

Delta Flow Factors Influencing Stray Rate of Escaping Adult San Joaquin River Fall-run Chinook Salmon (*Oncorhynchus tshawytscha*)

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ABSTRACT

Adult salmon that stray when they escape into non-natal streams to spawn is a natural phenomenon that promotes population growth and genetic diversity, but excessive stray rates impede adult abundance restoration efforts. Adult San Joaquin River (SJR) Basin fall-run Chinook salmon (*Oncorhynchus tshawytscha*) that return to freshwater to spawn migrate through the San Francisco Bay and Sacramento–San Joaquin River Delta (Delta). The Delta has been heavily affected by land development and water diversion. During the fall time-period for the years 1979 to 2007 Delta pumping facilities diverted on average 340% of the total inflow volume that entered the Delta from the SJR. The hypothesis tested in this paper is that river flow and Delta exports are not significantly correlated with SJR salmon stray rates. Adult coded-wire-tagged salmon recoveries from Central Valley rivers were used to estimate the percentage of SJR Basin salmon that strayed to the Sacramento River Basin. SJR salmon stray rates were negatively correlated ($P = 0.05$) with the average magnitude of pulse flows (e.g., 10 d) in mid- to late-October and positively correlated ($P = 0.10$) with mean Delta export

rates. It was not possible to differentiate between the effects of pulse flows in October and mean flows in October and November on stray rates because of the co-linearity between these two variables. Whether SJR-reduced pulse flow or elevated exports causes increased stray rates is unclear. Statistically speaking the results indicate that flow is the primary factor. However empirical data indicates that little if any pulse flow leaves the Delta when south Delta exports are elevated, so exports in combination with pulse flows may explain the elevated stray rates. For management purposes, we developed two statistical models that predict SJR salmon stray rate: (1) flow and export as co-independent variables; and (2) south Delta Export (E) and SJR inflow (I) in the form of an E:I ratio.

KEY WORDS

Fall-run, Chinook salmon, stray, Sacramento–San Joaquin Delta, flow, exports, age, hatchery.

INTRODUCTION

Over the past 2 decades large scale in-river flow and small scale non-flow restoration actions have been implemented to restore fall-run Chinook salmon (*Oncorhynchus tshawytscha*) in the San Joaquin River (SJR) basin. The primary purpose of these restora-

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tion actions is to ensure that mature fall-run salmon (salmon) return to the SJR basin to spawn. Results from previous studies indicate that Sacramento–San Joaquin River Delta (Delta) flow conditions when salmon escape the ocean (salmon escapement) may influence returning SJR origin salmon stray rates (Mesick 2001). Straying by SJR salmon hinders population goals and necessitates evaluating relationships between Delta flow conditions and SJR salmon straying into the Sacramento Basin. The specific hypothesis tested in this paper is that no statistically significant relationship between fall south Delta inflow and/or export flow conditions, and SJR origin salmon stray rates exists.

It is well established that some proportion of adult salmon, both wild and hatchery origin, stray from one river basin to another upon return to their natal home from the sea (Quinn 1993). Identifying what, if any, Sacramento–San Joaquin River Delta environmental factors increase the likelihood of SJR fall-run to stray into the Sacramento River Basin will help scientists, water project managers, and state and federal government regulators better manage Delta flow conditions (Hallock and others 1970; Mesick 2001) to accomplish their ultimate goal of restoring the SJR Basin fall-run salmon population. Published results of stray rate studies conducted within California rivers are few in number and are essentially limited to Snyder's (1931) work on the Klamath River, Hallock and others' (1970) work on the San Joaquin River, Sholes and Hallock's (1979) work on the Feather River, and Mesick's (2001) work on the San Joaquin River. Where necessary and applicable, stray rate information was gleaned from published stray rate research conducted in river basins in Oregon, Washington, Alaska, and Canada. Since Mesick's (2001) work directly relates to San Joaquin River salmon stray rates, his work is extensively cited.

Adult SJR Basin fall-run Chinook salmon that return to freshwater to spawn must pass through the San Francisco Bay (Bay) and Delta (Figure 1). The Delta has been heavily affected in the last century by land development and water diversion and comprises a labyrinth of man-made and natural channels that convey Delta inflow, direct water for diversion, and/or allow ocean-going ships to dock at Stockton for

commerce (Figure 2). The Delta today is effectively managed to store water upstream of the Delta and release it at times, and volumes, when pumping facilities in the south Delta can capture and convey it for agriculture and municipal use. The primary water diversions located in the south Delta are California's State Water Project (SWP) and the federal Central Valley Project (CVP) export pumping facilities located near Byron and Tracy, respectively (Figure 2). The CVP began operations in 1955, and the SWP in 1967. Smaller Delta diversions are made by the Contra Costa Canal Water District (CCC) at Rock Slough and Old River (Figure 2) and by the Solano County Water Agency from the North Bay Aqueduct (NBA) located on Barker Slough.

Historically the CVP, SWP, and CCC pumping facilities operate year-round and collectively have a combined pumping capacity of approximately $394.4 \text{ m}^3 \text{ s}^{-1}$ ($14,000 \text{ ft}^3 \text{ s}^{-1}$). In the 1990s, because of concern over excessive entrainment of spring-time emigrating juvenile Sacramento River and SJR salmon (various races), springtime diversions at the CVP and SWP were greatly curtailed with much of the displaced pumping moved to the fall when the adult fall-run migrate. Between 1979 and 2007, average October–November exports ranged from a low of 18% of SJR Basin flow to a maximum of more than 740%, averaging nearly 340% of the volume of water inflowing from the SJR. Water movements through the historic Old and Middle SJR channels (Figure 1) are affected by Delta pumping because these channels directly feed the CVP and SWP pumps. Most times, the river in these channels downstream of the pumps is pulled back upstream by the pumps. Rock barriers also have been placed in several locations in the south Delta to improve agricultural water quality and quantity by increasing surface water elevation. These barriers are collectively called the south Delta barriers and include the Head of Old River Barrier, Grant Line Canal Barrier, Old River at Tracy Barrier, and the Middle River Barrier (Figure 2). Some of the barriers are impassable for fish. Further, the Stockton Deep Water Ship Channel (SDWSC, Figure 2) can be a migration barrier for returning salmon during the fall because of low dissolved oxygen levels (e.g., $<5 \text{ mg L}^{-1}$) when flows are low (Hallock and others

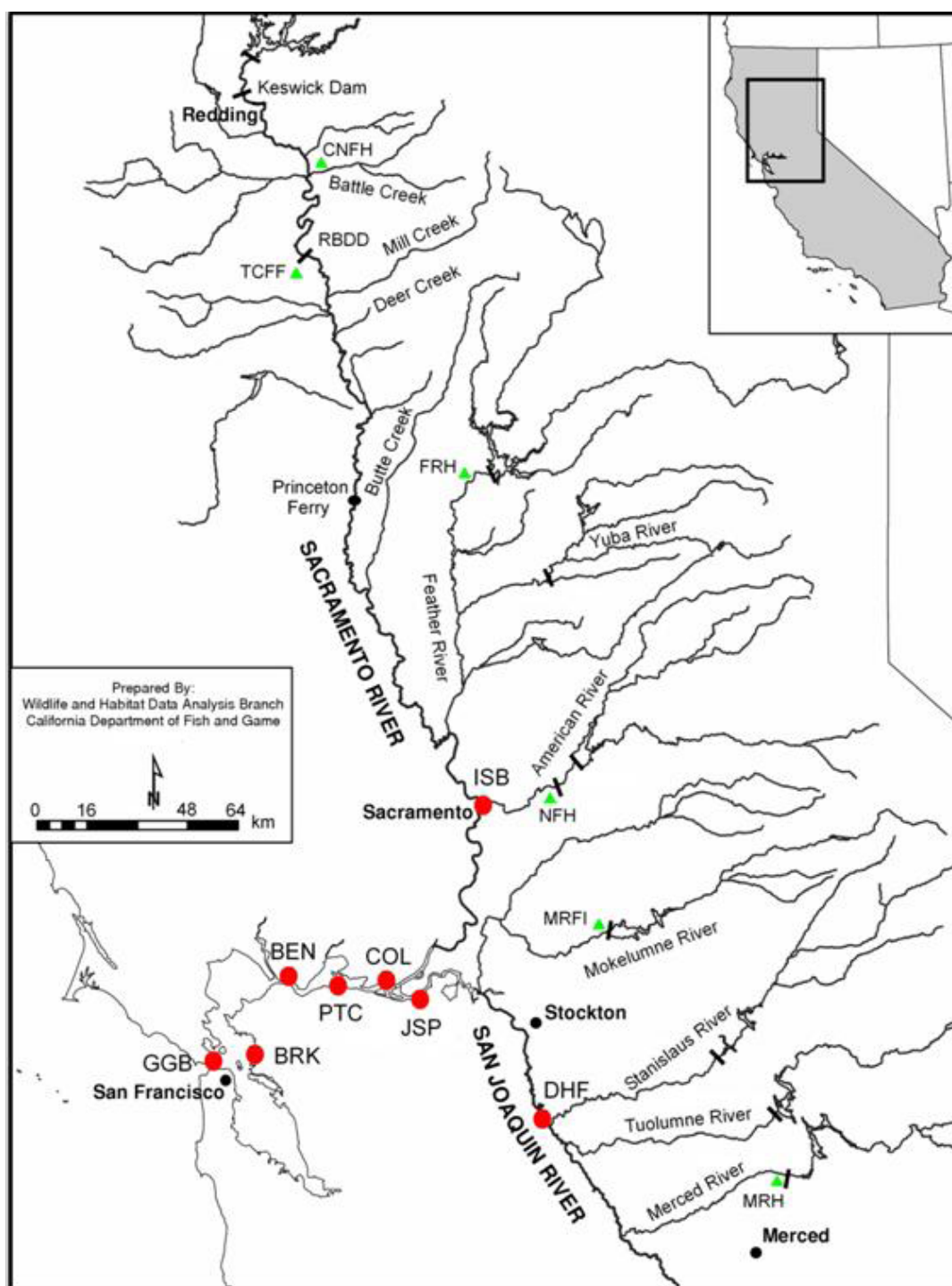


Figure 1 Map of the major Central Valley rivers, the Merced River Hatchery (MRH), Feather River Hatchery (FRH), Tehama Colusa Fish Facility (TCFF), Coleman National Fish Hatchery (CNFH), Mokelumne River Fish Installation (MRFI), and the Nimbus Fish Hatchery (NFH). Bay releases of tagged juveniles were made between Collinsville (COL) on the Sacramento River, Jersey Point (JSP) on the San Joaquin River, and the Golden Gate Bridge (GGB). Example release sites in the Bay include Berkeley (BRK), Benicia (BEN), and Port of Chicago (PTC). Delta releases were made upstream of COL and JSP to Durham Ferry (DHF) on the San Joaquin River and the I Street Bridge on the Sacramento River (ISB). Inland releases were made upstream of ISB and DHF.

