6
	ORE	228	17	2	0		
2011	SJL	919	5	1	0	348	95
	ORE	656	19	5	1		
2012	SJL	444	14	0	0	97	12
	ORE	9	1	0	0		
2013	SJL	106	0	0	1	2	0
	ORE	341	2	0	0		
2014	SJL	102	0	0	0	1	2
	ORE	9	0	0	0		
Total	SJL	1773	28	1	1	523	115
	ORE	1243	39	7	1		

Detection histories at CHP indicated detection (1) or non-detection (0) at the two parallel lines of acoustic receivers that formed the telemetry station. Detections at MAC and TRN were modeled only for tags detected at SJL

When route effects were used instead of year effects, the main effect of ORB.3rms remained significant ($P < 0.0001$), and the interaction effect between route and ORB flow was not significant ($P = 0.5896$). The year-effects model with ORB.3rms achieved acceptable model fit based on the area under the Receiver Operating Characteristic curve (AUC = 0.73) and on comparison of the predicted and observed joint probabilities of survival and detection at Chipps Island (Fig. 5). Survival from the head of Old River to Chipps Island was predicted to be higher for higher magnitudes of Old River flow as represented by the 3-day RMS flow at ORB (Fig. 6a). Using the estimated intercept for 2011, an increase in 3-day RMS flow at ORB from 7850 cfs to 10,750 cfs was predicted to increase the probability of survival to Chipps Island from 0.005 $\hat{SE}$ =0.006) to 0.057 $\hat{SE}$ =0.048) (Fig. 6a).

Other measures of interior Delta flow were also associated with survival from the head of Old River to Chipps Island, namely the 2-day and 3-day average net Middle River flow at MID, and the 2-day average net combined Old and Middle River flow represented by OMT (= ORB + MID) ($P \leq 0.0001$; Table 4). The year effects models using these flow metrics each had similar performance (ΔAIC≤0.54, AUC = 0.71), but had higher AIC than the model that used the 3-day RMS of ORB flow (ΔAIC≥4.41; Table 4). Each of these three average net flow metrics was moderately associated with survival when route effects were used in place of year effects ($P \leq 0.0138$), and none had a strongly significant interaction effect with route ($P \geq 0.0811$). Overall, the predictive power of the average net flow models was not as good as for the RMS model (ORB.3rms), in particular for the higher observed values (i.e., for 2010) (Fig. 5). Unlike the positive relationship estimated for RMS flow, survival to Chipps Island was negatively associated with the average net river flow at MID and OMT (e.g., Fig. 6b). Using the intercept for 2011, the model estimated that an increase of the 2-day average net OMT flow from −5800 cfs to 4670 cfs was associated with a decrease in survival to Chipps Island from 0.045 ($\hat{SE}$ =0.034) to 0.006 ($\hat{SE}$ =0.008) (Fig. 6b). Inferences for average OMT

Table 4 Single-variate regression results for survival from SJL/ORE to CHP, adjusted for fixed year effects, 2010–2013

Name	Type	Sign	P	ΔAIC	AUC
ORB.3rms	Flow	+	<0.0001	0	0.73
MID.2net	Flow	–	<0.0001	4.41	0.71
MID.3net	Flow	–	<0.0001	4.65	0.71
OMT.2net	Flow	–	0.0001	4.95	0.71
IE.2	I:E	–	0.0001	5.17	0.70
OMT.3net	Flow	–	0.0001	5.22	0.71
CVP.2	Exports	+	0.0001	5.48	0.70
ORB.2rms	Flow	+	0.0001	5.52	0.72
OMT.3rms	Flow	+	0.0001	5.56	0.71
ORB.2net	Flow	–	0.0001	6.01	0.71
MID.1net	Flow	–	0.0001	6.03	0.71
ORB.3net	Flow	–	0.0001	6.23	0.71
OMT.1net	Flow	–	0.0002	6.83	0.71
ORB.1net	Flow	–	0.0004	8.37	0.70
CVPSWP.2	Exports	+	0.0004	8.54	0.69
VNS.2	Inflow	–	0.2758	19.96	0.69

Results shown are restricted to covariates significant at the experimentwise 5% level (likelihood ratio test, test-wise α = 0.0009), and Delta inflow (VNS.2). See Table 2 for definitions of covariates. Sign refers to the estimated regression coefficient. AUC = area under the curve for the Receiver Operating Characteristic curve

