NRC Research Press

ARTICLE

Decoupling outmigration from marine survival indicates outsized influence of streamflow on cohort success for California's Chinook salmon populations

Cyril J. Michel

Abstract: Historically, marine survival estimates for salmon have been confounded with freshwater seaward migration (outmigration) survival. Telemetry studies have revealed low and variable survival during outmigration, suggesting marine mortality may not be the primary source of variability in cohort size as previously believed. Using a novel combination of tagging technologies, survival during these two life stages was decoupled over 5 years for Sacramento River Chinook salmon (*Oncorhynchus tshawytscha*). Outmigration survival ranged from 2.6% to 17%, and marine survival ranged from 4.2% to 22.8%. Influential environmental drivers in both life stages were also compared with smolt-to-adult ratios (SAR) for three Chinook salmon populations over 20 years. Streamflow during outmigration had higher correlation with SAR ($r^2 > 0.34$) than two marine productivity indices ($r^2 < 0.08$). The few SAR estimates that were poorly predicted by flow occurred during years with the lowest marine productivity, suggesting most interannual SAR fluctuations are explained by outmigration survival, but abnormally poor marine conditions also reduce SAR. The outsized influence of flow on SAR provides managers with a powerful mitigation tool in a watershed where flow is tightly regulated.

Résumé : Historiquement, une certaine confusion, associée à la survie durant la migration vers la mer (dévalaison), caractérise les estimations de la survie en mer des saumons. Des études de télémétrie ont révélé des taux de survie faibles et variables durant la dévalaison qui indiqueraient que, contrairement à la croyance antérieure, la mortalité en mer pourrait ne pas être la première source de variabilité de la taille des cohortes. L'utilisation d'une combinaison novatrice de technologies de marquage a permis de découpler la survie durant ces deux étapes du cycle de vie pendant une période de 5 ans pour des saumons quinnats (*Oncorhynchus tshawytscha*) du fleuve Sacramento. La survie durant la dévalaison allait de 2,6 % à 17 %, alors que la survie en mer allait de 4,2 % à 22,8 %. Les facteurs environnementaux exerçant une influence pendant les deux étapes du cycle de vie ont aussi été comparés aux rapports saumoneaux-adultes (RSA) pour trois populations de saumons quinnats sur 20 ans. Le débit durant la dévalaison présente une corrélation plus forte avec le RSA ($r^2 > 0{,}34$) que deux indices de productivité marine ($r^2 < 0{,}08$). Les quelques estimations du RSA que le débit ne prédit pas bien sont pour les années où la productivité marine était la plus faible, ce qui donne à penser que la plupart des fluctuations interannuelles du RSA s'expliquent par la survie durant la dévalaison, mais que des conditions marines anormalement mauvaises réduisent également le RSA. L'influence démesurée du débit sur le RSA fournit aux gestionnaires un puissant outil d'atténuation dans un bassin versant où le débit fait l'objet d'une régularisation serrée. [Traduit par la Rédaction]

Introduction

Convention is that variability in salmon cohort success is set during the early marine residence period. To date, direct evidence of how outmigration (freshwater plus estuarine) survival might be affecting overall cohort success has been scarce throughout the range of salmon populations. Historically, it has been difficult to parse out outmigration survival from marine survival, further obfuscating the causes and magnitude of outmigration mortality. Recent telemetry studies have estimated very low survival during the outmigration life stage of certain salmon stocks (Buchanan et al. 2013; Michel et al. 2015; Clark et al. 2016), suggesting that marine survival is likely higher than what the literature indicates. Many models attempting to explain marine survival using marine environmental indicators suffer from large amounts of unexplained variation in some years (Koslow et al. 2002; Logerwell et al. 2003; Sharma et al. 2013); and there is potential that variation due to outmigration survival has been incorrectly attributed to marine survival in these models. Through the accurate partitioning of outmigration and marine survival, it may be possible to identify new survival bottlenecks, which will require new and different management solutions.

Marine conditions are often blamed for poor cohort success of California's Central Valley Chinook salmon (*Oncorhynchus tshawytscha*) populations, but there is a building body of evidence to suggest that outmigration survival may be playing a large role (Buchanan et al. 2013; Michel et al. 2015). Gross et al. (1988) posited that anadromous life history strategies evolve in fishes when migration to the ocean provides gains to individual fitness that outweigh the costs of the migration itself. It is believed that salmon have evolved this life history strategy because the ocean provides a more favorable

Received 5 April 2018. Accepted 11 October 2018.

C.J. Michel. University of California, Santa Cruz, Institute of Marine Sciences, Affiliated with: Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 McAllister Way, Santa Cruz, CA 95060, USA.

Email for correspondence: cyril.michel@noaa.gov.

A correction was made to the e-First version of this paper on 25 April 2019 prior to the final issue publication. The current online and print versions are identical and both contain the correction.

trade-off between abundant food and predation risk. However, the Central Valley may be an example of a system where the costs of outmigration are high enough that the anadromous life history strategy is no longer sustainable and is only persisting through the assistance of humans (such as through hatcheries or transporting outmigrants past regions of poor survival). Three of the four distinct salmonid evolutionarily significant units that are found there are listed under the US Endangered Species Act, and the fourth is a "species of concern". Many inland stressors have been identified that have led to the decline of these populations, including the loss of 47% of spawning and rearing habitat due to dams without fish passage (Yoshiyama et al. 2001) and 97% of the productive floodplain rearing habitat to diking (Whipple et al. 2012). These dams and levees are one-time historical perturbations, but have ongoing impacts and will likely never be completely reversed. While it is almost certain that populations will not return to pre-dam and prediking levels without reversing these habitat changes, studies must also concentrate on the contemporary stressors that are governing annual outmigration survival dynamics, such as warm stream and estuary temperatures during outmigration, slow water velocities, low turbidity, and abundant predators (Baker et al. 1995; Newman and Rice 2002; Grossman 2016). However, these are just the symptoms of a larger problem: the fundamental alteration of the Central Valley hydrological regime. The dams and diversions of the Central Valley have resulted in the reduction and homogenization of river flows (Buer et al. 1989), which in turn can alter water temperatures, slow water velocities associated with large flow events, lower turbidity, and provide more suitable habitat for warm-water predator species. These same dams and diversions give resource managers tight control over streamflow and associated covariates. In contrast, managers have no control over the environmental variables that are thought to govern marine survival. Therefore, if outmigration survival is found to have a large influence on the magnitude and variability in cohort success, this suggests that managers can likely do more to help these populations.

A novel method of pairing outmigration survival estimates derived from an acoustic tagging study with smolt-to-adult ratio (SAR) estimates derived from coded-wire tag (CWT) recoveries from the same cohorts was used to investigate the relative importance of (*i*) freshwater and estuarine outmigration (hereinafter simply termed "outmigration") survival versus (*ii*) marine survival rates for Central Valley Chinook salmon over the 5-year time series of the acoustic tagging study. Expanding beyond this time series, many additional years of SAR estimates were regressed against environmental drivers that are believed to be influential on survival in each region to investigate the importance of these environmental drivers on smolt-to-adult dynamics and ultimately gain insights on where the majority of mortality might be occurring every year.

Methods

Study system

California's Central Valley includes the two largest rivers in the state. In the northern portion of the valley, the Sacramento River flows north to south and in the southern portion of the valley, the San Joaquin River flows south to north (Fig. 1). These two rivers meet to create the freshwater portion of their shared estuary: the Sacramento–San Joaquin River Delta (hereinafter "Delta"), an expansive and complex network of tidal freshwater river channels and sloughs. It is connected to the west by a series of increasingly saline bays, most notably the San Francisco Bay, which comprise the brackish portion of the estuary ("Bays" in Fig. 1). The estuary connects to the Pacific Ocean at the narrow passage at the Golden Gate, beyond which salmon have access to the productive waters of the Gulf of the Farallones.

Outmigration survival estimates

In an attempt to decouple outmigration and marine survival of Central Valley Chinook salmon, cohorts that were tagged using both acoustic tags (for estimation of outmigration survival) and CWTs (for estimation of overall cohort success) were identified. Outmigration survival estimates were used from two acoustic tagging studies conducted on hatchery-origin late-fall-run Chinook salmon from 2007 to 2011 (Michel et al. 2015; Iglesias et al. 2017). These studies released their acoustic tagged fish as part of larger hatchery releases that were also coded-wire tagged. CWTs are tiny, injectable, magnetized wire segments that are embossed with a release group serial code, with release groups of thousands of fish often sharing the same serial code. Recovery of tagged adults allows the estimation of SAR of these larger release groups. SAR represents the proportion of fish of a harvestable size recovered from the total number of juveniles released into the wild and was therefore used as an index of cohort success.