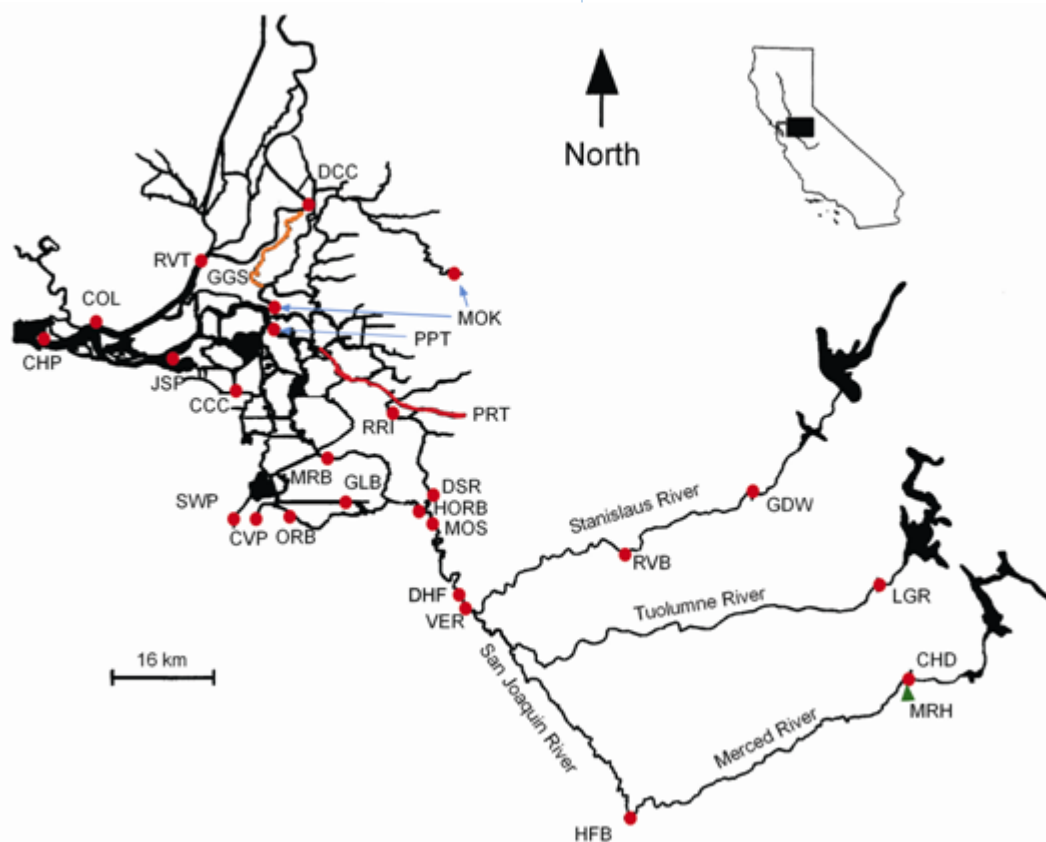


Figure 2 Map of the San Joaquin River and Delta showing the lowermost dams that block upstream passage for fall-run Chinook salmon including Goodwin Dam (GDW) on the Stanislaus River, La Grange Dam (LGR) on the Tuolumne River, Crocker-Huffman Dam (CHD) on the Merced River, and the Hills Ferry Barrier (HFB) on the mainstem San Joaquin River. The Merced River Hatchery (MRH) is shown as a green triangle. The lower Mokelumne River (MOK) is shown to its confluence with the SJR. Other study locations (red dots) include Riverbank (RVB), the State (SWP), Federal (CVP), and Contra Costa Canal (CCC) pumping facilities, stream gage at Vernalis (VER), Prisoner's Point (PPT), Durham Ferry (DHF), Mossdale (MOS), Dos Reis Road (DSR), Port of Stockton (PRT), Rough and Ready Island (RRI), Rio Vista (RVT), Delta Cross Channel (DCC), and Georgiana Slough (GGS, highlighted orange). The temporary rock barriers at the Head of the Old River (HORB), Grant Line Canal (GLB), Old River Barrier (ORB), and Middle River Barrier (MRB) are shown. The San Joaquin River mainstem downstream of the Port of Stockton (highlighted red) is dredged for ocean-going vessels. As defined here, releases of juvenile salmon in the Delta were made upstream of Jersey Point (JSP) to DHF on the San Joaquin River and upstream of Collinsville (COL) to the I Street Bridge (in the City of Sacramento, which is not shown) on the Sacramento River.

1970) or when water temperatures are high (Hallock and others 1970; Rich 2007). The SDWSC dissolved oxygen barrier can occur when SJR at Vernalis flows are less than approximately $42.5 \text{ m}^3 \text{ s}^{-1}$ ($1,500 \text{ ft}^3 \text{ s}^{-1}$). Water temperatures in the SJR can reach lethal levels and also block migration (Rich 2007) when temperatures exceed 21°C to 22°C (USEPA 2003). Reverse flows, physical barriers or chemical barriers that delay adult salmon migration may increase the likelihood of straying.

Chinook salmon rely primarily on olfactory cues to successfully migrate through the Delta's maze of waterways to home back to their natal river (Groves and others 1968; Mesick 2001). Juvenile salmon imprint by acquiring a series of chemical waypoints at every major confluence that enables them to relocate their river of origin (Quinn 1997; Williams 2006). Juvenile hatchery-reared salmon released downstream gather fewer chemical waypoints and are more likely to stray (CDFG and NOAA Fisheries 2001; Newman 2008). Adult SJR basin Chinook

pass through the Delta from late September through November, with peak immigration usually in October (Mesick 2001).

Since olfaction plays such a strong role in a salmon's ability to return (home) to its natal river of origin (Groves and others 1968; Quinn 1997; Williams 2006), providing sufficient water to enable salmon to home in on their natal river is paramount. The Sacramento River basin is approximately 2.5 times larger than the San Joaquin River basin, has a hydrograph dominated by fall and winter rainfall compared to the spring-time snow-melt hydrograph on the SJR, and can provide ten times greater fall Delta inflows than the SJR. Comparatively, the SJR is the most heavily diverted of the two rivers. The mainstem SJR is discontinuous (dry over 90% of the time in one or more reaches) upstream of its confluence with the Merced River (Figure 2) and provides flow to the Delta only in wet years (Rose 2000). Only the major east-side SJR tributaries flow year-round. The SJR is managed to provide fall pulse inflows to the south Delta, typically for 7 to 10 days in late October. The goal is to compensate for the extreme Delta inflow differential between the Sacramento River and SJR basins, to remove the SDWSC dissolved oxygen barrier, and to decrease water temperatures. A secondary purpose of the fall pulse flows is to reduce SJR salmon from straying into the Sacramento River basin by enabling salmon to successfully locate and immigrate into the SJR basin.

The term "straying" has four spatially implied definitions: (1) adult salmon returning to a non-natal river basin; (2) adult salmon returning to a non-natal sub-basin; (3) adult salmon returning to a non-natal tributary; and (4) adult salmon returning to a hatchery in their natal river if naturally spawned. For this reason, stray rates between studies cannot be directly compared without considering which straying definition was used. For the purpose of this paper, the term "stray" means an adult salmon that strayed into the wrong sub-basin of the Central Valley (i.e. the Sacramento River basin rather than the SJR basin).

Mesick (2001) evaluated the effects of SJR flows and Delta export rates during October on adult San Joaquin Chinook salmon stray rates. Mesick reviewed

the results of an earlier study (Hallock and others 1970) where adult San Joaquin salmon were tagged, then monitored (1964 to 1967), as they migrated through the Delta under varying environmental conditions (e.g. Delta inflow and export patterns, dissolved oxygen, and water temperature). Mesick also evaluated recovery data of coded-wire-tagged (CWT) adult salmon, released in years 1983 to 1996, that were reared at the California Department of Fish and Game's (CDFG's) Merced River Hatchery.

Mesick (2001) made two important observations from the Hallock and others (1970) data that describe adult migratory behavior through the Delta. First, adult San Joaquin salmon are migrating through the San Joaquin Delta near Prisoner's Point, which is about 5 km upstream from its confluence with the Mokelumne River (Figure 2), primarily during October, when they are likely to be susceptible to low SJR inflow and high Delta export conditions. Second, San Joaquin salmon migrate slowly through the Delta and do not enter the San Joaquin tributaries until approximately 4 weeks after they pass Prisoner's Point even if environmental conditions (dissolved oxygen, water temperature, and both south Delta inflow and exports levels) appear suitable for migration. These observations indicate that hydraulic conditions in the Delta are most likely to affect adult migrations during October rather than in November when they are observed on the spawning grounds in the tributaries.

Mesick (2001) found three primary flow factors that influence San Joaquin salmon stray rates. First, stray rates were directly correlated with the Delta export (E) to San Joaquin River Delta inflow (I) ratio (E:I). Second, the critical period to provide Delta flow protection (conditions conducive to SJR salmon migration) is between October 1st and 21st. Third, pulse flows from the SJR tributaries (the Merced, Tuolumne, and Stanislaus rivers) or, a reduction of Delta exports, that resulted in an E:I ratio of 3 (exports no greater than 300% of SJR inflow at Vernalis) for 8 to 12 days in mid-October were sufficient to keep stray rates at a minimum level (<3%). Mesick (2001) qualified his findings by saying that the accuracy of the estimated numbers of strays was questionable because of the uncertainties about the numbers of fish examined for CWTs within escapement surveys

conducted in Central Valley rivers. As a result, he was unable to discern the specific effects of flow versus export rates on SJR Basin salmon stray rates or determine the precise period when flows and export rates had the greatest effect. He qualified his analysis of the Hallock and others (1970) data by stating that although most of the tagged fish migrated into the Sacramento and Mokelumne basins when Vernalis flows were less than about $56.7 \text{ m}^3 \text{ s}^{-1}$ ($2,000 \text{ ft}^3 \text{ s}^{-1}$) and total exports exceeded 150% of Vernalis flows, there is uncertainty as to whether these were San Joaquin fish that strayed or Sacramento River fish that were captured in the San Joaquin River on their way to the Sacramento River via the Mokelumne River and Delta Cross Channel (Figure 2). He recommended that further studies were needed to refine the CWT return data in terms of the number of fish examined for tags during the carcass surveys and additional surveys for tags in all major tributaries of the Sacramento River Basin, particularly the main-stem Sacramento River.

Building on Mesick's (2001) work, we evaluated relationships between fall Delta flow conditions and San Joaquin salmon stray rates using coded-wire-tag (CWT) data collected from 1979 to 2007. We analyzed the data to determine the probability of an adult SJR salmon straying to the Sacramento River basin, given fall Delta flow conditions during their escapement. Pending analytical results, recommendations for controls that could be implemented as south Delta water quality control standards to provide a reasonable level of protection for returning adult SJR salmon could be considered and implemented. The specific hypothesis assessed, framed as a null hypothesis, is: fall south Delta inflow, export flow level, and barrier installation are not significantly correlated with SJR salmon stray rates.

METHODS

We developed three data sets in order to evaluate potential relationships between Delta flow patterns and SJR salmon stray rates. The data sets cover the years 1979 to 2007 and include those parameters we believe may significantly influence straying. The first data set includes coded wire tagged (CWT) salmon

releases and recoveries of Central Valley fall-run Chinook salmon from which stray rates were determined. The second data set includes fall Delta flow and export conditions. The third data set contains south Delta Barrier (SDB) annual construction dates and operational periods. The 1979 to 2007 time-period represents the principal time-period when Central Valley salmon were coded wire tagged and released, and covers the period having complete brood-year production cohorts. Methods used to develop the stray rate data are complicated and are only summarized here. For a full description of methods used to develop the stray rate data, and to see the stray, hydrodynamic, and barrier data sets used in our analyses, please refer to the Methods Appendix.