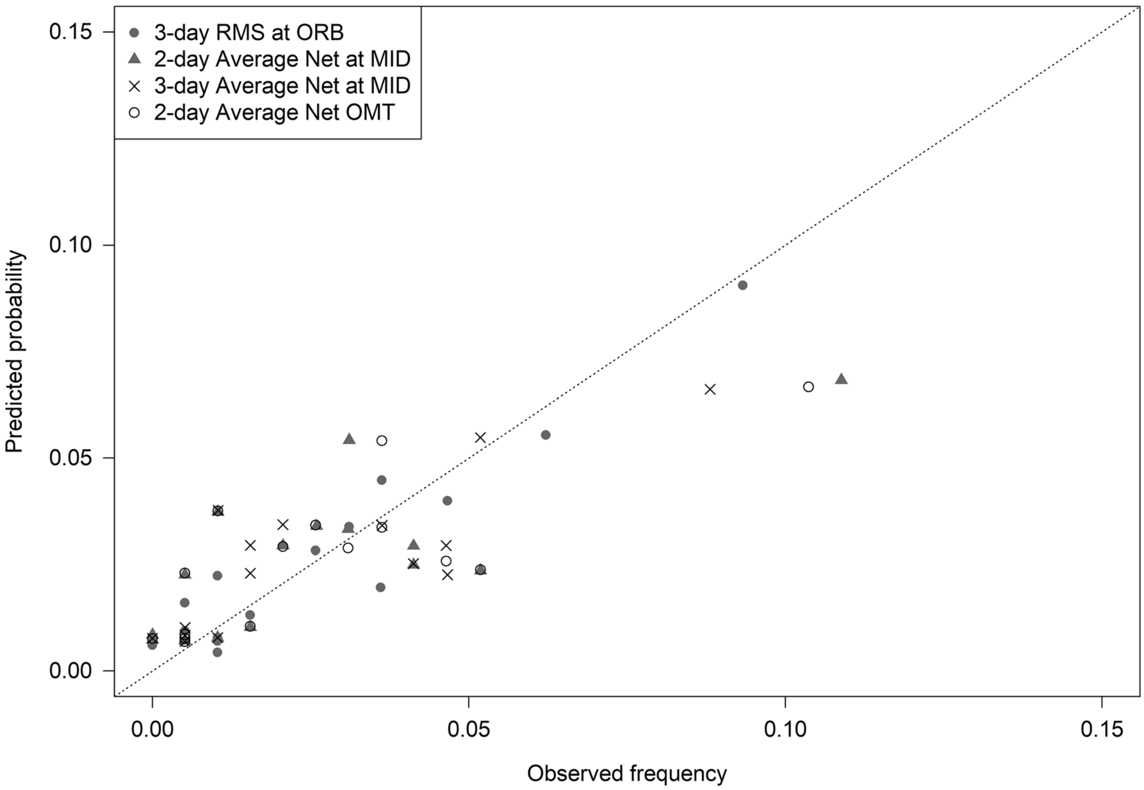

Fig. 5 Predicted probability versus observed frequency of the joint event of survival to and detection at Chipps Island (CHP) for the top four flow models for survival to Chipps Island from the head of Old River receivers (SJL and ORE). All models included fixed effects of year (2010–2013). Dashed line is 1–1 line