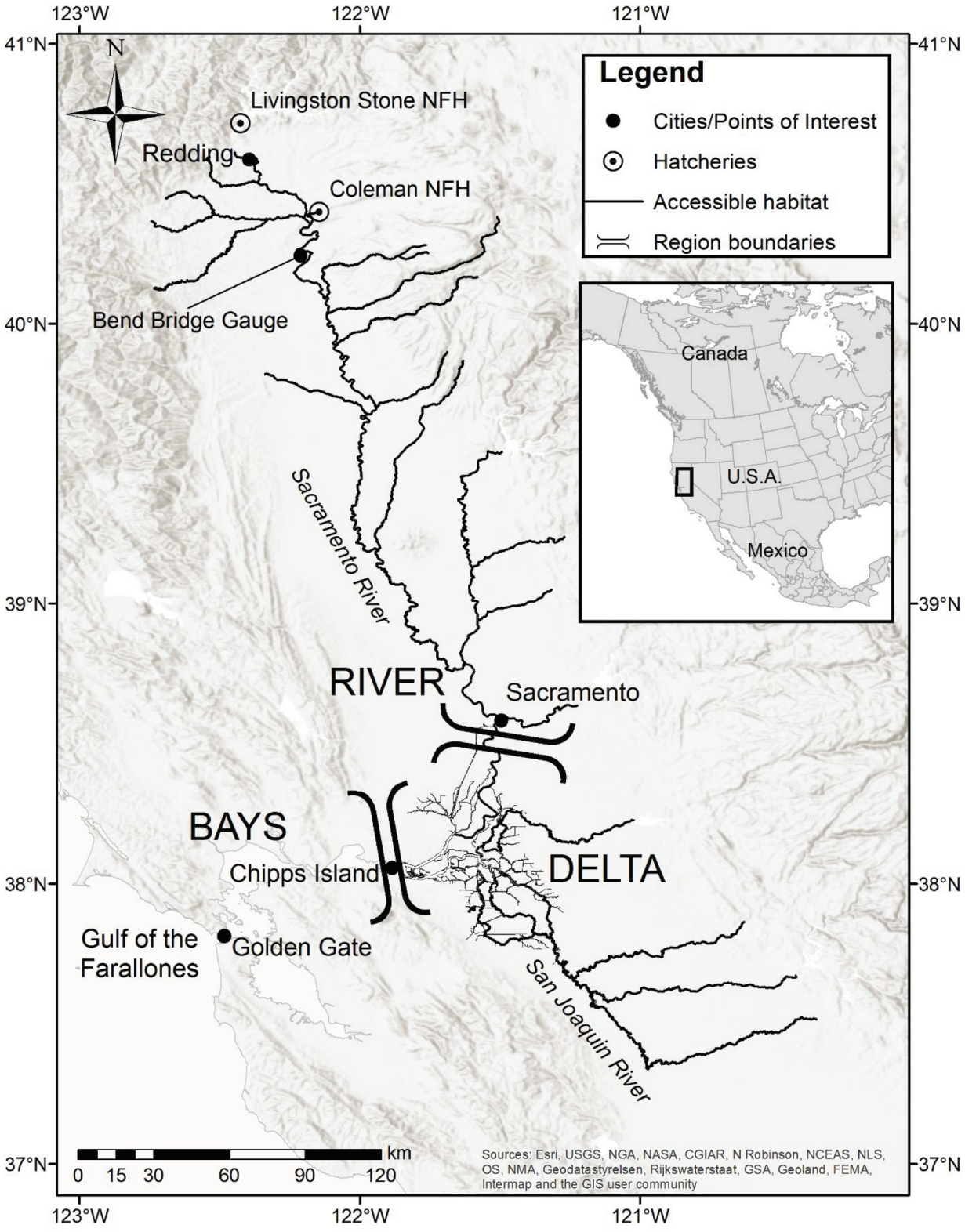
To assess the contribution of outmigration survival to overall SAR, and to factor out estimates of marine survival, I associated outmigration survival from acoustic tagged release groups to the SAR estimates from the most appropriate CWT release groups. However, some of the acoustic tagged release groups were not released in exact synchrony with a respective CWT release group. For these, if one or more CWT release groups were released within 7 days of the acoustic tag group's release date, that acoustic tag group's outmigration survival was associated to the respective CWT release group(s). For the purposes of these studies, outmigration survival was estimated as total survival from release to the Golden Gate Bridge, thereby including river and estuarine survival. For more information on the acoustic tagging, tracking, and estimation of survival for the acoustic tagging studies, refer to Michel et al. (2015).

Smolt-to-adult estimates

SAR is a survival metric often used for hatchery fish because of the fairly accurate estimates of how many smolts are released. Hatchery Chinook salmon are often raised up to the smolting stage before release, which is the beginning of the SAR period. The end of the SAR period is when a fish either returns to the spawning grounds or hatchery or is captured by commercial or recreational fisheries. These various recapture scenarios (strata) and their associated CWT recoveries occur after Chinook salmon have spent at least 1 year in the ocean (2+ years old) and can commonly occur for salmon that have spent as many as 3 years in the ocean (4+ years old; Fig. 2). SAR therefore represents the survival of a cohort from smolting to the point at which they reach harvestable and minimum reproductive (i.e., adult) size. Thus, survival during the SAR period for a CWT group will be the product of (*i*) "outmigration survival" (S_O) and (*ii*) "marine survival" (S_M), survival during the first year at sea plus an amalgamation of years 2, 3, and 4 survival depending on recapture time of individuals within the CWT group. Because of this complexity, SAR should be treated as an index of survival that primarily represents survival from hatchery release to age 2, with some additional mortality from latter periods (but that are thought to be relatively small contributions compared with critical survival bottlenecks of outmigration and the first year at sea; Magnusson and Hilborn 2003; Quinn 2005 and references therein).

The SAR in the Central Valley is most often calculated using CWT recoveries (CWT_R). Approximately 25% of all hatchery-origin fall-run Chinook salmon (since 2007) and 100% of all hatchery-origin late-fall-run and winter-run Chinook salmon (since 1992) in the Central Valley have CWTs inserted into their snouts as juveniles. Once the salmon attain harvestable size (hereinafter "adults"), the CWTs are recovered from the fisheries through creel surveys, from the spawning grounds through carcass surveys, and through the hatcheries (for additional details on recovery sources, refer to Table 1). All CWT data were downloaded from the Pacific States

Fig. 1. Map of the Central Valley, including portions of major rivers accessible to Chinook salmon populations delineated by major regions, cities, and points of interest and salmon hatcheries relevant to this study.



Marine Fisheries Commission's Regional Mark Processing Center's Regional Mark Information System database (http://www.rmpc.org/).

The first brood year (i.e., the year the eggs were spawned; "BY" hereinafter) for which SAR could be accurately estimated was 1999 for both winter- and fall-run Chinook salmon and 1993 for late-fall-run Chinook salmon (despite the absence of spawning ground and recreational river fishery recoveries until the late 1990s). Since an estimated 61% to 97% (mean 80%) of late-fall-run Chinook salmon escapement are counted at hatcheries (using

Fig. 2. A schematic representing the various recapture points for coded-wire tags (CWTs) along the salmon life cycle that contribute to the estimation of a smolt-to-adult ratio (SAR) for a given CWT group. The coloured arrows represent life stage transitions, each with inherent levels of natural mortality. The circle shape represents hatchery release, and rectangles represent CWT recoveries. Green shapes represent events that occur in fresh water, and blue shapes represent events that occur in the ocean. While recoveries of 5+-year-old salmon are possible, they are extremely rare and therefore not represented in this schematic. [Colour online.]

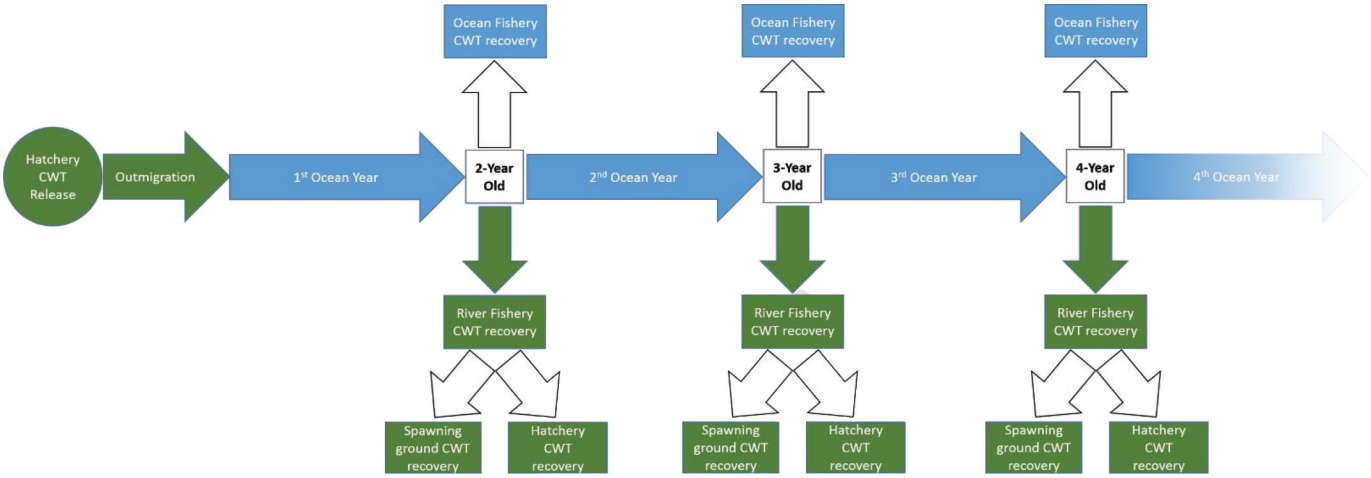


Table 1. The different sources of coded-wire tag (CWT) recoveries and the agency, method, and first collection year for each.