Stray rates of ocean-escaping SJR salmon were compared with two fall south Delta inflow indices: the first using average October and November flow (base flow) and the second using a 10-day pulse flow occurring in mid-October to late October into early November. We also looked at Delta export flow levels over the same time periods. Stray rates for SJR salmon were developed from adult inland recoveries of coded-wire-tagged, hatchery-origin juvenile releases into the San Joaquin and Sacramento river basins, Delta, and Bay over a 29-year period (1979 to 2007).

Adult Salmon Stray Rates

We define salmon strays as the SJR basin fish that returned to the Sacramento River basin to spawn and the Sacramento River basin fish that returned to the SJR basin to spawn. Central Valley fall-run Chinook salmon stray rates were estimated based on CWT recoveries of adult salmon during the spawning surveys that were conducted to estimate escapement. The juvenile salmon with CWTs were produced in Central Valley hatcheries including the Merced River Hatchery (MRH) and the Mokelumne River Fish Installation (MRFI) in the San Joaquin River basin, and the Nimbus Fish Hatchery (NFH), Feather River Hatchery (FRH), and Coleman National Fish Hatchery (CNFH) in the Sacramento River basin (Figure 1). The MRH, MRFI, NFH, FRH, and CNFH are located 271, 120, 134, 236, and 446 km upstream of the Sacramento-San Joaquin River confluence respectively. Juvenile

hatchery fish are trucked from the hatchery to various release locations and are not barged as occur in other river systems.

These hatchery-raised juveniles were released into three broad geographical areas identified as the Bay, Delta, and Inland release points. Bay releases occurred between Jersey Point on the San Joaquin and Collinsville on the Sacramento River, westward to the Golden Gate Bridge (Figure 1). Delta releases were made between Durham Ferry and Jersey Point on the SJR, and between the “I” Street Bridge (City of Sacramento) and Collinsville on the Sacramento River (Figure 1). Inland releases were made upstream of Durham Ferry and the “I” Street Bridge. To reduce the confounding effects of stray results caused by differences in juvenile release location (e.g. the farther downstream juveniles are released, the greater the stray probability (Quinn 1997; CDFG and NOAA Fisheries 2001; Newman 2008), only recoveries from inland releases were used to test our hypothesis.

MRH releases used in our analyses did not include any transfers of eggs or juveniles from other hatcheries; whereas, eggs and/or fry were routinely transferred from the FRH and NFH to the MRH. In general, the MRH released juveniles as yearling-sized fish from 1978 to 1985 during October (mean weight 56 g) and November (mean weight 60 g) and as sub-yearling-sized fish from 1986 to 2006 during April (mean weight 6 g) and May (mean weight 7 g). The FRH primarily released juveniles as yearling-sized fish from 1980 to 2002 during October (mean weight 42 g) and November (mean weight 60 g) and as sub-yearling-sized fish from 1975 to 2006 during April (mean weight 6 g), May (mean weight 6 g), and June (mean weight 8 g). The CNFH primarily released juveniles as sub-yearling-sized fish from 1975 to 2006 during March (mean weight 2 g), April (mean weight 5 g), and May (mean weight 6 g).

Developing stray rate data for Central Valley fall-run salmon required a multi-step approach: (1) assembling inland escapement estimates for each Central Valley river, (2) assembling the expanded number of CWT's recovered within each Central Valley fall-run escapement survey, and (3) identifying the proportion of each CWT code recovered in each Central Valley

river. We used the California Department of Fish and Game's (CDFG) fall-run escapement summary (GrandTab) for annual, river-by-river escapement data. We obtained CWT release data from the Pacific States Marine Fisheries Commission's (PSMFC's) Regional Mark Processing Center's Regional Mark Information System (RMIS) (data downloaded in 2011). We utilized CWT recovery data from annual escapement reports and/or personal contact with escapement survey crew leaders when additional information was necessary. The final form of the stray data consisted of annual summaries of the expanded number of fish that homed and strayed. Included in these expanded estimates were adjustments for number of fish that shed their tags, number of ad-clipped fish where tags were not recovered, and recovery number of untagged juvenile fish that were released alongside CWT marked juvenile releases. Annual summaries of hydrological data were also provided as discussed below.

To conduct this analysis, we assumed that CWT salmon recovery trends from juvenile salmon produced by the CDFG's MRH would also represent recoveries from naturally produced fish originating in the Merced, Tuolumne and Stanislaus rivers. Likewise, we assumed that the U.S. Fish and Wildlife Service's CNFH and the CDFG's FRH hatchery release-recovery trends would mirror those for all Sacramento Basin fall-run stocks. We believe this assumption is valid because Pacific salmon primarily home based on freshwater chemical olfactory cues imprinted when, as juveniles, they make their seaward migration (Quinn 1997; Williams 2006) and that water-borne odors would be similar for rivers within the same basin when compared with other basins. This assumption was indirectly corroborated by Barnett-Johnson and others (2008), who characterized Central Valley watersheds by Strontium isotope ($^{87}\text{Sr}:^{86}\text{Sr}$) ratios for purposes of identifying otolith markers for fall-run salmon, then by Miller and others (2010), who compared the water $\text{Sr}:\text{Ca}$ (mmol mol^{-1}) and $\text{Ba}:\text{Ca}$ ($\mu\text{mol mol}^{-1}$) ratios for Central Valley rivers to assess juvenile salmon river of origin via otolith $\text{Sr}:\text{Ca}$ and $\text{Ba}:\text{Ca}$ ratios. Collectively Barnett-Johnson and others (2008) and Miller and others (2010) found that water chemistry differed between the Sacramento

and SJR basins. We did not include the MRFI CWT release–recovery data in our analyses for two reasons. First, the flows in the lower Mokelumne are mixed with Sacramento River basin flows (because of the Delta Cross Channel and Georgiana Slough), which can allow Mokelumne River juvenile salmon to imprint upon both Mokelumne and Sacramento basin water, thus enabling the adults to “correctly” choose either the Sacramento or Mokelumne rivers upon return. Second, egg and/or fry transfers to the MRFI from the FRH and NFH may affect the homing behavior of the MRFI releases.

Delta Flow Conditions

Delta flow data for the fall period were obtained from Dayflow, which is a program developed, operated and maintained by the California Department of Water Resources (CDWR). The program was initially developed in 1978 to serve “as an accounting tool for determining historical Delta boundary hydrology” (CDWR 2011b). CDWR significantly updated the program in 2000 using Java, enabling input data stored as a HEC-DSS file, and output presented in an ASCII file. The computational scheme was modified in February 2002 based on a better understanding of the complex Delta conveyance system.

According to CDWR, “the Dayflow program presently provides the best estimate of historical mean daily flows: (1) through the Delta Cross Channel and Georgiana Slough; (2) past Jersey Point; and (3) past Chipps Island to San Francisco Bay (net Delta outflow). The degree of accuracy of Dayflow output is affected by the Dayflow computational scheme and the accuracy and limitations of the input data. The input data include the principal Delta stream inflows, Delta precipitation, Delta exports, and Delta gross channel depletions” (“Dayflow”).

All Dayflow calculations use daily flows and do not consider the travel time required for the water to move through the various channels in the Delta. The Dayflow computational scheme develops three types of quantities; net Delta outflow estimates at Chipps Island, interior Delta flow estimates at significant locations, and summary and fish-related parameters and indices.

Table 1 Delta Dayflow variables

SAC	Measured Sacramento flows at the “I” Street Bridge in Sacramento
SJR	Measured San Joaquin River flows at Vernalis
RIO	Calculated Sacramento River flows past Rio Vista
XGEO	Calculated flows of both the Delta Cross Channel and Georgiana Slough
QWEST	Calculated San Joaquin River flows at Jersey Point where reverse flows are indicated by a negative number
CCC	Measured Contra Costa Water District diversions at Rock Slough and Old River
SWP	Measured State Water Project exports from the Banks Pumping Plant or Clifton Court Intake
CVP	Measured Central Valley Project exports at Tracy
Exports	Sum of CCC + SWP + CVP

The time-period associated with the quantities generated by Dayflow range from October 1, 1955 through September 30, 2010. Our analyses included quantities from the years 1979 through 2007, to compare the results with fall-run Chinook salmon return data. The Dayflow variables are presented in Table 1 and the flow estimates are available at <http://www.water.ca.gov/dayflow/>.

Dayflow includes data representing total Delta exports (EXPORTS), which includes North Bay Aqueduct exports (NBAQ) along with the Contra Costa Water District Canal (CCC), State Water Project (SWP) and Central Valley Project (CVP) exports. NBAQ data were not used because these exports leave the Delta from the north. Therefore, in evaluating total exports for our analyses, we combined the CCC, SWP and CVP exports only. We also considered Old and Middle SJR (OMR) flows as measured at two U.S. Geological Survey (USGS) gaging stations: USGS 11312676 MIDDLE R AT MIDDLE RIVER CA and USGS 11313405 OLD R AT BACON ISLAND CA. The river at these locations is highly affected by both the SWP and CVP pumps that create reverse or upstream flows during the majority of the year. We gathered

Table 2 Cross-correlation matrix of Delta fall flow variables^a

	SAC	Exports	SJR	XGEO	QWEST	QRIO	OMR	Pulse SAC	Pulse Exports	Pulse SJR	Pulse XGEO	Pulse QWEST	Pulse QRIO	Pulse OMR
SAC	1													
Exports	-0.11	1												
SJR	0.88	-0.21	1											
XGEO	0.77	0.06	0.67	1										
QWEST	0.82	-0.58	0.88	0.67	1									
QRIO	0.99	-0.18	0.86	0.67	0.81	1								
OMR	0.40	-0.90	0.54	0.15	0.78	0.45	1							
Pulse SAC	0.85	0.08	0.84	0.73	0.68	0.79	0.23	1						
Pulse Exports	0.03	0.91	-0.07	0.08	-0.44	-0.02	-0.74	0.28	1					
Pulse SJR	0.84	-0.18	0.98	0.63	0.84	0.82	0.52	0.84	-0.02	1				
Pulse XGEO	0.70	-0.01	0.68	0.88	0.66	0.60	0.21	0.83	0.09	0.64	1			
Pulse QWEST	0.76	-0.55	0.85	0.67	0.96	0.73	0.73	0.70	-0.45	0.82	0.73	1		
Pulse QRIO	0.80	0.13	0.79	0.58	0.60	0.78	0.18	0.96	0.35	0.80	0.65	0.60	1	
Pulse OMR	0.40	-0.90	0.54	0.15	0.78	0.45	0.94	0.23	-0.74	0.52	0.21	0.73	0.18	1

a Table showing co-linearity comparison between various Delta flow metrics, including Sacramento River at Freeport (SAC), combined South Delta Exports (Exports), San Joaquin River at Vernalis (SJR), Delta Cross Channel and Georgiana Slough flow (XGEO), San Joaquin River flow past Jersey Point (QWEST), Sacramento River flow past Rio Vista (QRIO). Pulse metrics equal the average flow during the fall pulse flow time period. Non-pulse flow metrics are average flows for the October and November time period.

OMR flow data for both the October–November base flow period and the 10-day pulse flow period.

Fall Delta base flow (mean October and November flow) and pulse flow (10-day average of highest flow in October–November) data is provided in the Methods Appendix. In addition to average base and pulse flows, flow ratios (by example: the ratio of Delta exports to SJR inflow at Vernalis) are also presented in the Methods Appendix. We also developed a cross-correlation matrix table to identify co-linearity between any flow variables (Table 2).