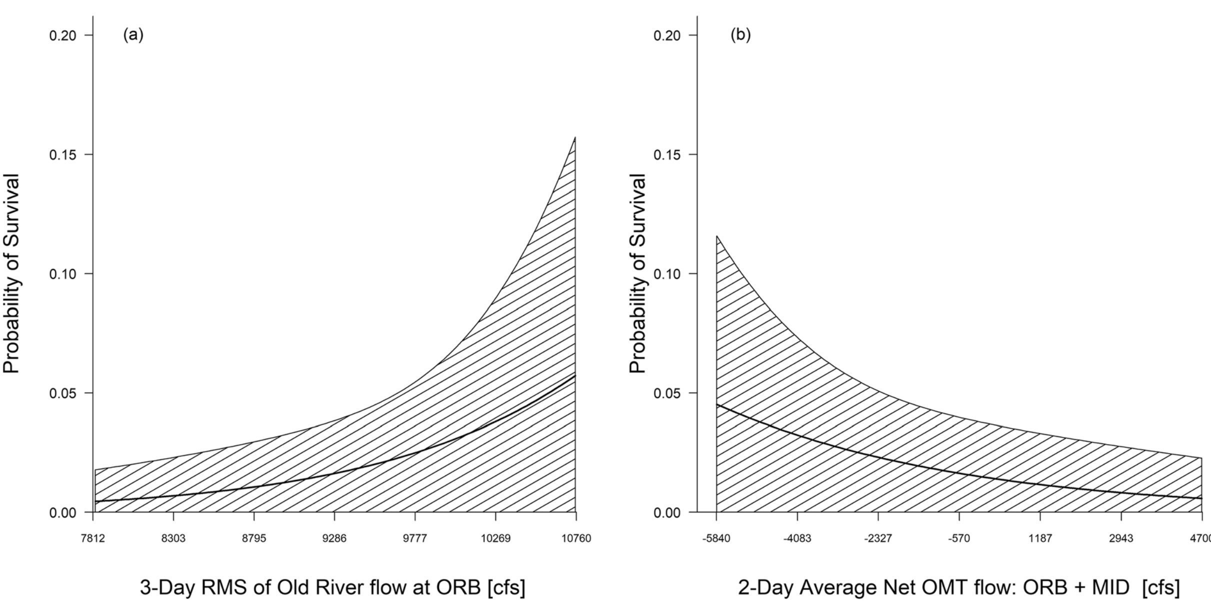

Fig. 6 Predicted probability and 95% confidence band of surviving from the head of Old River (SJL or ORE receivers) to Chipps Island (CHP receivers) as a function of (a) the 3-day Root Mean Square of Old River flow at the ORB gaging station, for l: $logit(S_{yi}) = \hat{\beta}_{0y} + 0.0009(SE = 0.0007) \times Q_{ORB.3rms,i}$, and (b) the 2-day average net OMT (=ORB + MID) flow, for l: $logit(S_{yi}) = \hat{\beta}_{0y} - 0.0002(SE = 0.0002) \times Q_{OMT.2net,i}$. Results are shown using 2011 i: (a) $\hat{\beta}_{0,2011} = -12.3143(SE = 6.5799)$ and (b) $\hat{\beta}_{0,2011} = -4.2098(SE = 0.7604)$

flows more negative than −5840 cfs or more positive than 4700 cfs are not warranted.

The association between Delta inflow and survival to Chipps Island was not significant within the years 2010–2013 ($P = 0.2758$; Table 4). There was little variation in San Joaquin River flow at VNS within the individual study years, compared to measures of flow in Old and Middle rivers represented by the ORB and MID stations and the combined OMT measure (Fig. 3), resulting in little opportunity to detect an inflow effect from the year-effects models. However, the effect of Delta inflow remained insignificant when route effects were used in place of year effects ($P = 0.2209$), and when neither year nor route effects were accounted for ($P = 0.2768$).

Survival models: Lathrop to Turner Cut Junction

The regression analysis modeled the joint probability of survival from SJL to the Turner Cut Junction and detection at the MAC or TRN telemetry stations. Estimated conditional detection probabilities at those sites were ≥ 0.97 for all release groups with sufficient detections to yield estimates, and were 1.0 (100%) for 25 of the 31 cases (Table 1). The consistently high detection probability estimates allow drawing inference from the modeling results to survival.

Both fixed year effects and fixed effects of the presence of the rock barrier at the head of Old River were separately significant in accounting for variability in survival and detection from SJL to the MAC and TRN telemetry stations ($P < 0.0001$). The year effects model was selected by AIC over the barrier model (ΔAIC = 137.35).

River flow measurements at the SLT and SJG gaging stations were unavailable in 2014, and measurements at the BDT gaging station were missing for more than one-third of the records from 2014 used in the analysis. Thus, 2014 was initially omitted from the data for fitting the survival model to the Turner Cut Junction receivers. Candidate models that used covariates other than the SLT, BDT, and SJG flow metrics were then refit using all data including those from 2014.

The flow models selected by AIC used the 1-day average net flow measured at OMT (combined ORB and MID), MID, or ORB, whether or not 2014 was included (Table 5). Among the flow models, these three covariates had nearly equal support (ΔAIC≤0.26). Model fit was moderate, based on the AUC (0.69 to 0.70) and on comparison of observed and predicted probabilities of survival and detection (Fig. 7). Higher levels of 1-day average net flow at the interior Delta stations were associated with higher probability of survival to the Turner Cut Junction (Fig. 8). Using the 2011 intercept, an increase in 1-day average net OMT flow from −6070 cfs to 5100 cfs was predicted to yield an increase in survival to the Turner Cut Junction from 0.38 $\widehat{SE} = 0.05$) to 0.58 $\widehat{SE} = 0.05$) (Fig. 8). The 1- and 2-day flow metrics at Garwood Bridge (SJG) also had significant associations with survival in this reach ($P \leq 0.0003$), although slightly less support than the interior Delta flow metrics (ΔAIC = 1.55 vs. OMT.1net) (Table 5). Higher SJG flow was predicted to yield higher survival. The association between Delta inflow at VNS and survival was positive and significant ($P = 0.0009$) but was not supported by AIC compared to the other flow models (ΔAIC = 6.04 vs. OMT.1net; Table 5).