Chinook salmon run	Recovery type	Recovery agency	Collection method	Brood year when first available
Winter	Ocean recreational fishery[a]	CDFW	Creel surveys	1991[b]
	Ocean commercial fishery[a]	CDFW	Creel surveys	1991[b]
	River recreational fishery	CDFW	Creel surveys	No fishery
	Spawning ground	USFWS	Carcass surveys	**1999**
	Hatchery	USFWS	Hatchery returns	1991[b]
Late-fall	Ocean recreational fishery[a]	CDFW	Creel surveys	1993[b]
	Ocean commercial fishery[a]	CDFW	Creel surveys	1993[b]
	River recreational fishery	CDFW	Creel surveys	1998
	Spawning ground	CDFW	Carcass surveys	1999
	Hatchery	USFWS	Hatchery returns	**1993**[b]
Fall	Ocean recreational fishery[a]	CDFW	Creel surveys	1979[b]
	Ocean commercial fishery[a]	CDFW	Creel surveys	1979[b]
	River recreational fishery	CDFW	Creel surveys	1998
	Spawning ground	CDFW	Carcass surveys	**1999**
	Hatchery	USFWS	Hatchery returns	1979[b]

Note: In the last column, years highlighted in bold represent the first brood year for which smolt-to-adult ratio (SAR) was estimated. CDFW, California Department of Fish and Wildlife; USFWS, United States Fish and Wildlife Service.

[a]Some ocean fishery recoveries are received from out-of-state sources.

[b]First year of consistent coded-wire tagging.

CWT data from recovery years 2000–2016 when spawning ground and recreational river fishery recoveries occurred), using only hatchery returns in years prior to the late 1990s could bias SAR estimates low for those years, but would likely still capture the major population trends.

For creel and carcass surveys, full coverage of all fishing areas and spawning grounds is not possible; sampling fractions (r) are therefore estimated per stratum (i.e., unique recovery type, area, and year combinations). Sampling fractions are the fraction of estimated total number of salmon caught (if a fishery) or that returned (if a hatchery or spawning area) that were examined for presence of a CWT per stratum, with some additional nuances outlined in Palmer-Zwahlen and Kormos (2015). Details on how total number of salmon per stratum were estimated can be found in O'Farrell et al. (2012). Expansion factors, the reciprocal of sampling fractions, are applied to the total CWTs observed per CWT release group that are recovered from that respective stratum to produce expanded CWT recoveries ($eCWT_R$). Finally, since Chinook salmon spawning age is variable (minimum age 2 years), SAR for the full cohort cannot be estimated until the CWTs from the fifth year after release are processed. Thus, SAR estimates beyond BY 2012 are not reported. Total expanded recoveries for each release group (N_e) is therefore estimated as

$$(1)\quad N_e = \sum_{y=1}^{Y} (eCWT_R \text{ Ocean Fishery} + eCWT_R \text{ River Fishery} + eCWT_R \text{ Spawning Grounds} + CWT_R \text{ Hatchery})$$

where Y is total number of return years for which CWTs are observed for that CWT release group. Note that hatchery CWT recoveries are not expanded because all CWTs are presumed to be recovered from hatchery returns.

SAR is expressed as the proportion of expanded recoveries (N_e) out of all smolts released from the hatchery for that CWT release group (N_r):

$$(2)\quad \text{SAR} = \frac{N_e}{N_r}$$

The standard error (SE) of the SAR for a CWT release group is a function of N_e, N_r, and the total number of observed CWTs (before expansion, N_d) (Skalski and Townsend 2005):

$$\text{SE(SAR)} = \sqrt{\frac{\frac{N_e}{N_r}\left(1 - \frac{N_e}{N_r}\right)}{N_r} + \frac{\left(\frac{1-r}{r^2}\right)N_d}{N_r^2}} \quad (3)$$

For proper variance calculation, sampling fractions are needed per stratum. However, protocols for estimating sampling fractions differed substantially by year and recapture type. Overall, the sampling fraction for all CWTs recovered (across the strata) per brood year and per population in this analysis was never below 0.21, and the mean was 0.35 for winter-run, 0.49 for fall-run, and 0.63 for late-fall-run. Therefore, a global sampling fraction (r) was applied to eq. 3 using a conservative estimate of 0.2:

$$\text{SE(SAR)} = \sqrt{\frac{\frac{N_e}{N_r}\left(1 - \frac{N_e}{N_r}\right)}{N_r} + \frac{\left(\frac{1-0.2}{0.2^2}\right)N_d}{N_r^2}} \quad (4)$$

When calculating SAR and SE for more CWT release groups that were released on the same day, N_e, N_r, and N_d were totaled among those CWT release groups. However, because there can be large heterogeneity in SAR estimates for different CWT release groups released in the same year, annual SAR and SEs are calculated differently (Skalski and Townsend 2005). Annual SAR is a weighted average across CWT release groups:

$$\widehat{\text{SAR}} = \frac{\sum_{k=1}^{K} N_{e_k}}{\sum_{k=1}^{K} N_{r_k}} \quad (5)$$

where K is the number of CWT release groups in a year. SE of the annual SAR is estimated as

$$\text{SE}(\widehat{\text{SAR}}) = \sqrt{\frac{\sum_{k=1}^{K} N_{r_k}(\text{SAR}_k - \text{SAR})^2}{(K-1)\sum_{k=1}^{K} N_{r_k}}} \quad (6)$$

For the late-fall-run and winter-run populations, the only hatcheries that release smolts in the Central Valley are the United States Fish and Wildlife Service's Coleman National Fish Hatchery (CNFH) and Livingston Stone National Fish Hatchery, respectively. Both of these hatcheries release the majority of their fish into the uppermost portions of the Sacramento River that is available to anadromy, more than 500 river kilometres from the Pacific Ocean. Because multiple hatcheries in the Central Valley release fall-run smolts, to compare fall-run release groups over the same outmigration corridor as the late-fall-run and winter-run groups, we used only fall-run CWT recoveries from CNFH release groups. All CWT release groups that were trucked and released downstream, a management strategy intended to artificially increase SARs (by reducing outmigration mortality) of hatchery smolts, were also excluded. This is because one of the main objectives of this study was to measure explicitly the magnitude and variability in natural outmigration survival.

SAR estimates are the combination of survival over a finite outmigration period and nondiscrete marine period (due to various CWT recapture times). To ascertain the magnitude of the bias introduced by the latter periods of the nondiscrete marine period on overall SAR, SAR estimates were compared with survival rates from hatchery release to the end of age 2 for winter-run Chinook salmon for the same brood years, as estimated from a Sacramento River winter-run Chinook salmon cohort reconstruction model (O'Farrell et al. 2012; data provided by M. O'Farrell, National Oceanic and Atmospheric Administration – National Marine Fisheries Service). This was done using a linear regression model fitted between the two variables, after logit-transformation (due to the range of both variables being bound by 0 and 1). Currently, a salmon cohort reconstruction model does not exist for Central Valley fall- or late-fall-run Chinook salmon.

Outmigration versus marine survival comparison

The outmigration survival component of SAR, as estimated from acoustic telemetry, was factored out to get an estimate of marine survival for those brood years:

$$S_M = \frac{\text{SAR}}{S_O} \quad (7)$$

To incorporate error in estimates of both SAR and S_O, I employed parametric bootstrapping. SAR was assumed to have a normal distribution on the real scale, and S_O was assumed to have a normal distribution on the logit scale. Given these distributions, SAR and S_O were generated 1000 times each and transformed back to the real scale, such that (SAR_1^*, SAR_2^*, …, SAR_{1000}^*) and ($S_{O_1}^*$, $S_{O_2}^*$, …, $S_{O_{1000}}^*$) yielded $S_{M_1}^*$, $S_{M_2}^*$, …, $S_{M_{1000}}^*$. Mean S_M and SE of the mean were estimated from these values on the logit scale and back-transformed to the real scale. The 95% confidence intervals were also generated given

$$\text{logit}^{-1}\left\{\text{logit}\left(\widehat{S_M}\right) \pm 1.96 \times \text{SE}\left[\text{logit}\left(\widehat{S_M}\right)\right]\right\} \quad (8)$$

This was done for late-fall-run Chinook salmon only and not for fall-run or winter-run Chinook salmon due to the lack of acoustic tag data old enough to estimate respective SAR values.

Freshwater outmigration survival versus SAR

Michel et al. (2015) demonstrated that much of the annual variability in outmigration survival may be occurring during the freshwater portions of the outmigration. To evaluate the effect of annual freshwater outmigration survival (S_{FW}) dynamics on SAR, a linear model was fitted to survival rates estimated from acoustic tags and the CWT-based SAR. The acoustic tag-estimated survival rates encompassed the river and Delta regions combined (i.e., from release to Chipps Island; data from Michel et al. 2015).

To incorporate error, I employed parametric bootstrapping for both SAR and S_{FW}. SAR data was generated 1000 times on the real scale, then transformed to the logit scale due to SAR being bounded by 0 and 1, such that [logit(SAR_1^*), logit(SAR_2^*), …, logit(SAR_{1000}^*)] data sets were created. S_{FW} was generated 1000 times on the logit scale, again because S_{FW} is bounded by 0 and 1, such that [logit($S_{FW_1}^*$), logit($S_{FW_2}^*$), …, logit($S_{FW_{1000}}^*$)] data sets were created. The SAR data sets were fitted to their respective S_{FW} data sets per iteration of 1000 different linear models, such that 1000 estimates of r^2 values were generated. The median, 5%, and 95% percentile values (i.e., 95% confidence intervals) of the r^2 estimates were then calculated.

Environmental covariates versus SAR

The relationship between SAR and variables that characterize the river and ocean environments were evaluated for each of the three Chinook salmon populations. Linear regression models were fitted between logit-transformed SAR estimates and environmental indices. Because extreme outliers can mask strong and persistent trends, Cook's distances were estimated for all points in all models (Cook 1977) to determine if any annual SAR values exert

Table 2. The estimated annual SAR (%), standard error (SE), and total number of release days for each run and each brood year.