South Delta Barriers

We obtained south Delta barrier (SDB) operational data from CDWR's South Delta Temporary Barriers Project (CDWR 2011a). Four barriers comprise CDWR's SDB Project: Head of Old River (HORB), Grant Line Canal, Middle River, and Old River at Tracy. As stated by CDWR, the objectives of the

SDB program are three-fold: (1) increase south Delta water levels (e.g., elevation) and circulation patterns to improve agricultural diversion water quality; (2) enhance the operational flexibility of the SWP and CVP; and (3) reduce effects on native and anadromous fish species.

The Head of Old River (HORB) barrier is a rock barrier—and the primary barrier, because it is intended to prevent SJR south Delta inflow from entering the Old River channel, which leads to the Delta export pumping facilities (i.e., the SWP and CVP), and maintains flow within the mainstem SJR and the SDWSC. The tidal effect and Sacramento River Basin flow contribution are greater downstream of the SDWSC than at the Head of the Old River and so the HORB reduces the amount of SJR flows that are diverted at the Delta pumping facilities relative to the amount of Sacramento River Basin flows diverted. Without the HORB, the majority of the SJR inflow enters the Old River depending on the diversion rate at the SWP

and CVP (Jassby 2005; SJRGA 2009; ICF 2010). From a fisheries management perspective, the purpose of the HORB is to concentrate flow into the main channel to attract adult immigrating salmon into the main SJR channel during the fall (fall HORB), to deter salmon from using non-main river channels, and keep springtime (spring HORB) emigrating juvenile salmon out of the Old River channel where entrainment into the south Delta pumps is possible.

The fall HORB is installed in most years and typically operates from September 15th to November 30th, which is intended to coincide with the SJR fall Chinook immigration time-period. The remaining three barriers, also temporary rock barriers, serve as agricultural barriers designed to improve water quality and operate during the agricultural irrigation season from April 15 through September 30 each year. From 1979 to 2007, the HORB operated in 19 years, the Old River at Tracy in 15 years, the Middle River in 20 years, and the Grant Line Canal in 11 years. State (CDWR) and federal (U.S. Bureau of Reclamation) agency regulatory requirements—both landowner and local reclamation district entry permits—and physical conditions determine barrier installation and removal dates (CDWR 2011a). By example, high SJR flows that occur in wetter years when upstream reservoir storage must be evacuated might preclude installation and operation of the HORB.

To analyze the influence SDB's have on SJR salmon stray rates we used an ordinal date format to make the SDB's fall operating dates consistent across years. (The SDB operating dates are provided in the Methods Appendix.) To further ensure SDB operational consistency across years, the earliest date a barrier was considered to have been installed was September 1st (ordinal day 245). This date was chosen as the start date to coincide with Delta salmon immigration timing as described in Hallock and others (1970).

Statistical Analysis

The goals of the statistical analyses include estimating the independent associations of flow and exports upon SJR stray rates (explanatory analysis), as well as determining whether any particular combination of predictors was significantly better at predict-

ing stray rates. The objective of the explanatory analysis was to examine the probability of escaping salmon straying relative to Delta flow conditions. Specifically, given the denominator as adjusted estimates of the number of CWT fish retrieved, we examined whether the probability of being a stray (specifically, a SJR fish returning to the Sacramento River Basin) was a function of various flows: SAC (Sacramento River at Freeport), SJR (San Joaquin River flow at Vernalis), Exports (Delta Exports), QRIO (Sacramento River flow past Rio Vista), QWEST (SJR flow past Jersey Point), and XGEO (Delta Cross Channel and Georgiana Slough flow), and OMR (combined Old and Middle River flow). The individual adult return rates for each CWT code were adjusted by (1) observed carcasses with adipose fin clips but no information for the tag code and (2) releases of unmarked juveniles with CWT marked juveniles that may have affected CWT return rates (see Methods Appendix). They also include stray rate estimates for rivers that lacked direct CWT recovery data, such as the mainstem Sacramento River from 1986 to 2000 (see Methods Appendix). The mean annual return rate for individual tag codes for each adult age was used as the unit of the statistical analysis.

As mentioned above, there is very high correlation among many of the average and pulse flow annual summaries. Due to this co-linearity, we included only pulse flows for the SJR and the corresponding SJR pulse flow period for the exports in our analysis. Also because of the co-linearity of flow variables, we did not analyze ratios between these explanatory variables—not because the other variables are not causally important, but only because the covariance among them is such that it is impossible, given the available data, to distinguish (estimate) the relative effects with the modest sample size (number of years) available. In addition, we examined the number of operating days for each barrier and its association with stray rates. (We note that the number of days and the start day for barrier operations cannot be examined independently in the same model, so we used the number of days as a proxy for both variables).

For each paired analysis between either SJR or export pulse flow level and stray rate we: (1) performed LOWESS smoothing (Cleveland 1979) on the proportions to examine (semi-parametrically) the stray

response and provide in visual form the variability of stray rates around the predicted mean; (2) examined the logistic regressions of average trends (in the logit scale) of the probability of being a stray versus these flow levels, adjusting for the age of fish; and (3) derived our *P*-value for resulting trends (relative to flow independence and stray probability) via an age-conditioned pseudo-exact permutation test.

For the multivariable regression models, we used the nonparametric bootstrap (Efron and Tibshirani 1993) to derive inference, treating the year as the unit. We note that sometimes the bootstrap-based *P*-values can be quite different from the corresponding permutation ones (for analyses that are equivalent), suggesting that the dispersion can be so great relative to sample size that even robust inference can be potentially biased, which is why we emphasize the permutation method when appropriate.

For both SJR fall pulse and export flow levels, we (1) performed LOWESS smoothing on the stray proportions (Figures 3 and 4); (2) examined the logistic regressions of “average” trends in the logit scale) of the probability of being a stray versus these flow variables; and (3) derived our *P*-value for these trends (relative to flow independence and stray probability) via bootstrapping. For the bootstrapping, one thousand bootstrapped re-samplings of the data were generated. Coefficients for each re-sampling were estimated and their dispersion was used to calculate the standard error of the estimates. Such bootstrapped estimates are to some level robust when data does not necessarily fully conform to the assumptions of the normal linear regression model. In this case, the data was overdispersed (i.e., there was greater variance than would be predicted by a binomial model) and significance estimates that did not take this into account would have resulted in a high overestimation of statistical significance.

Finally for the pure prediction model procedure we compared the fit of competing models in predicting future stray rates by using a cross-validation technique, with known theoretical properties related to selecting the “optimal” model (Van der laan and others 2007), to compare five simple models (all of them containing indicators for age groups): (1) including

log (SJR Pulse Flow) and log (Exports); (2) log(SJR Pulse Flow) and log (pulse OMR flows); (3) log (exports/SJR Pulse Flows) ratio; (4) log (SJR Pulse Flow) alone; and (5) log (Exports) alone. We note that both Models 4 and 5 are sub-models of 1 (for Model 4, it assumes the coefficient associated with log (SJR pulse flow) equals the negative of that on log (exports), whereas for Model 5, it just assumes the coefficient on exports is 0). Thus, under the typical assumptions, a likelihood ratio test could provide a measure of the relative fits of the model. However, in this case, we examine it empirically via 10-fold cross-validation. Specifically, the sample is divided into 10 equal parts (say validation samples) and for each of these, one (a) removes them from the data, (b) fits Models 1 through 5 on the other portion (the so-called training sample), and (c) uses these fits to predict on the left out sample. Thus, the procedure results in a column of observed stray rates, and five predicted stray rates (one for each model) where the predictions were derived independently of the corresponding outcome.

RESULTS

Stray Rates in General

Our analysis indicates that the stray rates for Sacramento Basin hatchery origin salmon, released upstream of the Delta, average less than 1% (range = 0 to 6%). Comparatively, for SJR Basin hatchery-origin salmon, stray rates average 18% (range = 0 to 70%). When stray results are considered for Delta and Bay releases, the average Sacramento hatchery-origin stray rates are 0.5% and 1%, respectively. SJR basin hatchery-origin stray rates, corresponding with Delta and Bay releases, are 35% and 85%, respectively.

Cross Correlation of Delta Flow Variables

Exports correlate negatively to the OMR flows (Old and Middle SJR). As exports increase OMR flows become more negative. All non-export Delta flow variables are highly positively correlated with one another (Table 2). That is, as one variable rises in value so do the others. The positive correlation results

indicate that any of the non-export flow variables can be used to some extent as a proxy for all the flow variables. Since SJR fall pulse flow is, biologically speaking, the flow variable of importance it is used as the variable to determine if Delta inflow is significantly correlated with stray rate probability. Due to the extreme co-linearity between fall base flows and 10-day pulse flows (correlation = 0.97), we cannot determine which has the most important influence. If SJR base flow was used as the flow metric instead of pulse flow, the results for pulse flow presented below could be applied to base flow using the following linear regression equation between base and pulse flow levels:

$$SJRBaseFlow = 0.786 \times SJRPulseFlow, R^2 = 0.97$$

Delta Flow Variables and Stray Rates

Graphical comparisons of the probability of SJR salmon straying as a function of SJR fall pulse flow, south Delta exports, and the ratio (E:I) of south Delta exports (E) to SJR fall pulse flow (I) are provided in Figures 3, 4 and 5, respectively. Though there is a significant amount of variability between years, general trends are identifiable. For SJR fall pulse flow,

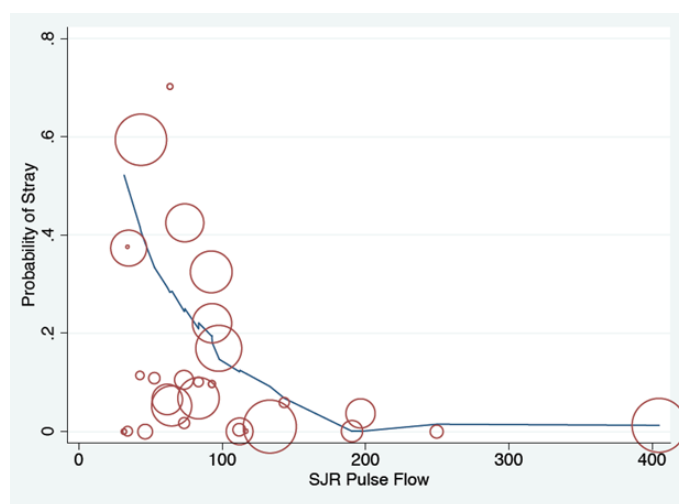


Figure 3 Plot showing the smooth of probability of San Joaquin River salmon straying as a function of San Joaquin River inflow level ($\text{m}^3 \text{s}^{-1}$) to the South Delta. Bubble size reflects relative number of coded-wire-tag recoveries across years. Smooth line is weighted by total recapture size.

salmon stray rate probability peaks (~50%) when flow levels are less than $30 \text{ m}^3 \text{s}^{-1}$ ($1,060 \text{ ft}^3 \text{s}^{-1}$) and are reduced substantially (~5%) when pulse flow levels increase to $150 \text{ m}^3 \text{s}^{-1}$ ($5,297 \text{ ft}^3 \text{s}^{-1}$). For south Delta exports, salmon stray rate probability peaks (20%) when export levels exceed $141.6 \text{ m}^3 \text{s}^{-1}$ ($5,000 \text{ ft}^3 \text{s}^{-1}$) and are substantially lower (~3%)

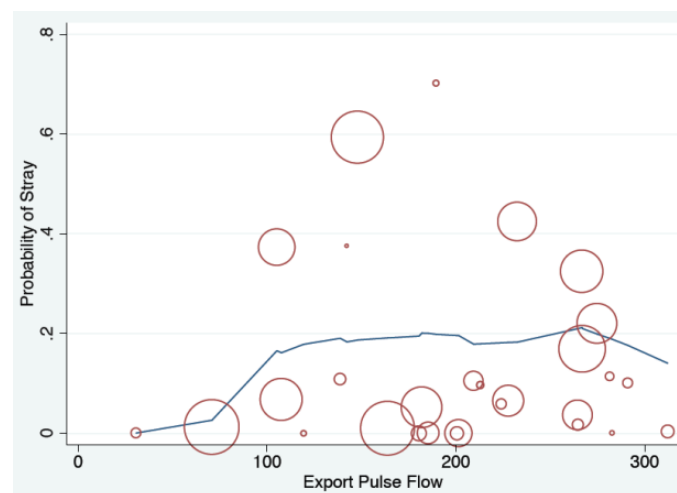


Figure 4 Plot showing the smooth of probability of San Joaquin River salmon straying as a function of South Delta export level ($\text{m}^3 \text{s}^{-1}$). Bubble size reflects relative number of coded-wire-tag recoveries across years. Smooth line is weighted by total recapture size.