The covariate with the strongest support (smallest AIC) in modeling survival to the Turner Cut Junction was not a flow metric but rather the salinity measure X2 (2-day average) (ΔAIC≥42.90 compared to the flow models; Table 5). Higher levels of X2, which indicated a greater extent inland of the salt intrusion measured from the Golden Gate Bridge, were strongly associated with lower survival to the Turner Cut Junction ($P < 0.0001$).

Discussion

This paper updated previous analyses of Delta survival relative to Delta inflow using spatially and temporally-detailed acoustic telemetry data in individual-based regression models, and also included other measures of river flow in the Delta. Whether or not average differences in survival between years or migration routes were accounted for, the relationship between Delta inflow and survival from the head of Old River to Chipps Island was not significant for these years ($P \geq 0.2209$). This is in contrast to previous results from CWT data (Newman 2008) and adult escapement data (SJRGA 2007). It also differs from more recent analyses of acoustic-telemetry data in the Sacramento River that found a positive relationship between mainstem Sacramento River flow and survival to Chipps Island for late-fall-run Chinook Salmon migrating from the Sacramento River (Perry 2010). The findings here are consistent with the

Table 5 Single-variate regression results for the joint probability of survival from SJL to Turner Cut Junction and detection at MAC or TRN, adjusted for fixed year effects, 2010–2013 and 2010–2014

		2010–2013				2010–2014			
Name	Type	Sign	P	ΔAIC	AUC	Sign	P	ΔAIC	AUC
X2.2	Salinity	–	<0.0001	0	0.67	–	<0.0001	0	0.70
Tslt.2	Temp	–	<0.0001	13.60	0.68	–	<0.0001	11.67	0.71
OMT.1net	Flow	+	<0.0001	42.90	0.67	+	<0.0001	43.03	0.70
MID.1net	Flow	+	<0.0001	43.09	0.67	+	<0.0001	43.17	0.69
ORB.1net	Flow	+	<0.0001	43.10	0.67	+	<0.0001	43.29	0.70
CVP.2	Exports	–	<0.0001	43.31	0.66	–	<0.0001	43.44	0.68
CVPSWP.2	Exports	–	0.0001	43.98	0.67	–	0.0001	44.20	0.69
SJG.1net	Flow	+	0.0001	44.45	0.66				
SWP.2	Exports	–	0.0001	44.73	0.67	–	0.0001	45.00	0.69
MID.2net	Flow	+	0.0001	45.13	0.67	+	0.0001	45.26	0.69
IE.2	I:E	+	0.0001	45.14	0.66	+	0.0001	45.04	0.69
SJG.1rms	Flow	+	0.0002	45.65	0.66				
OMT.2net	Flow	+	0.0002	45.79	0.67	+	0.0002	45.97	0.69
SJG.2net	Flow	+	0.0002	45.96	0.65				
MID.3net	Flow	+	0.0002	46.17	0.66	+	0.0002	46.38	0.69
SJG.2rms	Flow	+	0.0003	46.57	0.66				
OMT.3net[a]	Flow	+	0.0003	46.65	0.66	+	0.0003		0.69
ORB.2net	Flow	+	0.0003	46.78	0.67	+	0.0003	47.05	0.69
ORB.3net	Flow	+	0.0004	47.41	0.66	+	0.0004	47.75	0.69
VNS.2	Inflow	+	0.0012	49.31	0.65	+	0.0009	49.07	0.68

Results shown are restricted to covariates significant at the experimentwise 5% level either with or without 2014 (likelihood ratio test); the test-wise α is 0.0009 without 2014, and 0.0014 with 2014. See Table 2 for definitions of covariates. Sign refers to the estimated regression coefficient. AUC = area under the curve for the Receiver Operating Characteristic curve

[a] OMT.3net was missing for 1 tag in 2014

conclusions of Zeug and Cavallo (2013), who found low support for hydrodynamic conditions represented by Delta inflow and export rates to drive survival. However, their analysis did not separate Delta survival from ocean survival, or Delta inflow from export rates.

Although within-season variability in Delta inflow did not appear closely related to the survival pattern from the head of Old River to Chipps Island, measures of flow within the Delta were associated with survival. Surprisingly, it was not the measures of San Joaquin River flow in the Delta (SLT, BDT, or SJG) that stood out, but rather measures of interior Delta flow conditions in Old and Middle rivers. In particular, the long-term volume of Old River flow measured at Bacon Island, represented by the 3-day RMS, was positively associated with survival to Chipps Island, even though most fish did not pass that location on their migration through the Delta: the majority (89%) of the tagged fish from the Old River route that were detected at Chipps Island each year passed through the CVP holding tank and salvage, and the fish in the San Joaquin River route mostly avoided the interior Delta. Furthermore, there was no evidence of a different survival relationship with interior Delta flow in the two major migration routes. The apparent mismatch between this key flow metric and the migrating population suggests that the ORB flow measure represents conditions throughout the northern portion of the South Delta, rather than strictly localized conditions. That it is the 3-day summary measure rather than a shorter measure also suggests that it is the conditions encountered downstream that drive total Delta survival.