	Late-fall-run			Winter-run			Fall-run		
Brood year	SAR (%)	SE	Total release days	SAR (%)	SE	Total release days	SAR (%)	SE	Total release days
1993	0.50	0.07	3	—	—	—	—	—	—
1994	1.80	0.42	5	—	—	—	—	—	—
1995	1.02	0.13	5	—	—	—	—	—	—
1996	1.64	0.23	5	—	—	—	—	—	—
1997	0.69	0.10	6	—	—	—	—	—	—
1998	0.85	0.08	3	—	—	—	—	—	—
1999	1.03	0.14	5	2.23	0.21	1	3.29	0.14	3
2000	0.77	0.11	4	0.34	0.03	1	0.78	0.05	4
2001	1.10	0.19	4	0.24	0.02	1	0.70	0.06	5
2002	1.44	0.25	4	1.88	0.09	1	0.94	0.12	2
2003	1.44	0.16	4	1.38	0.07	1	0.30	0.04	1
2004	0.26	0.07	4	0.08	0.01	1	0.10	0.03	2
2005	1.72	0.24	3	0.11	0.01	1	0.02	0.01	2
2006	0.87	0.16	3	0.29	0.04	1	0.04	0.01	4
2007	0.79	0.16	3	0.28	0.05	1	0.13	0.01	4
2008	0.56	0.05	4	0.05	0.01	1	0.59	0.04	3
2009	0.58	0.10	3	0.59	0.04	2	2.39	0.09	3
2010	1.21	0.14	3	0.43	0.06	1	1.46	0.08	4
2011	0.91	0.09	5	0.42	0.03	1	0.45	0.04	3
2012	0.88	0.10	4	0.62	0.07	1	0.15	0.02	3

Note: Standard errors were calculated using eq. 6.

excessive leverage on the linear regressions. The linear regression model was fitted with and without any annual SAR value with a Cook's distance > 1.

Environmental covariates thought to influence survival during the outmigration and marine survival life stages were selected in an attempt to determine the relative contribution of these factors on cohort success. For the river environment, the literature suggests that flow may have the greatest influence on outmigration survival (Newman and Rice 2002; Smith et al. 2003; Michel et al. 2015). Flow values (cubic feet per second; 1 ft^3 = 28.3 L) were used from the United States Geological Survey's Bend Bridge gauging station on the Sacramento River (USGS station number 11377100). This gauge is located approximately 20 and 60 river kilometres downstream from the release locations used by the CNFH and LSFH, respectively. Distribution of flow values was right-skewed and thus log-transformed for normality.

A single variable (upwelling) and a multivariate index of productivity were chosen for the marine environment. Upwelling is a key variable in determining the quality of marine conditions for salmon (Kope and Botsford 1990; Scheuerell and Williams 2005; Wells et al. 2016). Mean monthly coastal upwelling index as computed by the National Oceanic and Atmospheric Administration's National Marine Fisheries Service for the 39°N, 125°W station, the closest station to the Gulf of the Farallones (https://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html), was used as the single covariate. The upwelling index represents wind-driven, cross-shore transports computed from surface pressure analyses (in cubic metres per second along each 100 metres of coastline). The Multivariate Ocean Climate Indicator (MOCI) as described in Garcia-Reyes and Sydeman (2017) was used as the multivariate index of productivity. This unitless environmental indicator, specific to California's continental shelf, synthesizes numerous ocean and atmospheric variables to give an index of the state of the ecosystem productivity (http://www.faralloninstitute.org/moci). The MOCI is estimated for both the Northern California region (38°N to 42°N) and the Central California region (34.5°N to 38°N). Since juvenile salmon from the Central Valley are known to occupy both these regions (MacFarlane 2010), the mean seasonal MOCI between these regions was used. Low MOCI values represent high marine productivity, and high MOCI values represent low marine productivity.

Daily mean flow at Bend Bridge was averaged over a 14-day window, starting the day of release, for each CWT release group, to represent the mean river travel time from release to Delta entry (as estimated for acoustic tagged hatchery-origin late-fall-run Chinook salmon smolts; Michel et al. 2012). These release-group-specific 14-day mean flows were then averaged per year and weighted to the size of each CWT release group. For the marine environment, the first few months at sea is the most critical survival period of the marine phase of a salmon's life history (Kilduff et al, 2014), specifically during the first spring at sea for Central Valley salmon stocks and mediated through environmental drivers such as upwelling (Wells et al. 2012; Woodson et al. 2013). Therefore, the mean monthly upwelling index across the months of March, April, and May for the year of outmigration were used, as well as the mean of the Northern and Central California spring MOCI.

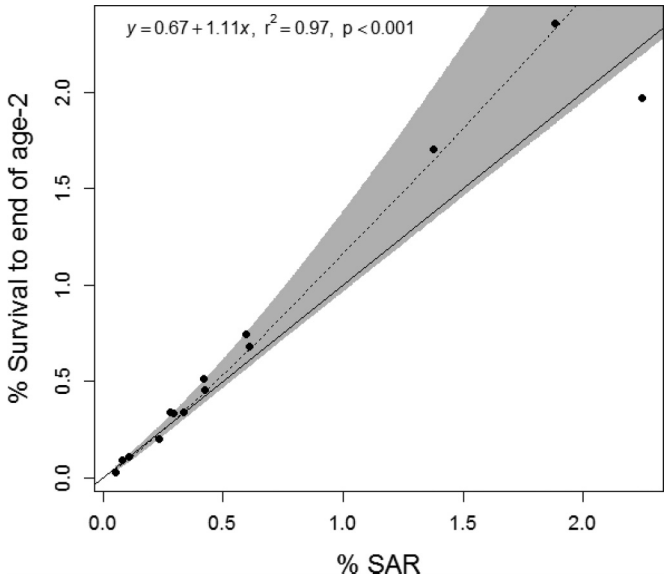
The residuals of the flow linear models were graphically compared with upwelling and MOCI to evaluate if any variability in SAR that was unexplained by flow could be explained by the marine environmental covariates. Two contour plots were generated by interpolating the known SAR values (all three salmon populations combined, to increase resolution) across a grid of flow and either upwelling or MOCI values (using Akima interpolation; Akima 1970), bounded by the limits of the current data set. Because SAR values could be influenced by population-specific life history strategies, annual logit-scale SAR values were standardized within populations (i.e., z score: subtracting the mean and dividing by the standard deviation for each SAR value) and then combined. All analyses were performed using program R (version 3.5.1) along with the "akima" package (Akima and Gebhardt 2016).

Results

Smolt-to-adult estimates

Annual SAR values were estimated for 20 consecutive years for late-fall-run and 14 consecutive years for winter-run and fall-run Chinook. The number of CWTs released per run and per year ranged from 30 451 to 3 128 686. Annual SAR ranged from 0.02% to 3.29% overall, and mean annual SAR for these years were 1.00% (0.1 SE) for late-fall-run Chinook salmon, 0.64% (0.18 SE) for winter-run Chinook salmon, and 0.81% (0.26 SE) for fall-run Chinook salmon (Table 2).

Fig. 3. The relationship between winter-run Chinook salmon SAR values (%) and survival from hatchery release to the end of age 2 (%). The solid black line represents the 1:1 line. The black dotted line represents the linear model between these two variables, and the grey shaded area is the 95% confidence interval around the linear model. The intercept, slope, r^2, and significance of the linear model is provided in the top left corner of the plot frame.



There was a strong positive relationship between the winter-run Chinook salmon SAR values and hatchery release to end of age 2 survival, as estimated by cohort reconstruction (r^2 = 0.95; Fig. 3). Because the two variables are approximately equal under the same conditions (95% confidence intervals of the linear model between these two variables overlap the 1:1 line), SAR was used to represent the combined outmigration and marine survival during the first year at sea.

Outmigration versus marine survival comparison

Overall, outmigration survival ranged from 2.6% to 17%, and marine survival ranged from 4.2% to 22.8% for eight late-fall-run Chinook salmon CWT release groups (or cluster of release groups) from brood years 2007 through 2010 (Fig. 4). For the eight CWT release groups, five were estimated to have higher marine survival than the respective outmigration survival estimate, two groups had the opposite pattern, and one group had approximately equal survival in both periods. SAR estimates were distributed above and below the BY 1993–2012 long-term median SAR (0.81%; represented by the black dashed line in Fig. 4), suggesting that these release groups experienced overall survival that was roughly representative of the larger pool of CWT release group SAR estimates.

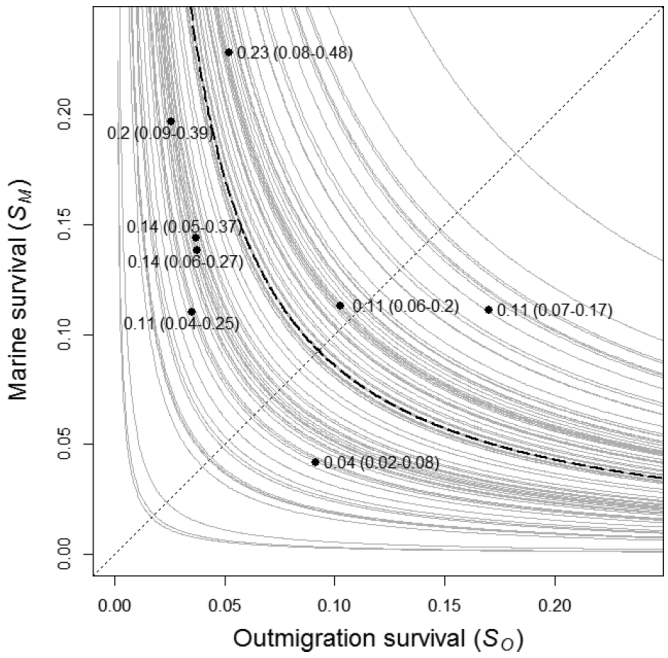
Freshwater outmigration survival versus SAR

Freshwater survival had a strong positive relationship with overall SAR for these same eight CWT release group clusters (r^2 = 0.62; Fig. 5), indicating freshwater outmigration survival was an important factor in overall SAR for those cohorts.