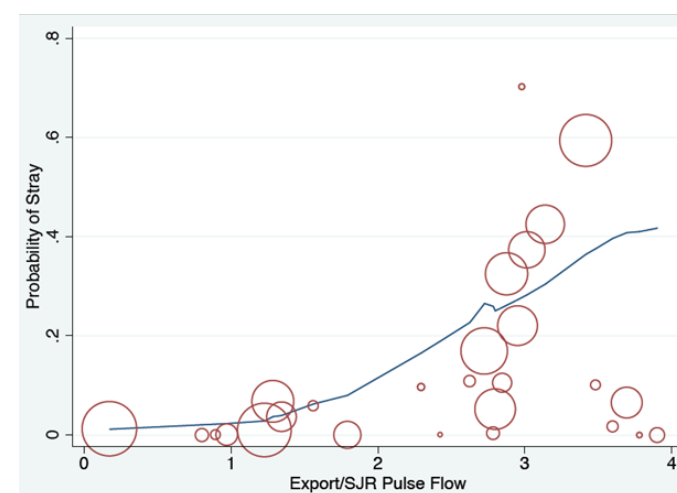


Figure 5 Plot showing the smooth of probability of San Joaquin River salmon straying as a function of South Delta export (E) ($\text{m}^3 \text{s}^{-1}$) to San Joaquin River Pulse Flow (I) level ($\text{m}^3 \text{s}^{-1}$) ratio (E:I). Bubble size reflects relative number of coded-wire-tag recoveries across years. Smooth line is weighted by total recapture size.

Table 3 Results of Delta flow variables and San Joaquin River salmon stray rate

	Coefficient ^a	Standard error ^b	p-value	95% confidence interval for coefficient	Unadjusted coefficient ^c	Unadjusted p-value ^c
Constant	5.349	9.231	0.562	–12.74 – 23.44		
ln(SJR)	–2.568	0.786	0.001	–4.108 – –1.029	–1.9	0.016
ln(Exports)	1.570	0.868	0.07	–0.131 – 3.271	0.53	0.56
Age 3^d	–0.596	0.628	0.343	–1.827 – 0.636		
Age 4^d	–0.846	0.726	0.244	–2.268 – 0.577		

a Example calculation using most likely coefficients. Assume a SJR pulse flow of 8,000 and an Export pulse flow of 6,000 (in cfs; U.S.) for a group of salmon aged 3. The following is used to calculate the probability of straying for this group:

$$\text{logit}(P\text{Stray}) = 5.35 + (-2.57 \ln(8,000) + 1.57 \ln(6,000) + (-0.596 \times 1) + (-0.846 \times 0))$$

$$\text{logit}(P\text{Stray}) = \ln\left(\frac{P\text{Stray}}{1 - P\text{Stray}}\right) = -4.68$$

$$P\text{Stray} = 0.0092$$

b Standard Error calculated using nonparametric bootstrapping, randomly re-sampling years with replacement (Efron and Tibshirani 1993).

c Coefficient based on unadjusted logistic regression, p-value based on the permutation distribution of corresponding Wald Statistic.

d Age is a dummy variable that is 1 when the salmon is that age and 0 otherwise.

when export flow levels are reduced to $56.6 \text{ m}^3 \text{ s}^{-1}$ ($2,000 \text{ ft}^3 \text{ s}^{-1}$). For E:I ratio, salmon stray rate probability peaks (~40%) when the ratio approaches a 4:1 level, and is substantially reduced (~10%) when the ratio is less than 2:1.

Table 3 contains the results of the logistic regression that predicts stray rates as a function of SJR fall pulse flow, export flow and salmon age. Of the independent fall Delta pulse inflow variables analyzed, only SJR flow was significant ($P = 0.05$), according to the bootstrapping estimate of error, and has a negative association with SJR salmon stray rate (Figure 3). Combined south Delta export pulse flow was close to significant ($P = 0.10$) and has a positive association with SJR salmon stray rate (Figure 4). The smooth lines depicted in Figures 3 and 4 are weighted by the proportional number of CWT recoveries. Equation 1 determines SJR salmon stray rate, by age, as a func-

tion of SJR pulse flow magnitude and south Delta combined export level in non-ratio format.

When the five competing models previously discussed—(1) log (SJR Pulse Flow) and log (Exports), (2) log (SJR Pulse Flow) and log (pulse OMR flows), (3) log (Exports/SJR Pulse Flows), (4) log (SJR Pulse Flow), and (5) log (Exports)—were compared via cross-validation, the results, given the relatively large residual variation seen in all the observed versus the cross-validated predictions (for all the competing models) were quite large, one can not definitely rank the predictive accuracy of any of them versus the others. It appears that models including either SJR flow and exports or both do relatively well, still with relatively modest cross-validated R^2 values of around 0.2. It is important to note that we repeated this analysis with many different splits, and also with different cross-validation folds (up to 40-fold) to avoid

Equation 1

$$\text{StrayRate} = \frac{1}{1 + e^{-(1.790 - 2.568 \ln(\text{SJRPulseFlow}) + 1.570 \ln(\text{ExportPulseFlow}) - (0.5956 \text{Age3}) - (0.8455 \text{Age4})}}$$

NOTE: To calculate stray rate for age-2 salmon, set both the age-3 and the age-4 terms to zero. For age-3 salmon stray rates, set the age-3 term to 1 and the age-4 term to zero. For age-4 salmon stray rates, set the age-3 term to zero and the age-4 term to 1. For cubic feet per second (cfs; U.S.) units, simply substitute the intercept value of 1.790 with 5.349. The equation beneath Table 3 is the same equation described here but it is converted, for convenience, to standard units.

making conclusions based on any cross-validation configuration. These results suggest that, based on existing data, models that include exports and pulse flow, either as a ratio, or separate terms, appear to be as good or better than competing models with other hydrological measures. It is important to note that these cross validation results, which were intended to evaluate competing model prediction accuracy, do not contradict results obtained from a robust analysis assessing what is a significant association of stray rate. The single factor that is controlling stray rate, from a statistically significant perspective, is SJR flow.

In conclusion, since the biology of salmon indicates that a model including SJR flow is biologically necessary (salmon navigate based upon juvenile river imprinting), we must include SJR flow in a management model. There are several ways to link flow and exports to stray rates. Whether or not to include either co-variate (flow and exports), and how, depends entirely upon the objective. If the objective is explanation, then a model that includes both flow and exports independent of one another is warranted (Model 1). Alternatively, if the goal is pure prediction, then a model that has flow alone (Model 4) is acceptable given that flow is the only variable associated with SJR salmon stray rates at a statistically significant level. However, since we cannot say with statistical certainty whether flow or exports is the primary determinant influencing SJR salmon stray rates, exports can also be included in the management model in the form of an E:I ratio (Model 3). Equation 2 determines SJR salmon stray rate, by age, as a function of south Delta combined export to SJR inflow ratio (E:I).

Equation 2

$$\text{StrayRate} = \frac{1}{1 + e^{-(3.25 + 2.41 \ln(\text{ExportPulseFlow} / \text{SJRPulseFlow}) - (0.64 \text{Age3}) - (1.01 \text{Age4}))}}$$

NOTE: To calculate stray rate for age-2 salmon, set both the age-3 and the age-4 terms to zero. For age-3 salmon stray rates, set the age-3 term to 1 and the age-4 term to zero. For age-4 salmon stray rates, set the age-3 term to zero and the age-4 term to 1. No modifications to this equation are required for cubic feet per second (cfs; U.S.) unit calculations.

South Delta Barriers and SJR Salmon Stray Rate

We also examined the operating days for each of the barriers and their association with stray rates. The total operating days and the initial operating day for each barrier cannot be examined independently in the same model, so we used the total barrier operating days as a proxy for both variables. None of the barriers produced a significant effect on salmon stray rates at either the $P = 0.05$ or 0.10 levels. This indicates that, for south Delta Barriers, neither barrier construction date, nor total operating days, are positively or negatively influencing SJR salmon stray rates in a statistically significant manner. The implication of this finding is that barrier operation for whatever purpose, even if to influence SJR salmon stray rate, is not reducing—or increasing—SJR salmon stray rate at a statistically detectable level.

DISCUSSION

Our results suggest that the percentage of SJR fall-run Chinook salmon straying into the Sacramento River Basin (1979 to 2007) was as high as 70% (fall 2007). Straying was inversely correlated with pulsed flows in the mainstem SJR at Vernalis ($P = 0.05$) and directly correlated with Delta export levels at a nearly significant level ($P = 0.10$). Our estimated stray rates were more than twice as high as those reported by Mesick (2001), because Mesick did not have complete estimates of the number of adult salmon carcasses that were examined for CWTs during the Sacramento River Basin surveys.

Although stray rates were most highly correlated with pulsed SJR flows, we cannot differentiate between the 10-day pulse flows in October–November and mean

October and November base flows. Mean and pulse fall SJR flows are positively cross correlated to a very high degree (adjusted R -square of 0.97 at $P = 0.05$). Fall flows are highly regulated (controlled) in the SJR basin and are tied to SJR basin water year type (critical, dry, below normal, above normal, wet); whereby, annual flow schedules are derived pursuant to regulatory instream flow requirements. Thus, as water year type increases as a result of greater snowmelt runoff, both fall base and pulse flows increase concurrently. The cross correlation between mean and pulse flows makes it uncertain which of the two flow metrics is responsible for attracting SJR salmon to their natal river. However, it is logical that since adult salmon migrate over several months that the mean flow rate in September through November would affect the largest number of salmon.