Current management of the water facilities limits the amount of upstream-directed (i.e., negative) flow in the Old and Middle rivers in the interior Delta during the spring via the concept of “reverse OMR flows;” the

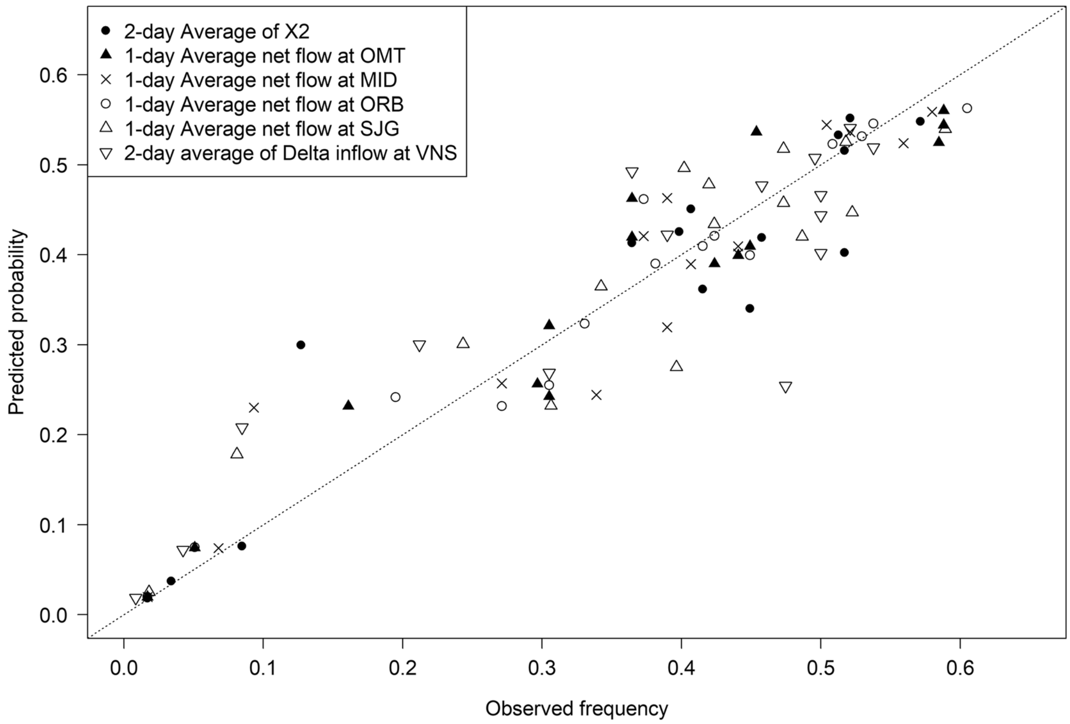

Fig. 7 Predicted probability versus observed frequency of the joint event of survival to and detection at MAC or TRN from the SJL receivers for the top model (X2), top four flow models, and Delta inflow (VNS.2) model for survival to the Turner Cut Junction from the head of Old River receivers at SJL. All models included fixed effects of year (2010–2014); the SJG flow model omits 2014. Dashed line is 1–1 line

amount of negative flow is controlled by adjusting pumping rates at the water facilities (NOAA 2009b). The OMR index measure used in management is based on Delta inflow at Vernalis and water diversion and pumping rates out of the Delta, and represents average tidally-filtered ORB and MID flow (Hutton 2008). This analysis did not use the complicated formulation of the OMR index, but instead approximated it via the sum of the 15-min event flow data at the ORB and MID gaging stations (i.e., OMT = ORB + MID). Rather than using as a covariate the proportion of time flows were either negative or more negative than a cutoff such as −5000 cfs, the average net flow over varying durations was used. Conditions with more negative average net flow will, generally, also be those conditions under which OMR flows are more negative. The results here show that the average net flow in the interior Delta is not as associated with variability in Delta survival as is the volume of flow regardless of flow direction, represented by the RMS. Furthermore, the association that was observed between average net flow and survival was negative, implying that for these fish and within these study years, survival was higher when average net flow was more negative; this is counter to the OMR-based management. However, this finding is limited by several considerations. First, there was a small range of average net flow values observed in the interior Delta during most years (Fig. 3), reflecting the fact that these data were collected when the OMR restrictions were in place. Thus, there was limited ability to gauge the effectiveness of those restrictions for improving salmon survival. Second, approximately half of the tagged salmon detected at Chipps Island in this study went through CVP salvage and were transported by truck to the Delta exit. To the extent that negative values of the OMT net flow measures and OMR index reflect higher rates of pumping at CVP, the negative association between interior Delta net flow measures and survival to Chipps Island may reflect the relative viability of the CVP salvage route over the non-salvage routes in the context of very low survival overall. If survival in the non-salvage routes improves, the relationship between net interior Delta flow and survival may change.