Environmental covariates versus SAR

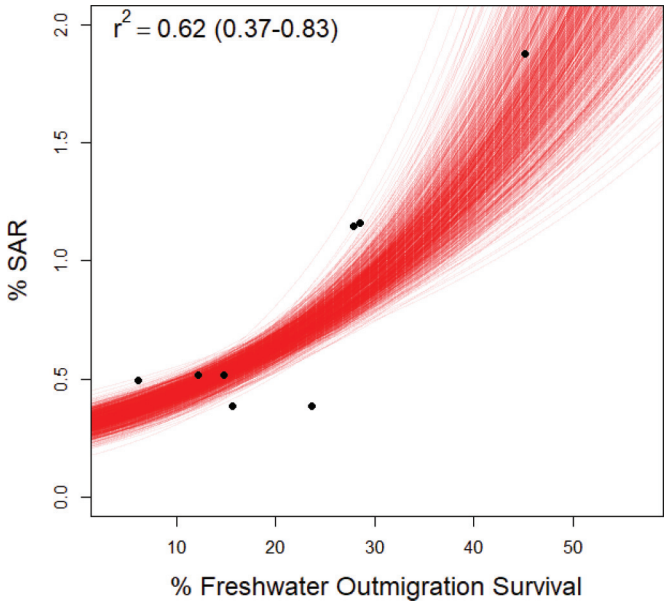
Flow during outmigration was a strong predictor of SAR in all three of the Chinook salmon runs (r^2 = 0.45 for late-fall-run, 0.57 for winter-run, and 0.35 for fall-run Chinook salmon, after removing the extreme outliers identified by Cook's distance), while both upwelling and MOCI during the first spring at sea had little influence over SAR (Fig. 6). All points in all linear models had Cook's distances < 1 with the exception of 20.0 and 1.9 for outmigration year (i.e., brood year + 1; "OY" hereinafter) 2006 in both the fall-run and winter-run Chinook salmon linear models between SAR and flow (red labeled points in Figs. 6*d* and 6*g*). The r^2 of the linear regressions with the outlier included was 0.08 for fall-run and 0.16 for winter-run (linear regressions shown in Figs. 6*d* and 6*g* do not include the OY 2006 year). In both cases, these outliers had lower SAR than what would be predicted by flow during outmigration given the remainder of the data sets.

Fig. 4. The range of possible relationships between outmigration survival and marine survival given known CWT release group SAR values for late-fall-run Chinook salmon. Each grey line represents the SAR value for a specific CWT release group, and the point along each line that represents the actual outmigration and marine survival for each release group is unknown, with the exception of the years for which acoustic tagging data outmigration survival estimates existed (black points, respective marine survival estimates with bootstrapped 95% confidence intervals represented alongside). The black dashed line represents the median SAR for all CWT release groups. The black dotted line represents the location where outmigration and marine survival are equal (i.e., 1:1 line); if a point falls above this line, marine survival was higher than outmigration survival.



The residuals from the three flow regressions were plotted against spring upwelling index and spring MOCI. For fall-run and winter-run Chinook salmon OY 2006, the residual was predicted based on the linear regression that was fitted to the data set that did not include OY 2006 (due to having a Cook's distance > 1). Model performance was poorest in predicting annual SAR in years with some of the lowest upwelling and MOCI indices (Fig. 7). Specifically, for late-fall-run Chinook salmon, model performance was poor in OYs 1998 and 2005, years with the lowest spring upwelling indices and the highest MOCI indices (i.e., low productivity) from the 20-year time series. For winter-run Chinook salmon, the flow model performed poorly in explaining the low SAR that occurred for salmon outmigrating during OY 2005 and 2006; these same years also had the first and third lowest spring upwelling index values and the highest MOCI index values for the 14-year time series. For fall-run Chinook salmon, the model poorly explained the low SAR for outmigrating salmon in OY 2006, the year with the third lowest spring upwelling index and the second highest MOCI index for the 14-year time series.

Fig. 5. The relationship between freshwater outmigration survival (i.e., release to Chipps Island) for acoustic-tagged late-fall-run Chinook salmon release groups and their associated SAR (%). The red lines represents 1000 linear models between 1000 parametric bootstrapped samples of these two variables, with the mean r^2 (and bootstrapped 95% confidence intervals) of these models represented in the top left corner. [Colour online.]



For all three runs, flow was the primary driver of year-to-year variation in SAR for the variables tested (Fig. 6), with marine productivity only playing a major role in annual dynamics when productivity was at low levels (Fig. 7). High SAR values tended to only occur when flow was higher than average and productivity was not near abnormally low levels (Fig. 8). The OY 2014–2017 cohorts (for which SAR values are not yet available) are predicted to have poor SAR based on the trends seen in the existing data with the exception of the OY 2015 late-fall Chinook salmon and all three runs in OY 2017 as predicted by the upwelling contour plot (Fig. 8). The MOCI contour plot has all three runs in OY 2017 falling outside the bounds of the contour plot.

Discussion

This study indicates that outmigration survival, and the conditions that affect it, are the primary drivers of SAR dynamics, and marine survival likely plays a critical role only in years with abnormally unfavorable marine conditions for salmon. Lindley et al. (2009) also suggested that ocean conditions can have infrequent and yet drastic effects on salmon cohorts, while the long-term, steady degradation of the freshwater environment likely plays a larger role in population health of Central Valley Chinook salmon populations. In a sense, these populations are extremely stressed due to the degraded freshwater environment, and cumulative to this, poor marine conditions can then result in extremely low survival rates.

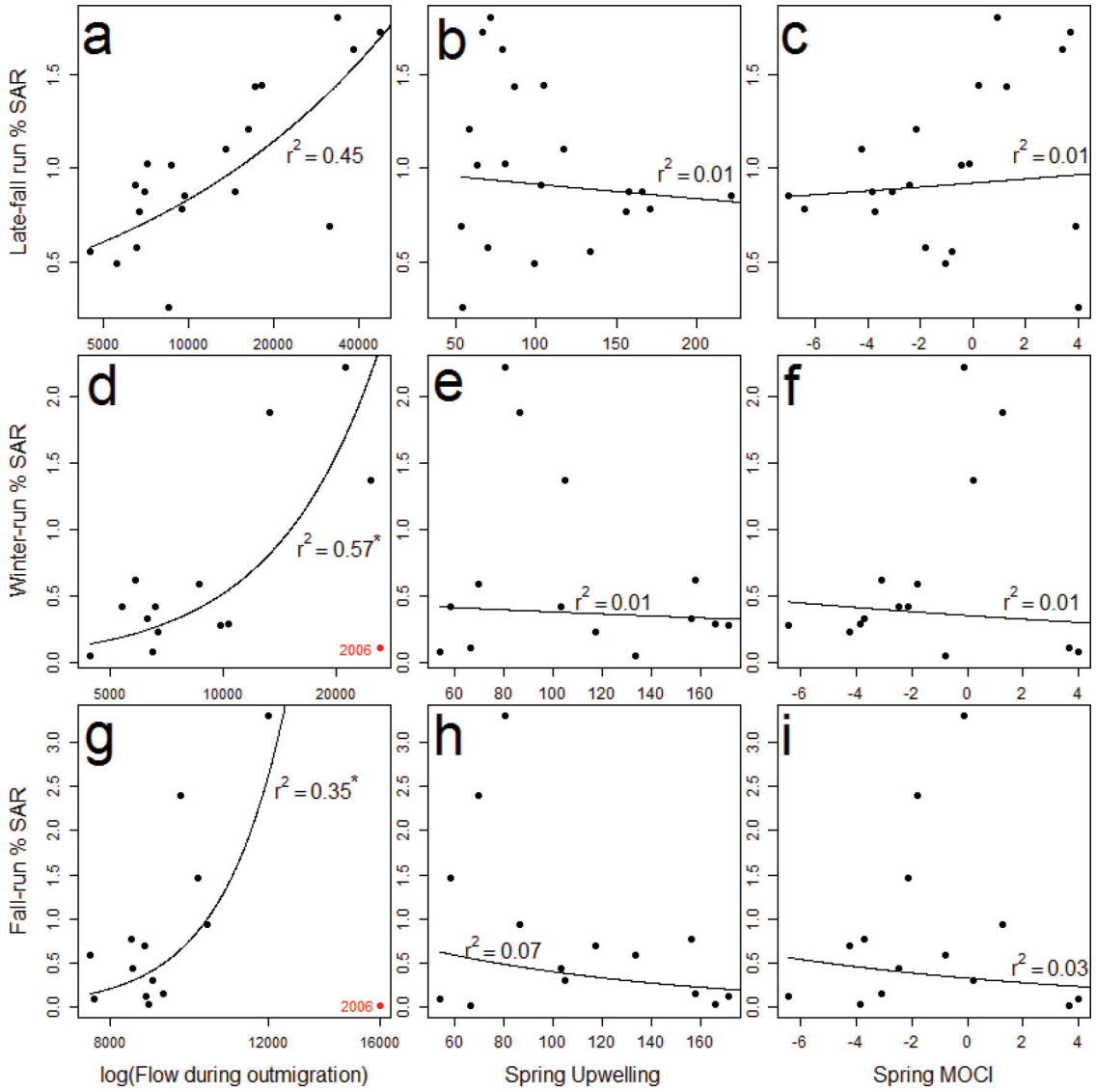
This study used a novel combination of short-term acoustic tagging data paired with long-term CWT recovery data to estimate marine survival rates for California Chinook salmon populations. The results indicated that marine survival for California Chinook salmon populations is similar in scale to outmigration survival. Given that these marine survival estimates are confounded with return river survival, net marine survival is likely higher than outmigration survival in most years. Two studies have found exceptionally low outmigration survival rates for California Central Valley Chinook salmon stocks compared with other large west coast rivers (Buchanan et al. 2013; Michel et al. 2015). Given these low outmigration survival rates, it would be mathematically impossible for these fished populations to be sustainable if marine survival was much lower than outmigration survival and hatchery propagation did not exist (Michel et al. 2015). Indeed, the average annual SAR estimates in this study were below 1% for all three populations; for Upper Columbia River and Snake River Chinook salmon populations, the Columbia River Basin Fish and Wildlife Program suggests that a minimum of 2% SAR is required for population survival and 4% for population recovery (NPCC 2009). This study is an additional line of evidence suggesting that for California Central Valley Chinook salmon populations, the risks of outmigration may now be too high and these populations are likely no longer sustainable.