It is uncertain whether SJR flows or Delta exports have the greatest effect on SJR stray rates, because exports were so high in most years that it appears that little if any SJR flow (i.e., olfactory migration cue) was conveyed to the Bay during the fall (Figure 6). The calculated QWEST (SJR flow past Jersey Point and the Central Delta outflow point) flow levels can be strongly negative even in wetter years (2005 and 2006). A negative QWEST flow means that the SJR is flowing 'backward' (i.e. upstream) and tends to occur when the combined SWP and CVP exports exceed the flow in the SJR. October and November QWEST flows for the years from 1979 through 2007 ranged from $-70.8 \text{ m}^3 \text{ s}^{-1}$ ($-2,500 \text{ ft}^3 \text{ s}^{-1}$; 2005) to $651.3 \text{ m}^3 \text{ s}^{-1}$ ($23,000 \text{ ft}^3 \text{ s}^{-1}$; 1983). Negative fall base and pulse flows at QWEST occurred in 14 (48%) of years analyzed. Even in some years when QWEST is positive for the fall base and pulse flow period, exports may exceed SJR flow but Sacramento flow that has been diverted into the Central Delta (identified as XGEO: flow through the Cross-Delta Canal and the Georgiana Slough) adds to the QWEST. Median XGEO flows ($150.4 \text{ m}^3 \text{ s}^{-1}$; $5,310 \text{ ft}^3 \text{ s}^{-1}$) from 1979 through 2007 are nearly double the SJR flows ($66.1 \text{ m}^3 \text{ s}^{-1}$; $2,333 \text{ ft}^3 \text{ s}^{-1}$). Median fall pulse flows show a similar disparity between XGEO flows ($145.9 \text{ m}^3 \text{ s}^{-1}$; $5,152 \text{ ft}^3 \text{ s}^{-1}$) and SJR flows ($83.6 \text{ m}^3 \text{ s}^{-1}$; $2,951 \text{ ft}^3 \text{ s}^{-1}$).

Exports and SJR flow are not correlated; thus, both should be included as potential model parameters. A permutation test is the best statistical method to evaluate the individual linkage of each parameter with stray rate, which reveals flow is significant (0.05) and exports are nearly so (0.10). The permutation method does not allow simultaneous assessment of both parameters to get the best inference so another test is used (bootstrapping). The bootstrap method reveals flow is still significant but exports are not. However, we cannot say that exports are not truly significant, given the limited sample size, and, according to the competing model evaluation, a model with exports performed as well as one with SJR pulse flow alone. Therefore both flow and export parameters can be included in a single model in the form of an E:I ratio.

An example of daily SJR fall flow for a single year (2009) is provided in Figure 6 where SJR flow is measured at four gaging stations in the Delta. SJR flows, as measured at Vernalis, indicate that pulse flows experienced at Vernalis (rkm 118; rm 73) are barely detectable at Garwood Bridge (rkm 68; rm 42) and are non-detectable at both Prisoner's Point (rkm 40; rm 25) and Jersey Point (rkm 16; rm 10). In fact, not only did the SJR fall pulse flows in late October not make it to both Prisoner's Point and Jersey Point in 2009, both of these locations had strong negative flows occurring at the same time pulse flows were supposed to be flowing through the south Delta. Note that the flows depicted in Figure 6 give the impression that all SJR pulse flow is constrained within the main SJR channel, but it is not. Given the labyrinthine nature of the south Delta (Figure 2), and the ability of SJR pulse flow to enter and proceed through the SJR Old River channel, SJR pulse flow can re-enter the main SJR channel between Jersey Point (rkm 16; rm 10) and Prisoner's Point (rkm 40; rm 25). If SJR pulse flows that enter the Old River contribute to flow in the SJR at Jersey Point, it may be that SJR salmon that successfully migrate through the south Delta may be detecting the SJR via Old River, rather than mainstem SJR flow. It is also unknown how tidal influence affects fall pulse flow hydraulic continuity and ability of escaping salmon to detect the SJR. Further research is needed to determine whether SJR fall pulse flows do, or do

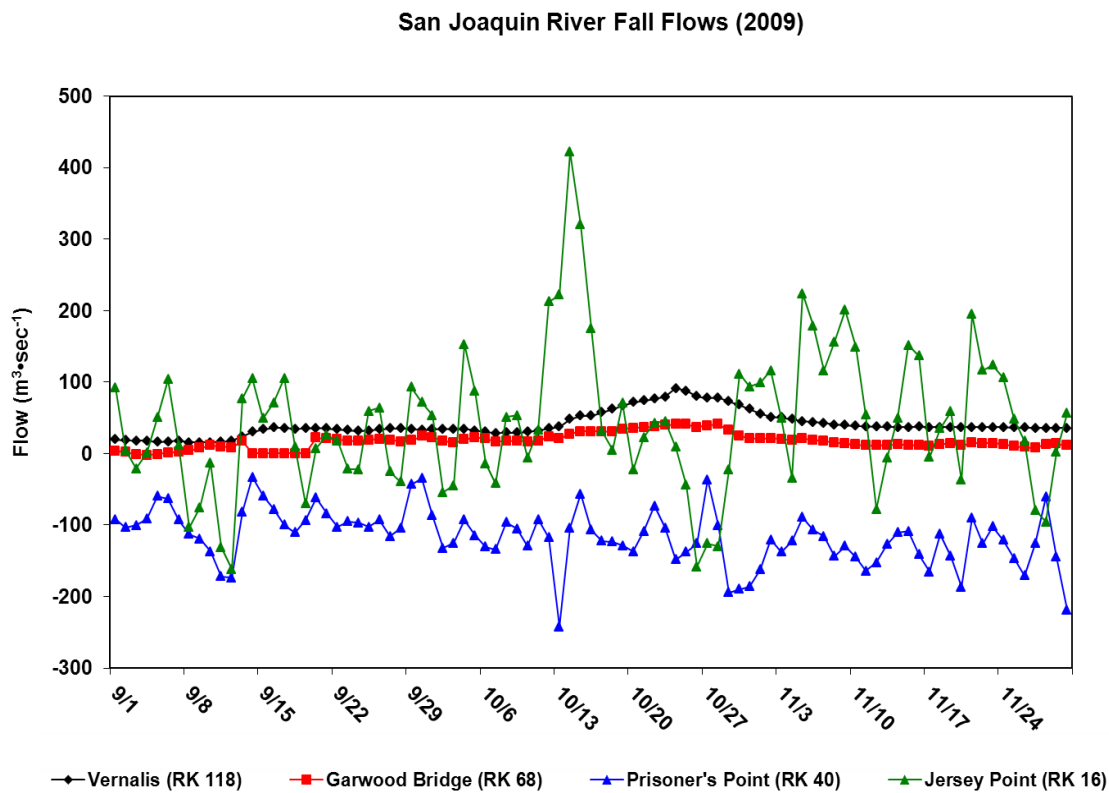


Figure 6 San Joaquin River flows at four locations from the entrance to the South Delta (Vernalis), through the interior of the Delta (Prisoner's Point and Garwood Bridge), and near the exit point of the Delta (Jersey Point). River kilometer (RK) is the distance measured from the San Joaquin-Sacramento River confluence to each location.

not, make their way to the SJR main river channel upstream of the confluence of the San Joaquin River and Sacramento River.

Our results also indicated that the south Delta barriers, including the fall HORB, have little if any influence on reducing SJR salmon stray rates. Although, the flow through the main SJR channel was reduced if the HORB was not installed, and the majority of the flow was conveyed towards the CVP and SWP pumping facilities via the Old River (Jassby 2005; SJRGA 2009; ICF 2010), the statistical analyses suggest that SJR stray rates were unaffected by whether SJR water flowed in the SDWSC or through the Old and Middle rivers. This is logical because SJR origin migrating adults would need to detect their natal SJR flow at the confluence of the San Joaquin and Sacramento Rivers to home successfully.

Juvenile Release Location and Stray Rates

Comparing stray rates for Sacramento River and SJR basin hatchery releases by broad geographical location (Figure 7) indicates that there is a ten-fold difference in stray rate for SJR salmon compared to that for Sacramento Basin salmon. Adult salmon stray rates for Sacramento Basin origin juvenile releases made upstream of the Delta averaged 0.1%; whereas, adult salmon stray rates for San Joaquin origin juvenile salmon releases made upstream of the Delta averaged 18%. For both Sacramento and San Joaquin adult salmon, straying increased sharply the farther downstream juvenile salmon were released. Sacramento salmon straying by release location averaged 0.1% (0 to 6.1%), 0.5% (0 to 3.4%), and 1.1% (0 to 7.8%), respectively for inland, Delta, and Bay releases. For San Joaquin salmon, adult straying by juvenile release location averaged 18% (0 to 70.1%),

35% (0 to 75%), and 85% (37.4% to 100%), respectively for inland, Delta, and Bay releases.

The coded-wire-tag release-recovery data indicate that releasing juvenile salmon farther downstream substantially increases juvenile-to-adult survival rates. This practice is called out-planting and while it increases survival, it appears to come at a cost in the form of higher stray rates than if releases occurred upstream at or near the hatchery (Ebel and others 1973; Slatick and others 1975; Ebel 1980). There is conflicting information in the literature about whether or not transportation of juveniles, from point of capture or rearing, to downstream locations, increases straying. Ebel and others (1973), Slatick and others (1975), and Ebel (1980), represent three separate studies documenting the effect of transporting juveniles on their survival and homing success as adult fish. Observed adult recoveries for both transported

(barged) and non-transported fish in the Snake–Columbia River system, found that the homing ability of Chinook salmon was not impaired even when juveniles were transported 400 km (249 miles) downstream. Conversely, in a more recent study Keefer and others (2008), who also reported stray results from a long distance juvenile transportation study conducted in the Snake–Columbia River system, found that stray rates were higher for transported (barge) juveniles than for non-transported juveniles. Vreeland and others (1975) and Solazzi and others (1991), who conducted separate juvenile transportation studies using coho salmon (*Onchorhynchus kisutch*), found that transported (trucked) juveniles had lower homing (i.e. higher stray) rates than non-transported juveniles. These studies suggest that transportation of juveniles to downstream locations increases juvenile-to-adult survival but provide contradictory results for influ-

Stray Comparison by Geographic Release Location
Average Rates for Years 1979-2007

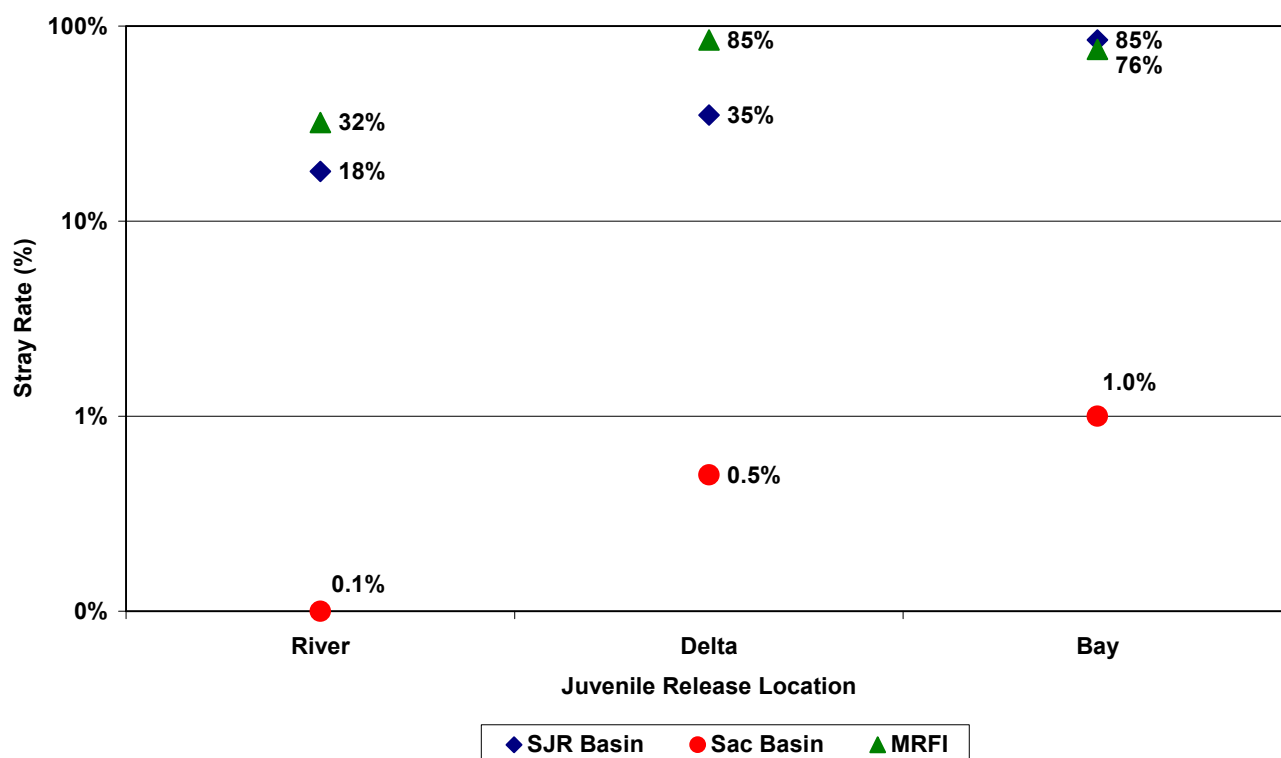


Figure 7 Plot showing stray rates for Sacramento River and San Joaquin River basin origin fall-run Chinook salmon by geographic location of release (River, Delta, and Bay) from the hatchery of origin during their juvenile emigration

ence upon adult homing. Our results indicate that juveniles released farther downstream will stray at greater rates (Figure 7).