Management via OMR is designed to protect ESA-listed species such as winter-run Chinook Salmon by

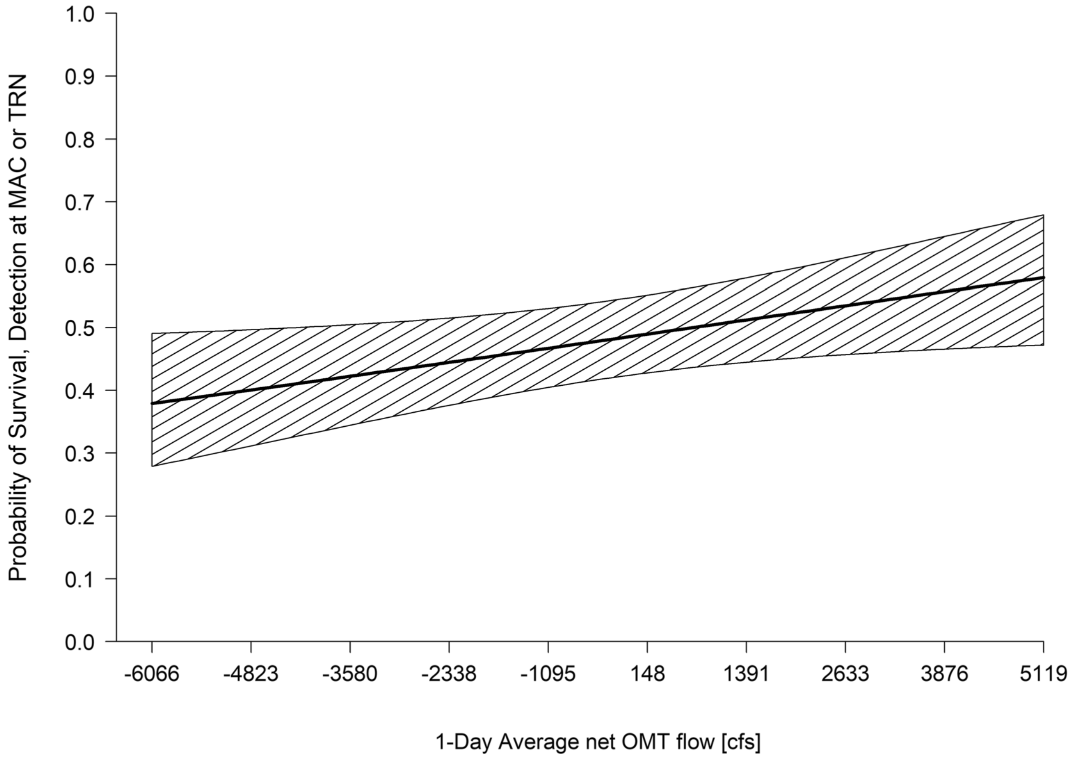

Fig. 8 Predicted joint probability and 95% confidence band of surviving (S) from the SJL receivers to the Turner Cut Junction and detection (P) at the MAC or TRN receivers as a function of the 1-day average net OMT flow, for : $logit\left((SP)_{yi}\right) \sim \hat{\beta}_{oy} + 0.00007(SE = 0.00003) \times Q_{OMT.1net,i}$. Results are shown using 2011 t: $\hat{\beta}_{0,2011} = -0.0520(SE = 0.1208)$. Negative values of average net flow occur when flow reverses

keeping them away from the water pumping facilities (NOAA 2009b). Because winter-run Chinook Salmon migrate solely from upstream in the Sacramento River, they approach the delta from the north and thus have the opportunity to avoid entering the southern portion of the Sacramento-San Joaquin delta entirely. Perry et al. (2010) observed higher survival of late-fall-run Chinook Salmon from the Sacramento River basin that avoided entering the southern delta. San Joaquin River basin salmonids, on the other hand, originate south of the delta and cannot avoid entering the relatively risky southern delta as they migrate seaward. It is possible that the protective measures designed for Sacramento River basin salmon, or even for San Joaquin River basin steelhead, are less effective for San Joaquin River basin salmon, especially in the context of consistently low Delta survival.