The idea that the contribution of marine survival to cohort success has been overestimated over the past decades of salmon research is an emerging concept and is not unique to California or Chinook salmon. It has been suggested for Atlantic salmon (*Salmo salar*) in the Bay of Fundy, Canada (Lacroix 2008), for steelhead (*Oncorhynchus mykiss*) in the Cheakamus River, British Columbia (Melnychuk et al. 2014), and for sockeye salmon (*Oncorhynchus nerka*) in the Fraser River, British Columbia (Clark et al. 2016). The emergence of this concept is fundamentally linked to the advent of acoustic tags small enough for tagging juvenile salmon, because accurate estimates of outmigration survival before acoustic tags was difficult if not impossible. Without an estimate of outmigration survival, outmigration survival and marine survival cannot be parsed, which may lead researchers to believe that marine survival was driving population declines. Potential factors leading to this misconception include the fact that less is known about marine survival dynamics, marine residency is substantially longer in duration than the outmigration period, and recruitment is set during early marine residence for many strictly marine fishes, and this concept was transferred to salmon. Managers and biologists should ensure that salmon life cycle and forecast models incorporate some index of outmigration survival.

Streamflow during outmigration was found to have a large influence on SAR dynamics. Over 35% of all variability in annual SAR dynamics can be explained by flow during outmigration for three different Chinook salmon populations (after removal of an extreme outlier). Flow has been found by numerous studies to have strong influences on outmigration survival of salmon populations worldwide, including Central Valley Chinook salmon populations (Kjelson and Brandes 1989; Zeug et al. 2014). Increases in flow usually cause or are coincident with changes in many other river conditions that are beneficial to the survival of outmigrating salmon, such as increased water velocities (Hogasen 1998), decreased water temperatures (Smith et al. 2003), increased turbidity (Gregory and Levings 1998), and increases in habitat area that reduce exposure to predators and increase growth opportunities (Sommer et al. 2001). Among existing studies, this is one of only a few studies have demonstrated that flow can ultimately have a strong influence on overall cohort success in the Central Valley (Sturrock et al. 2015; Wells et al. 2017).

These results demonstrate that marine survival is also a major contributor to overall cohort strength. While the indices used for marine productivity in this analysis did not show strong relationships with SAR, this is not evidence of a lack of influence of marine survival on SAR variability, as they cannot capture all the relevant factors (e.g., abundance of predators, alternative prey, etc.). Moreover, the magnitude of marine survival was found to be as large a contributor to SAR as outmigration survival. Furthermore, three of the study years showed evidence of poor marine productivity leading to low SAR, all of which were corroborated with existing literature. The first of these 3 years, 1998, was a record El Nino – Southern Oscillation (ENSO) event with drastic effects on the California marine ecosystem (Lynn et al. 1998), which likely had a strong negative impact on marine survival of

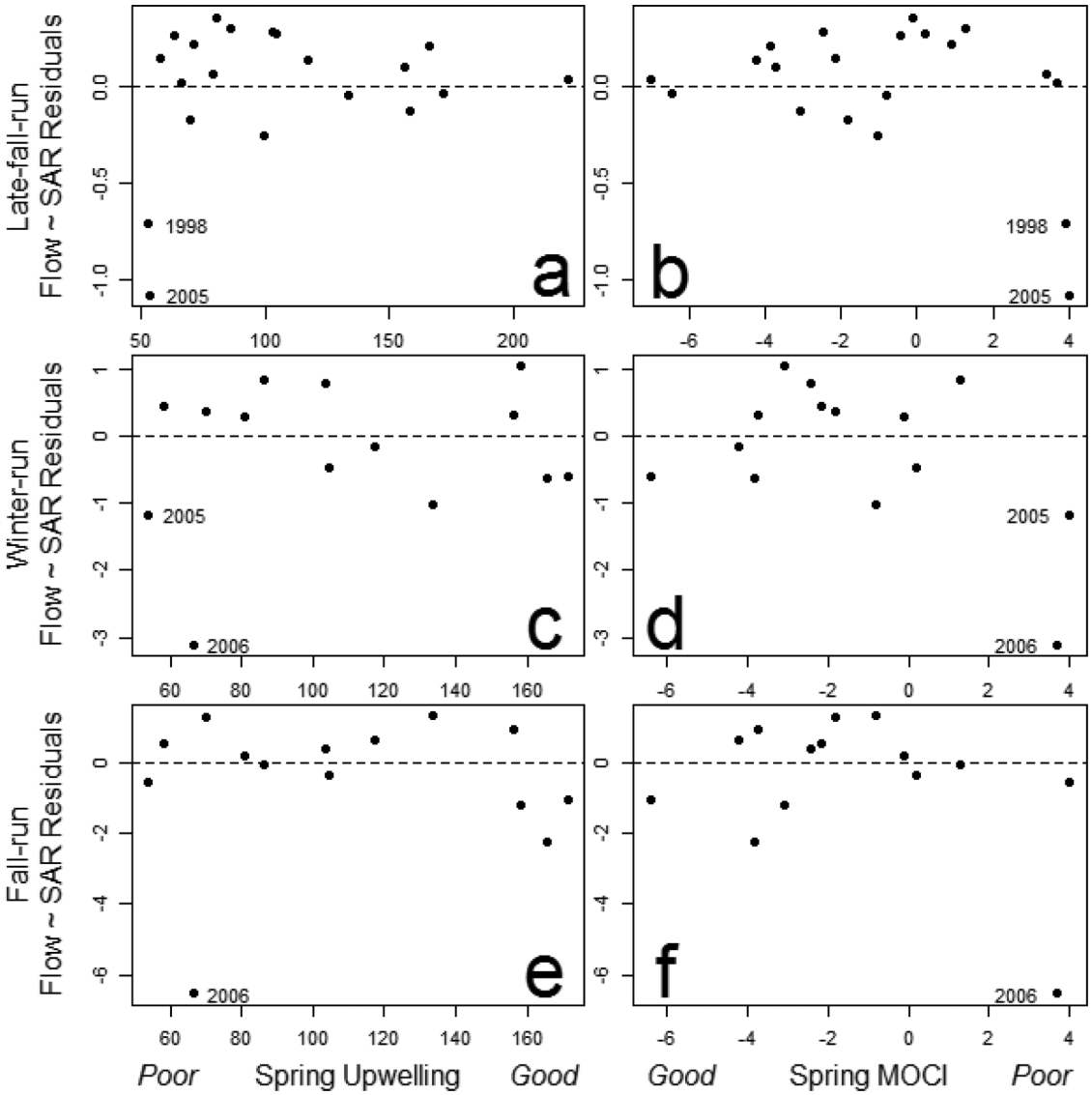
Fig. 6. The relationship between annual SAR and (1) flow during outmigration (*a*, *d*, *g*), (2) upwelling during the first spring at sea (*b*, *e*, *h*), and (3) Multivariate Ocean Climate Indicator (MOCI) during the first spring at sea (*c*, *f*, *i*), for late-fall-run Chinook salmon (*a*, *b*, *c*), winter-run Chinook salmon (*d*, *e*, *f*), and fall-run Chinook salmon (*g*, *h*, *i*). The solid lines in all panels represent the linear model for that relationship, as well as the r^2 value. Note that the r^2 values in plots *d* and *g* did not include the OY 2006 because it was determined to be an outlier (data point represented in red). [Colour online.]



salmon (Pearcy and Schoener 1987; Johnson 1988). In 2005, during the well-documented delayed spring upwelling and resulting poor productivity of the northern California Current (Schwing et al. 2006; Barth et al. 2007), there was evidence of strong size and growth-rate selective early-marine mortality of Central Valley Chinook salmon (Woodson et al. 2013). In 2006, spring upwelling was similarly delayed as in 2005, especially off the coast of Central California where juvenile Central Valley Chinook salmon first recruit to after leaving the San Francisco Bay, leading to a similar situation of poor productivity (Lindley et al. 2009 and references therein). It is widely accepted that the poor early-marine survival of Central Valley fall-run Chinook salmon in the springs of 2005 and 2006 were the proximate causes of the collapse of that stock and the temporary closure of the fishery (Lindley et al. 2009), and in this analysis, the otherwise strong positive relationship between flow and SAR for fall-run and winter-run Chinook salmon was likely overshadowed by abnormally poor early-marine survival in OY 2006, as demonstrated by the high Cook's distances of those points.