One consequence arising from transporting hatchery juveniles to downstream releases locations is that hatchery fish from the MRH, and MRFI stray throughout the Central Valley at high rates. Though Sacramento River basin salmon exhibited relatively low stray rates (1% or less), regardless of release location in comparison to SJR basin salmon, the straying of Sacramento River basin salmon to the SJR could still be problematic given the order-of-magnitude difference in fall-run escapement between the two basins. For example, from 1979 to 2007, average annual escapement for Sacramento River and SJR adult salmon was 288,313 (ranging from 86,698 to 834,900) and 16,160 (ranging from 590 to 69,847), respectively (CDFG GrandTab 2010). If we assume a 1% stray rate and an escapement of 500,000 spawners for Sacramento River basin salmon, this would result in 5,000 salmon straying into the SJR basin. This level of Sacramento River basin salmon straying into the SJR can swamp SJR escapement, given that the combined SJR escapement has been less than 5,000 spawners in several years during the 1979 through 2007 time-period. This may have significant implications for Central Valley salmon management and may help explain why recent genetic testing indicates that the Central Valley fall-run Chinook salmon population is homogeneous (Banks and others 2000; Williamson and May 2005; Garza and others 2008; California HSRG 2012).

Stray Rate Comparisons

What is a “normal” (i.e., natural) stray rate for fall-run Chinook salmon? According to Quinn (1997), background levels of between 2% to 5% appear to be normal stray rates for hatchery salmon, but not many studies have been conducted for wild salmon. Williams (2006) reported a Mokelumne River wild fall-run Chinook stray rate of 7.3%, with the caveat that this population is heavily influenced by hatchery production and receives eggs and fry transferred from Sacramento River Basin hatcheries (FRH and NFH). CDFG Mokelumne River Hatchery annual reports

confirm that large numbers of eggs and juveniles have been transported from Sacramento River Basin hatcheries (FRH and NFH) to the Mokelumne River Hatchery (Estey 1988; Anderson 2010). What a “normal” stray rate is depends on the definition of stray rate being referenced. There can be a wide range of stray rates for Chinook salmon depending on how straying is defined. Looking closely into the factors that influence straying, such as environmental conditions at the time of return (water temperature and flow rates in both natal rivers and rivers located adjacent to the natal river [Quinn 1997]), there is near unanimous agreement—from studies conducted in the lower Columbia River Basin, U.S. (Quinn 1993), Puget Sound and Strait of Georgia, Southern Canada (Candy and Beacham 2000), and New Zealand (Unwin and Quinn 1993)—that it is relatively rare that adult Chinook salmon stray into non-natal river basins to spawn. For reference and context, in this case the entire Central Valley is a single river basin. In other words, it would be a relatively rare event to have a naturally produced Central Valley salmon stray to a non-Central Valley river basin (say the Klamath River).

Whether or not there exists a difference in stray tendency for wild versus hatchery-reared salmon is largely unknown given the few homing studies conducted using wild salmon. Comparisons of straying between wild and hatchery-reared salmon, though few, have shown results indicating that tagged wild juveniles strayed less as returning adults than hatchery reared-released salmon; although, these results are not consistent. In one study, rearing of juvenile wild fall-run Chinook in a hatchery for a short time period increased their adult straying rate relative to wild fish not reared in the hatchery (McIsaac 1990). However, wild and hatchery-reared juvenile salmon showed similar stray rates in studies with coho salmon (Labelle 1992) and Atlantic salmon (*Salmo salar*; Jonsson and others 1991, as cited in Quinn 1997).

Straying by Age

The age of adults returning may contribute to stray rate variability in salmon. In some studies, older Chinook salmon strayed more than younger fish

(Quinn and Fresh 1984; McIsaac and Quinn 1988; Quinn and others 1991; Unwin and Quinn 1992; Pascual and Quinn 1994). In contrast, Hard and Heard (1999, as cited in Candy and Beacham 2000) studied stray rates among transplanted Alaskan hatchery populations of Chinook salmon and found that straying is highest for younger fish (jack males). They hypothesized that these fish may stray at higher rates in order to expand their population by straying into non-natal rivers and spawning with uncontested females. We also found that younger age SJR salmon strayed at higher rates than did older salmon though these differences in stray rates were not statistically significant. Candy and Beacham (2000) found no consistent trend of increased stray rate with age.

Coded Wire Tag Recovery Effort

Candy and Beacham (2000) reported that recovery effort influenced stray rates with the highest stray rates and number of fish recovered occurring in regions where the highest recovery effort occurred. Their finding was consistent with Pascual and others (1995) who found that the highest stray rates occurred in the lower Columbia River and attributed this finding to this area having the highest number of potential recovery sites. Development of the Central Valley fall-run Chinook salmon CWT database uncovered similar findings. Both number of fish tagged (CWT) and CWT recovery effort in the Central Valley has fluctuated widely over time. This variability in both tagging and recovery effort results in high levels of analytical uncertainty because, as described in the Methods Appendix, missing CWT data gaps need to be filled in. That said, both Central Valley CWT tagging and recovery effort have improved over time as resources to conduct monitoring (funding and staffing) have been made available. The constant fractional marking (CFM) program of hatchery produced Central Valley fall-run Chinook salmon initiated in 2007 (PSMFC 2008) will provide more reliable results as CFM continues (Newman and others 2004) and consistent recovery effort throughout the Central Valley occurs (Hicks 2003; Hankin and others 2005).

Policy and Management Implications

Although this statistical analysis shows that both south Delta exports and SJR flow affect SJR salmon stray rates, the relative role of flow and exports is uncertain, as is the period when flow management affects stray rates. Based on our statistical results alone, the SJR flow metric (either base or pulse) is more predictive metric than one that includes exports. However, since Delta exports can cause severe negative flows in the south Delta, and occurrence of negative flows are likely to negatively affect (disorient) escaping salmon populations that migrate through the Delta because of reduced chemical olfaction cue signals (Keefer and others 2006), further study is warranted to determine whether negative flows make it more difficult for returning SJR salmon to successfully locate and migrate into the SJR.

Since the Merced River (Mesick 2010), Tuolumne River (Mesick 2009), and Stanislaus River (Carl Mesick, USFWS, pers. comm., 2012) salmon populations have been identified as being at a high risk of extinction, we further suggest evaluating whether or not increasing fall south Delta inflows (pulse or base) from each of the tributaries in the SJR could reduce SJR salmon stray rates to a natural level (<5%). Each stream's fall flow contribution might also be managed to be proportional to its unimpaired watershed runoff size (i.e., ecological fair share contribution). This could ensure that each river provides equitable homing cues. Further research on such tributary effects is probably just as important as further monitoring of the effects of exports. Further research is also needed regarding the implementation of the SJR mainstem Friant Restoration Program (SJRRP 2011) and how these new fall flows influence SJR salmon straying.

The state and federal fish agencies should consider studies to determine how the following pairing of factors influences SJR salmon stray rates: (1) the relative roles of south Delta exports and SJR flow; (2) the timing of pulse flows and export reductions; and (3) the role of pulse flows versus base flows. Because of the large number of study factors involved, it may be necessary to test a different set of conditions each year until a statistically valid model can be developed.

(e.g., ~20 years). The test conditions should include the timing, duration, and magnitude of flow releases, including source of SJR tributary flow releases, and Delta exports. It would be important to hold these conditions constant through the migratory period each year to the extent possible. The homing success and movement timing of adult SJR salmon into and through the Delta and SJR tributaries should also be monitored. The analysis of salmon migration patterns and stray rates should include water quality indices such as water temperature and dissolved oxygen concentration as well as for flow and exports in the Delta. The role of tidal action influence upon stray rates should also be considered.

Lastly, we recommend developing a stray rate target that could consist of a single number, or range, that can be used to evaluate the effectiveness of management actions to achieve the biological management goal. An example goal could be to reduce SJR salmon stray rates to levels that are comparable with Sacramento River fall-run stray rates (i.e. <1% for river releases, see Figure 7). Equalizing salmon stray rates among the Sacramento and SJR basins would facilitate progress toward achieving SJR salmon restoration goals (i.e. reduce genetic homogenization, increase natural spawner abundance, and reduce migration barriers that impede upstream movement of spawners). The recommendation to do the aforementioned studies should not be used as a reason to defer taking action now to improve Delta flow conditions to reduce straying of SJR salmon, given that SJR flow, whether it be base or pulse, has been identified as a controlling factor. Furthering our understanding about how the above mentioned factors influence straying of SJR salmon should be built upon the premise of increasing SJR flow, base and/or pulse, into the south Delta during the fall time-period.

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REFERENCES

- Anderson R. 2010. Annual report: Mokelumne River Hatchery, 2007–2008. Draft administrative report. Sacramento (CA): California Department of Fish and Game. 20 p.
- Banks M, Rashbrook V, Calvetta M, Dean C, Hedgecock D. 2000. Analysis of microsatellite DNA resolves genetic structure and diversity of Chinook salmon (*Oncorhynchus tshawytscha*) in California's Central Valley. *Canadian Journal of Fisheries and Aquatic Science* 57:915–927.
- Barnett-Johnson R, Pearson T, Ramos F, Grimes C, McFarlane R. 2008. Tracking natal origins of salmon using isotopes, otoliths, and landscape geology. *Limnology and Oceanography* 53(4):1633–1642.
- [California HSRG] California Hatchery Scientific Review Group. 2012. California hatchery review report. Prepared for the U.S. Fish and Wildlife Service and Pacific States Marine Fisheries Commission. 100 p.
- Candy J, Beacham T. 2000. Patterns of homing and straying in Southern British Columbia coded-wire tagged Chinook salmon (*Oncorhynchus tshawytscha*) populations. *Fisheries Research* 47:41–46.
- [CDFG] California Department of Fish and Game. 2010. Grandtab, Fisheries Branch Anadromous Resources Assessment–Chinook salmon. March 9, 2010. Available from: <http://www.calfish.org/portals/0/Programs/AdditionalPrograms/CDFGFisheriesBranch/tabid/104/Default.aspx>

[CDFG and NOAA Fisheries] California Department of Fish and Game, National Oceanic and Atmospheric Administration–Fisheries. 2001. Final report on anadromous salmonid fish hatcheries in California. Joint hatchery review. California Department of Fish and Game and National Marine Fisheries Service, Southwest Region (now National Oceanic and Atmospheric Administration–Fisheries). 35 p.