The pattern observed between flow and survival from Lathrop to the Turner Cut Junction is considerably different than for Delta survival to Chipps Island. Delta inflow is marginally associated with survival, although still not among the top flow measures, likewise for the San Joaquin River flow measured at Garwood Bridge (SJG) (Table 5). Interior Delta flow remains the flow measure most associated with survival, but there is now a positive association between the average net flow in the interior Delta and survival (Table 5, Fig. 8). It is notable that none of the fish in this analysis experienced the interior Delta or even the more tidal regions north of the Turner Cut Junction during the migration and survival process modeled. Thus, it seems likely that the selected interior Delta flow measures are surrogates for favorable environmental conditions throughout the region. One component of those favorable conditions may be the extent of the salt intrusion upstream from the Golden Gate Bridge, as represented by the salinity measure X2. A model of survival from SJL to the Turner Cut Junction using X2 accounted for considerably more variability in MAC and TRN detections than the best of the flow models (ΔAIC≥42.09). Newman and Rice (2002) likewise noted that salinity was competitive with river flow in accounting for variability in survival of Sacramento River salmon, although they observed a positive association between salinity and survival; they also noted that salinity level is confounded with river flow. Thus, the association between salinity and survival may partly reflect flow conditions. Additionally, salinity may influence the distribution and relative densities of native and non-native fish species in the Delta, some of which are suspected predators of juvenile salmon (e.g., Striped Bass *Morone saxatilis*, Largemouth Bass *Micropterus salmoides*; Nobriga and Feyrer 2007; Young et al. 2018). The X2 salinity metric is influenced by the relative amount of freshwater entering the Delta compared to tidal action. The majority of the freshwater entering the Delta comes from the Sacramento River (Cavallo et al. 2013), so Delta inflow at Vernalis has less potential to drive X2 than Delta inflow from the Sacramento River. Inflow from the Sacramento River is managed by reservoir releases upstream of the Delta and operation of the Delta Cross Channel, which connects the Sacramento River to the Delta more directly and can be closed via operable gates. Sacramento River inflow is generally managed to protect ESA-listed species from the Sacramento River basin, but these findings suggest that it may affect Delta survival of San Joaquin River salmon as well. If this is the case, then a proposal to divert Sacramento River water directly to the water pumping facilities via tunnels (NOAA 2017) may harm San Joaquin River-origin salmon.

The low survival to Chipps Island in the wet year of 2011 was unexpected, based on previous understanding of how survival depends on inflow. Delta inflow was high in 2011, and survival was higher in 2011 to the Turner Cut Junction compared to drier years, but total survival was low to Chipps Island. One possible explanation is that the overall shape of the hydrograph may be as important as the actual inflow values. The 2011 study fish were released after the peak Vernalis flow that spring (Fig. 2); although they experienced high flow conditions, they may have missed migrating on the spate (McCormick et al. 1998) and any protection that strategy may provide (e.g., predator-swamping), in particular in the region downstream of Turner Cut. A similar regional pattern of survival was observed in 2011 for late-fall-run Chinook Salmon from the Sacramento River, in which survival was higher than in low flow years through the more riverine reaches but not in the more brackish reaches; nevertheless, total Delta survival of the Sacramento River salmon was higher in 2011 than in drier years (Michel et al. 2015). Our findings are also consistent with Perry et al. (2018), who found that survival of Sacramento River late-fall-run Chinook salmon was positively related to Delta inflow only in reaches where increased inflow changed river flow from bidirectional to unidirectional, similar to the reach from SJL to the Turner Cut Junction.

The complex nature of hydrodynamics and fish migration and survival in the Delta is apparent when comparing the results for survival from the head of Old River to the Turner Cut Junction to results for survival to Chipps Island. Higher survival to the Turner Cut Junction is associated with higher average net interior Delta flow, although more with lower X2. Higher survival from the head of Old River to Chipps Island, via both routes, is associated with lower average net interior Delta flow, although more with higher RMS (i.e., volume) of Old River flow at Bacon Island. To the extent that average net interior Delta flow is related to survival in these different regions and spatial scales, the pattern is contradictory: positive on one spatial scale and negative on the other. The Turner Cut Junction is located approximately where the more riverine region of the San Joaquin River transitions to a distinctly more tidal environment, although all regions of the Delta are influenced by tides and the location where reverse flows are first encountered varies with Delta inflow. Different processes are driving survival in different regions of the Delta, even within a common migration route. The lesson for managers is that a one-size-fits-all approach is unlikely to create conditions that promote higher survival through the entire Delta. It is necessary both to get fish down to the tidally-driven areas (e.g., higher total Delta inflow), and to get them through those areas to exit the Delta. The small survival differences associated with changes in flow conditions observed in this investigation indicate that achieving the latter goal may require more systemic approaches than simply short-term adjustments of inflow and exports, including large-scale habitat restoration within the Delta.