These results also provide insights into how river and marine conditions might have varied influences on different salmon populations. High flows during outmigration benefited all three populations, despite the juveniles leaving at different sizes and at different times of the year. However, marine productivity seems to have affected the different runs differently in some years. For example, the late-fall-run Chinook salmon did not experience the OY 2006 crash, while the winter-run and fall-run did, despite all three benefitting from relatively high flows during outmigration. This could be due to the late-fall-run's predisposition to a larger size at ocean entry, especially if size-selective mortality is at play (which is often seen during poor ocean conditions; Holtby et al. 1990; Saloniemi et al. 2004; Woodson et al. 2013). Lindley et al. (2009) reported on this discrepancy between the fall-run and late-fall-run Chinook salmon in those years: "Curiously, Sacramento River late-fall-run Chinook salmon escapement has declined only modestly since 2002, while the [Sacramento River fall-run] in the same river basin fell to record low levels." This is strong support for the concept of allowing Central Valley salmon to exhibit many

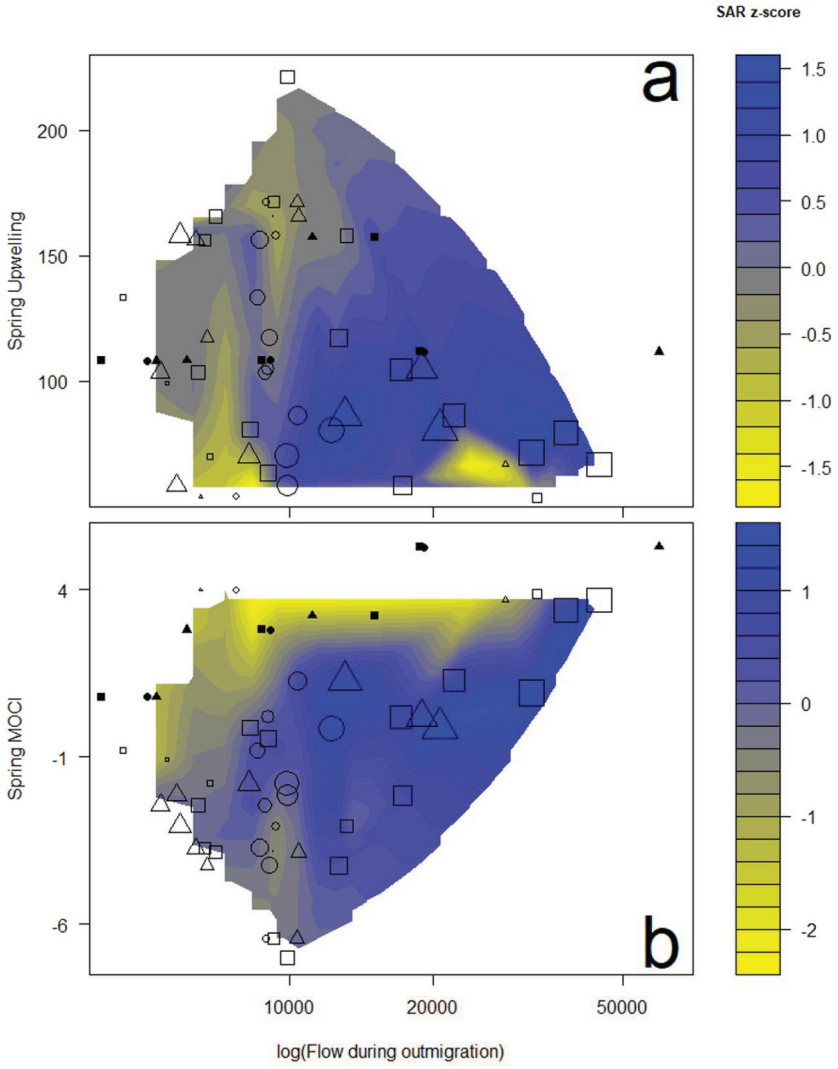
Fig. 7. The relationship between the residuals from the flow versus SAR linear model and spring upwelling during the first spring at sea (*a*, *c*, *e*) and between the residuals from the flow versus SAR linear model and spring MOCI during the first spring at sea (*b*, *d*, *f*). The dotted lines in all panels represent the zero line for residuals. The points with the largest negative residual values have been labeled with their year of ocean entry. The closer points fall to the zero line, the better they were predicted by the flow model. The three different runs of Chinook salmon are represented: late-fall-run (*a*, *b*); winter-run (*c*, *d*); and fall-run (*e*, *f*).



life history strategies and thereby diversifying the Central Valley salmon's portfolio and increasing population stability (Schindler et al. 2010; Carlson and Satterthwaite 2011).

As with many large-scale correlative survival studies, there are noteworthy caveats. Firstly, the survival estimates used in this analysis are for hatchery-origin fish only. While the trends discovered in this analysis likely effect wild populations similarly, empirical estimates of SAR for wild Central Valley Chinook salmon do not currently exist. Secondly, the effects of acoustic tagging on juvenile salmon can bias survival estimates low, through mortality related to the tag or surgery, mortality due to behavioral changes, or tag shedding. A subset of the fish used to generate the acoustic tag survival estimates used here from Michel et al. (2015) were also submitted to a laboratory tag effects study. In that study, no fish shed their tags over 160 days (exceeding the maximum outmigration time), and tagged fish growth and survival was not significantly different from that of untagged fish (Ammann et al. 2013). However, no tests were conducted to address mortality related to behavioral changes, and therefore it is conceivable that outmigration survival estimates used in this study were biased low. Thirdly, the strong relationship between flow during outmigration and SAR may be mediated in some part through marine survival. Climatic dynamics that led to increases or decreases in precipitation over the inland portions of the salmon's range may have also influenced marine conditions in a manner not captured by the marine productivity indices, but had an influence on SAR nonetheless. A similar scenario was demonstrated by Lawson et al. (2004) with coho salmon (*Oncorhynchus kisutch*) populations in the Pacific Northwest. One potential avenue for a post hoc investigation of this concept would be to look for correlation between flow during outmigration and the marine productivity indices. Using the combined data sets, the r^2 for a linear model between flow during outmigration and spring upwelling was 0.07 and was 0.19 between flow and spring MOCI, showing some evidence of relationships between these freshwater and marine indices. These relationships are likely driven by the trend that years with extremely high flows typically have low spring productivity (see conspicuous lack of points in upper-right quadrant of Fig. 8*a* and

Fig. 8. The influence of flow during outmigration and spring upwelling during the first year at sea on SAR (*a*) and flow during outmigration and spring MOCI during the first year at sea on SAR (*b*). Logit-scale SAR values have been standardized; yellow colours represent low SAR values, and blue colours represent high SAR values. Empty symbols represent the location of actual data that were interpolated across; size of these symbols increases proportionally with standardized SAR values. Solid black symbols represent conditions experienced by cohorts for which SAR values are not yet available, spanning OY 2014–2017. Squares represent late-fall-run Chinook salmon, circles are for fall-run Chinook salmon, and triangles are for winter-run Chinook salmon (no point exists for OY 2015 fall-run because no Coleman National Fish Hatchery salmon were released in the river that year). [Colour online.]



lower-right quadrant of Fig. 8*b*). This phenomenon may be in part explained by the effects of ENSO, which often manifests itself in California with heavy precipitation and low productivity of coastal waters (Schonher and Nicholson 1989; Jacox et al. 2015). In the 1 year that contradicted this trend in this data set, OY 2005, when flow during outmigration and ocean productivity were both extremely low, SAR values were at their lowest levels (lowest for late-fall-run, second lowest for winter-run, and third lowest for fall-run). For salmon, it is perhaps a fortunate climatic concurrence that low marine productivity seems to be frequently associated with high outmigration flows in California.

The management implications of this study are important; while we do not have the luxury of mitigation actions when it comes to marine conditions, we have some control over conditions in the freshwater environment, and therefore potentially control over 35% of the annual variability in salmon population abundances, and thus can somewhat buffer these populations from the negative effects of poor marine conditions. Managers should explore approaches to increase river flow and other associated beneficial river conditions during the outmigration season of Central Valley Chinook salmon populations.

Acknowledgements

I thank A. Osterback and S. Hayes for thoughtful discussions that led to the genesis of this study. I also thank B. Wells and N. Mantua for further discussions that led to a refinement of the manuscript. I am indebted to A. Ammann, who was instrumental in developing the different acoustic tag studies that have allowed this analysis. The Red Bluff USFWS office, in particular K. Offill, R. Null, and K. Niemela, provided additional data where the RMIS database was lacking. Finally, I thank E. Danner, S. Lindley, M. O'Farrell, W. Satterthwaite, and the anonymous reviewers for insightful reviews of the manuscript. Support for this project was provided by the National Marine Fisheries Service – Southwest Fisheries Science Center. Funding for the project that generated acoustic tag survival estimates (as part of Michel et al. (2015)) was provided by a CALFED Bay Delta program grant, project U-05-SC-047.

References

Akima, H. 1970. A new method of interpolation and smooth curve fitting based on local procedures. J. Assoc. Comput. Mach. **17**: 589–602. doi:10.1145/321607.321609.

Akima, H., and Gebhardt, A. 2016. akima: interpolation of irregularly and regularly spaced data. R package version 0.6-2 [online]. Available from https://CRAN.R-project.org/package=akima.