[CDWR] California Department of Water Resources. 2011a. South Delta Temporary Barriers program [website]. Available from: http://baydeltaoffice.water.ca.gov/sdb/tbp/index_tbp.cfm.

[CDWR] California Department of Water Resources. 2011b. DAYFLOW program documentation [website]. Available from: <http://www.water.ca.gov/dayflow/documentation/dayflowDoc.cfm#Introduction>.

Cleveland W. 1979. Robust locally weighted regression and smoothing scatterplots. *Journal of the American Statistical Association*. 74:829–836.

Ebel WJ. 1980. Transportation of chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, smolts in the Columbia River and effects on adult returns. *Fishery Bulletin* 78:491–505.

Ebel W, Park D, Johnsen R. 1973. Effects of transportation on survival and homing of Snake River chinook salmon and steelhead trout. *Fishery Bulletin* 71:549–563.

Efron B, Tibshirani R. 1993. An introduction to the bootstrap. Boca Raton (FL): Chapman & Hall/CRC. 433 p.

Estey DF. 1988. Annual report: Mokelumne River Hatchery, 1987–88. Administrative Report No. 89-3. Sacramento (CA): California Department of Fish and Game. 11 p.

Garza J, Blankenship S, Lemaire C, Charrier G. 2008. Genetic population structure of Chinook salmon (*Oncorhynchus tshawytscha*) in California's Central Valley. Comprehensive evaluation of population structure and diversity for Central Valley Chinook salmon. Final report for CALFED project. Santa Cruz (CA): Institute of Marine Sciences, University of California, Santa Cruz, California and NOAA Southwest Fisheries Science Center. 84 p.

Groves A, Collins G, Trefethen P. 1968. Roles of olfaction and vision in choice of spawning site by homing adult Chinook salmon. *Journal of the Fisheries Research Board of Canada* 25:867–76.

Hallock R, Elwell R, Fry D. 1970. Migrations of adult king salmon *Oncorhynchus tshawytscha* in the San Joaquin Delta; as demonstrated by the use of sonic tags. *Fish Bulletin* 151. Sacramento (CA): California Department of Fish and Game. 92 p.

Hankin D, Clark J, Deriso R, Garza J, Morishima G, Riddell B, Schwarz S. 2005. Expert panel on the future of the coded wire tag Program for Pacific Salmon. Pacific Salmon Commission Technical Report No. 18. Vancouver, BC: Pacific Salmon Commission. 230 p.

Hard J, Heard R. 1999. Analysis of straying variation in Alaskan hatchery Chinook salmon (*Oncorhynchus tshawytscha*) following transplantation. *Canadian Journal of Fisheries Science* 56:578–589.

Hicks A. 2003. A discussion and analysis of four constant fractional marking alternatives for California's Central Valley salmon hatcheries [master's thesis]. Available from: University of Idaho. 97 p.

[ICF] ICF International. 2010. Effects of the head of Old River barrier on flow and water quality in the San Joaquin River and Stockton Deep Water Ship Channel. ICF 01111.07. Prepared for the Department of Water Resources. 65 p.

Jassby AD. 2005. Phytoplankton regulation in a eutrophic tidal river (San Joaquin River, California). San Francisco Estuary and Watershed Science [Internet]. Available from: <http://escholarship.org/uc/item/9jb2t96d>.

Jonsson B, Jonsson N, Hansen L. 1991. Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. *Aquaculture* 98:69–71.

Keefer M, Caudill C, Peery C, Bjornn T. 2006. Route selection in a large river during the homing migration of Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Science* 63:1752–1762.

- Keefer M, Caudill C, Peery C, Lee S. 2008. Transporting juvenile salmonids around dams impairs adult migration. *Ecological Applications* 18:1888–1900.
- Labelle M. 1992. Straying patterns of Coho salmon (*Onchorhynchus kisutch*) stocks from Southeast Vancouver Island, British Columbia. *Canadian Journal of Fisheries and Aquatic Science* 49:1843–1855.
- Mclsaac D. 1990. Factors affecting the abundance of 1977–1979 brood wild fall Chinook salmon (*Oncorhynchus tshawytscha*) in the Lewis River, Washington [dissertation]. Available from: University of Washington, Seattle. 174 p.
- Mclsaac D, Quinn T. 1988. Evidence for a hereditary component in homing behavior of Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 45:2201–2205.
- Mesick C. 2001. The effects of San Joaquin River flows and Delta export rates during October on the number of adult San Joaquin Chinook salmon that stray. In: Brown RL, editor. *Fish Bulletin* 179: Contributions to the biology of Central Valley salmonids. Volume 2. Sacramento (CA): California Department of Fish and Game. p 139–161.
- Mesick C. 2009. The high risk of extinction for the natural fall-run Chinook salmon population in the lower Tuolumne River due to insufficient instream flow releases. U.S. Fish and Wildlife Service Report submitted to the State Water Resources Control Board. Stockton (CA): U.S. Fish and Wildlife Service. 78 p.
- Mesick C. 2010. The high risk of extinction for the natural fall-run Chinook salmon population in the lower Merced River due to insufficient instream flow releases. Report prepared for California Sportfishing Protection Alliance. El Dorado (CA): Carl Mesick Consultants. 111 p.
- Miller J, Gray Q, Merz J. 2010. Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook salmon (*Onchorhynchus tshawytscha*). *Marine Ecology Progress Series* 408:227–240.
- Newman K. 2008. An evaluation of four Sacramento–San Joaquin River Delta juvenile salmon survival studies. Report produced for the CALFED Science Program, Project number SCI-06-G06-299. March 31, 2008. Stockton (CA): U.S. Fish and Wildlife Service, Stockton Fish and Wildlife Office 182 p.
- Newman K, Hicks A, Hankin D. 2004. A marking, tagging, and recovery program for Central Valley hatchery Chinook salmon. Unpublished report to Central Valley Salmonid Project Work Team. July 7, 2004. 72 p.
- Pascual M, Quinn T. 1994. Geographical patterns of straying of fall run Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), from Columbia River (USA) Hatcheries. *Aquaculture and Fisheries Management* 25(Supplement 2):17–30.
- Pascual M, Quinn T, Fuss H. 1995. Factors affecting the homing of fall Chinook salmon from Columbia River Hatcheries. *Transactions of the American Fisheries Society* 124:308–320.
- [PSMFC] Pacific States Marine Fisheries Commission. 2008. Constant fractional marking/tagging program for Central Valley fall-run Chinook salmon. Report produced for the CALFED Ecosystem Restoration Program, Sacramento, CA. Final project report P0685610 dated November 2008. Red Bluff (CA): Pacific States Marine Fisheries Commission. 54 p.
- Quinn T. 1993. A review of homing and straying of wild and hatchery-produced salmon. *Fisheries Research* 18:29–44.
- Quinn T. 1997. Homing, straying, and colonization. In: Grant, WS, editor. Genetic effects of straying of non-native fish hatchery fish into natural populations: proceedings of the workshop. U.S. Dep. Commerce, NOAA Tech Memo. NMFS-NWFSC-30. 130 p.
- Quinn T, Fresh K. 1984. Homing and straying in Chinook salmon (*Onchorhynchus tshawytscha*) from Cowlitz River Hatchery, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 41:1078–1082.

Quinn T, Nemeth R, McIssac D. 1991. Homing and straying patterns of fall Chinook salmon in the Lower Columbia River. *Transactions of the American Fisheries Society* 120:150–156.

Rich A. 2007. Impacts of water temperature on fall-run Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) in the San Joaquin River system. Publication prepared for the California Department of Fish and Game and submitted to the California Central Valley Water Resources Control Board. San Anselmo (CA): A.A. Rich and Associates. 46 p.

Rose E. 2000. The San Joaquin a river betrayed. Clovis (CA): Quill Driver Books/Word Dancer Press, Inc. 160 p.

Sholes W, Hallock R. 1979. An evaluation of rearing fall-run Chinook salmon (*Oncorhynchus tshawytscha*) to yearlings at Feather River Hatchery, with a comparison of returns from hatchery and downstream Releases. *California Fish and Game* 65:239–255.

[SJRG] San Joaquin River Group Authority. 2009. San Joaquin River Agreement–Vernalis Adaptive Management Plan, Annual Technical Report 2008. Prepared for the California Water Resources Control Board in compliance with D-1641. Modesto (CA): San Joaquin River Group Authority. 132 p.

[SJRRP] San Joaquin River Restoration Program. 2011. Final Supplemental Environmental Assessment. Interim Flows Project–Water Year 2012. Sacramento (CA): U.S. Department of Interior, Bureau of Reclamation Mid-Pacific Regional Office. 94 p. Available from: http://www.usbr.gov/mp/nepa/documentShow.cfm?Doc_ID=8385.

Slatick E, Park D, Ebel W. 1975. Further studies regarding effects of transportation on survival and homing of Snake River chinook salmon and steelhead trout. *Fishery Bulletin* 73:925–931.

Snyder J. 1931. Salmon of the Klamath River. *California Fish and Game Fish Bulletin* 34:1–130.

Solazzi M, Nickelson T, Johnson S. 1991. Survival, contribution, and return of hatchery coho salmon (*Oncorhynchus kisutch*) released from freshwater, estuarine, and marine environments. *Canadian Journal of Fisheries and Aquatic Sciences* 48:248–253.

Unwin M, Quinn T. 1993. Homing and straying patterns of Chinook salmon (*Oncorhynchus tshawytscha*) from a New Zealand Hatchery: spatial distribution of strays and effects of release Date. *Canadian Journal of Fisheries and Aquatic Sciences* 50(6):1168–1175.

[USEPA] U.S. Environmental Protection Agency. 1986. Ambient water quality criteria for dissolved oxygen. EPA 440/5-86-003. Washington, D.C.: Office of Water Regulations and Standards Criteria and Standards Division, USEPA. 54 p. Available from: <http://www.epa.gov/cgi-bin/claritgw?op=Display&document=clserv:OAR:0579;&rank=4&template=epa>.

[USEPA] U.S. Environmental Protection Agency. 2003. EPA region 10 guidance for Pacific northwest state and tribal temperature water quality standards. EPA 910-B-03-002. Washington, D.C.: Office of Water Regulations and Standards Criteria and Standards Division, USEPA. 49 p. Van Der Laan M, Polley E, Hubbard A. 2007. Super learner. *Statistical Applications in Genetics and Molecular Biology* 6(1):Article 25.

Vreeland R, Wahle R, Arp A. 1975. Homing behavior and contribution to Columbia River fisheries of marked coho salmon released at two locations. *Fishery Bulletin* 73:717–725.

Williams J. 2006. Central Valley salmon: a perspective on Chinook and steelhead in the Central Valley of California. *San Francisco Estuary and Watershed Science* [Internet]. Available from: <http://escholarship.org/uc/item/21v9x1t7>.

Williamson K, May B. 2005. Homogenization of fall-run Chinook salmon gene pools in the Central Valley of California, USA. *North American Journal of Fisheries Management* 25:993–1009.