There were limitations to the current analysis. There were only four years of data available for modeling survival to Chipps Island using individual-based covariates, and sample sizes were small and Chipps Island detections sparse in some of those years. Similarly, efforts to account for effects of the barrier, which affects both fish and flow routing at the head of Old River, were hampered by having only two years of observations with the barrier in place, one of which had no detections at Chipps Island and was missing flow data in the San Joaquin River. Additionally, because of changes in funding and study objectives between years, the study design was unbalanced, with the majority of records coming from 2011. Accounting for year effects helps limit the impact of the unbalanced study design on results, but the results are necessarily heavily driven by patterns observed in 2011.

The lack of associations observed between Delta inflow and survival may be due to a truly weak relationship, or it may be due to the small number of study years and limited range of inflow values observed within each year. Additional years of study using sufficient sample sizes may help settle uncertainties and inconsistencies with previous results, but will depend on achieving adequate range of inflow values each year to see any existing pattern. Another possible explanation for surprising patterns is that survival in the Delta may be too low to exhibit the variability necessary to detect associations. If survival is low partly because fish condition is poor when entering the Delta, then there may be too few salmon surviving at all to detect an effect of flow (e.g., the extreme drought years of 2013 and 2014). The factors that promote survival when conditions are very poor may be different from the factors that promote survival when conditions are better. For example, it is unclear how much the results here reflect the relative success of the salvage route compared to non-salvage routes, which is expected to change if overall Delta survival improves.

The flow metrics used in this analysis represent a variety of locations throughout the Delta, three time scales, and two types of data summaries (average net flow and RMS flow). They reflect different time signatures in the Delta hydrodynamics and different characteristics of localized and regional flow patterns. Cavallo et al. (2013) advises against relying on any single hydrodynamic metric to characterize flow patterns in the San Joaquin River, advice that is supported by the inconsistency of findings of the survival modeling on the two different spatial scales here. More nuanced relationships between flow and survival may be developed using either sophisticated flow metrics or by combining different types of flow metrics. The latter would require more degrees of freedom each year for fitting and testing the model, which would necessitate additional field study.

Next steps for this type of investigation include analyzing data from the more recent study years (2015, 2016, and 2017). However, these studies also suffered from either very low survival or low effective samples sizes, so the best hope for additional resolution via new data is to implement larger field studies designed for a flow investigation. Using the existing data, it may be possible to incorporate travel time into the survival model, either to better model the conditions experienced by the migrating salmon on a smaller spatial scale, or to model survival as a function of travel time (e.g., Perry et al. 2018). Improved flow metrics may be achievable from simulated hydrodynamic models, although there have been concerns raised about the adequacy of such models in the South Delta (e.g., SST 2017).

Despite the limitations due to sample size and flow metrics, the existing analysis demonstrates the limitations of a conceptual model that relies on simple measures such as Delta inflow rather than flow metrics that better represent the conditions fish experience within the Delta. Improving hydrodynamic model simulations may allow managers to better model how different management scenarios are likely to affect flow conditions, and then relate predictions to observed salmon survival. Successful management of Central Valley salmon populations requires improved understanding of salmon interactions with their environment and how different conditions in the complex Delta region can promote survival through this critical life history stage.

Acknowledgments The 2010 study and the first two release groups from 2011 were part of the Vernalis Adaptive Management Program (VAMP) study, and the last two groups from 2011 were part of the South Delta Temporary Barriers study funded by the California Department of Water Resources (CDWR) (SJRGA 2011, 2013). The VAMP program was funded by the San Joaquin River Group Authority. The 2012–2014 studies were part of the South Delta Chinook Salmon survival study, and were conducted jointly by the U.S. Fish and Wildlife Service, the U.S. Bureau of Reclamation (USBR), the U.S. Geological Survey, and the University of Washington, and funded by the Central Valley Project Improvement Act's Comprehensive Monitoring and Assessment Program, CDWR, and the USBR. Funds for this analysis were provided by the USBR through the Interagency Ecological Program. The authors are grateful to the many people and agencies who funded, oversaw, and implemented fish tagging, care, and release, and acoustic receiver installation, maintenance, retrieval, and processing; to Chris Holbrook (USGS) for assistance in mapping the Delta; and to two anonymous reviewers for helpful comments on earlier drafts of the manuscript.

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