Ammann, A.J., Michel, C.J., and MacFarlane, R.B. 2013. The effects of surgically implanted acoustic transmitters on laboratory growth, survival and tag retention in hatchery yearling Chinook salmon. Environ. Biol. Fishes, **96**: 135–143. doi:10.1007/s10641-011-9941-9.

Baker, P.F., Speed, T.P., and Ligon, F.K. 1995. Estimating the influence of temperature on the survival of chinook salmon smolts (*Oncorhynchus tshawytscha*) migrating through the Sacramento – San Joaquin River Delta of California. Can. J. Fish. Aquat. Sci. **52**(4): 855–863. doi:10.1139/f95-085.

Barth, J.A., Menge, B.A., Lubchenco, J., Chan, F., Bane, J.M., Kirincich, A.R., McManus, M.A., Nielsen, K.J., Pierce, S.D., and Washburn, L. 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. Proc. Natl. Acad. Sci. **104**: 3719–3724. doi:10.1073/pnas.0700462104. PMID:17360419.

Buchanan, R.A., Skalski, J.R., Brandes, P.L., and Fuller, A. 2013. Route use and survival of juvenile chinook salmon through the San Joaquin River Delta. N. Am. J. Fish. Manage. **33**: 216–229. doi:10.1080/02755947.2012.728178.

Buer, K., Forwalter, D., Kissel, M., and Stohler, B. 1989. The Middle Sacramento River: Human impacts on physical and ecological processes along a meandering river. USDA Forest Service General Technical Report.

Carlson, S.M., and Satterthwaite, W.H. 2011. Weakened portfolio effect in a collapsed salmon population complex. Can. J. Fish. Aquat. Sci. **68**(9): 1579–1589. doi:10.1139/f2011-084.

Clark, T.D., Furey, N.B., Rechisky, E.L., Gale, M.K., Jeffries, K.M., Porter, A.D., Casselman, M.T., Lotto, A.G., Patterson, D.A., Cooke, S.J., Farrell, A.P., Welch, D.W., and Hinch, S.G. 2016. Tracking wild sockeye salmon smolts to the ocean reveals distinct regions of nocturnal movement and high mortality. Ecol. Appl. **26**: 959–978. doi:10.1890/15-0632. PMID:27509741.

Cook, R.D. 1977. Detection of influential observation in linear regression. Technometrics, **19**: 15–18. doi:10.1080/00401706.1977.10489493.

Garcia-Reyes, M., and Sydeman, W.J. 2017. California Multivariate Ocean Climate Indicator (MOCI) and marine ecosystem dynamics. Ecol. Indic. **72**: 521–529. doi:10.1016/j.ecolind.2016.08.045.

Gregory, R.S., and Levings, C.D. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Trans. Am. Fish. Soc. **127**: 275–285. doi:10.1577/1548-8659(1998)127<0275:TRPOMJ>2.0.CO;2.

Gross, M.R., Coleman, R.M., and McDowall, R.M. 1988. Aquatic productivity and the evolution of diadromous fish migration. Science, **239**: 1291–1293. doi:10.1126/science.239.4845.1291. PMID:17833216.

Grossman, G.D. 2016. Predation on fishes in the Sacramento–San Joaquin Delta: current knowledge and future directions. San Francisco Estuary and Watershed Science 14.

Hogasen, H.R. 1998. Physiological changes associated with the diadromous migration of salmonids. Can. Spec. Publ. Fish. Aquat. Sci. **127**: i–viii, 1–128.

Holtby, L.B., Andersen, B.C., and Kadowaki, R.K. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **47**(11): 2181–2194. doi:10.1139/f90-243.

Iglesias, I.S., Henderson, M.A., Michel, C.J., Ammann, A.J., and Huff, D.D. 2017. Chinook salmon smolt mortality zones and the influence of environmental factors on out-migration success in the Sacramento River Basin. NOAA–National Marine Fisheries Service Report prepared for United States Fish and Wildlife Service.

Jacox, M.G., Fiechter, J., Moore, A.M., and Edwards, C.A. 2015. ENSO and the California Current coastal upwelling response. J. Geophys. Res. Oceans, **120**: 1691–1702. doi:10.1002/2014JC010650.

Johnson, S.L. 1988. The effects of the 1983 El Niño on Oregon's coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon. Fish. Res. **6**: 105–123. doi:10.1016/0165-7836(88)90031-8.

Kilduff, D.P., Botsford, L.W., and Teo, S.L.H. 2014. Spatial and temporal covariability in early ocean survival of Chinook salmon (*Oncorhynchus tshawytscha*) along the west coast of North America. ICES J. Mar. Sci. **71**(7): 1671–1682. doi:10.1093/icesjms/fsu031.

Kjelson, M.A., and Brandes, P.L. 1989. The use of smolt survival estimates to quantify the effects of habitat changes on salmonid stocks in the Sacramento-San Joaquin River, California. *In* Proceedings of the National Workshop on the Effects of Habitat Alteration on Salmonid Stocks. *Edited by* C.D. Levings, L.B. Holtby, and M.A. Henderson. Canadian Special Publication of Fisheries and Aquatic Sciences. pp. 100–115.

Kope, R.G., and Botsford, L.W. 1990. Determination of factors affecting recruitment of chinook salmon *Oncorhynchus tshawytscha* in central California. Fish. Bull. **88**: 257–269.

Koslow, J.A., Hobday, A.J., and Boehlert, G.W. 2002. Climate variability and marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon production area. Fish. Oceanogr. **11**: 65–77. doi:10.1046/j.1365-2419.2002.00187.x.

Lacroix, G.L. 2008. Influence of origin on migration and survival of Atlantic salmon (*Salmo salar*) in the Bay of Fundy, Canada. Can. J. Fish. Aquat. Sci. **65**(9): 2063–2079. doi:10.1139/F08-119.

Lawson, P.W., Logerwell, E.A., Mantua, N.J., Francis, R.C., and Agostini, V.N. 2004. Environmental factors influencing freshwater survival and smolt production in Pacific Northwest coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **61**(3): 360–373. doi:10.1139/f04-003.

Lindley, S.T., Grimes, C.B., Mohr, M.S., Peterson, W., Stein, J., Anderson, J.T., Botsford, L.W., Bottom, D.L., Busack, C.A., Collier, T.K., Ferguson, J., Garza, J.C., Grover, A.M., Hankin, D.G., Kope, R.G., Lawson, P.W., Low, A., MacFarlane, R.B., Moore, K., Palmer-Zwahlen, M., Schwing, F.B., Smith, J., Tracy, C., Webb, R., Wells, B.K., and Williams, T.H. 2009. What caused the Sacramento River fall Chinook stock collapse? NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-447.

Logerwell, E.A., Mantua, N., Lawson, P.W., Francis, R.C., and Agostini, V.N. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fish. Oceanogr. **12**: 554–568. doi:10.1046/j.1365-2419.2003.00238.x.

Lynn, R.J., Baumgartner, T., Garcia, J., Collins, C.A., Hayward, T.L., Hyrenback, K.D., Mantyla, A.W., Murphree, T., Shankle, A., Schwing, F.B., Sakuma, K.M., and Tegner, M.J. 1998. The state of the California Current, 1997–1998: transition to El Nino conditions. California Cooperative Oceanic Fisheries Investigations Report 39.

MacFarlane, R.B. 2010. Energy dynamics and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from the Central Valley of California during the estuarine phase and first ocean year. Can. J. Fish. Aquat. Sci. **67**(10): 1549–1565. doi:10.1139/F10-080.

Magnusson, A., and Hilborn, R. 2003. Estuarine influence on survival rates of Coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific coast. Estuaries, **26**: 1094–1103. doi:10.1007/BF02803366.

Melnychuk, M.C., Korman, J., Hausch, S., Welch, D.W., McCubbing, D.J.F., and Walters, C.J. 2014. Marine survival difference between wild and hatchery-reared steelhead trout determined during early downstream migration. Can. J. Fish. Aquat. Sci. **71**(6): 831–846. doi:10.1139/cjfas-2013-0165.

Michel, C.J., Ammann, A.J., Chapman, E.D., Sandstrom, P.T., Fish, H.E., Thomas, M.J., Singer, G.P., Lindley, S.T., Klimley, A.P., and Macfarlane, R.B. 2012. The effects of environmental factors on the migratory movement patterns of Sacramento River yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*). Environ. Biol. Fishes, **96**: 257–271. doi:10.1007/s10641-012-9990-8.

Michel, C.J., Ammann, A.J., Lindley, S.T., Sandstrom, P.T., Chapman, E.D., Thomas, M.J., Singer, G.P., Klimley, A.P., and MacFarlane, R.B. 2015. Chinook salmon outmigration survival in wet and dry years in California's Sacramento River. Can. J. Fish. Aquat. Sci. **72**(11): 1749–1759. doi:10.1139/cjfas-2014-0528.

Newman, K.B., and Rice, J. 2002. Modeling the survival of chinook salmon smolts outmigrating through the Lower Sacramento River System. J. Am. Stat. Assoc. **97**: 983–993. doi:10.1198/016214502388618771.

NPCC. 2009. Columbia River Basin Fish and Wildlife Program. Council Document 2009 — Appendix E: Subbasin Measures [online]. Northwest Power and Conservation Council. Available from https://www.nwcouncil.org/fw/program/program-2009-amendments.

O'Farrell, M.R., Mohr, M.S., Grover, A.M., and Satterthwaite, W.H. 2012. Sacramento River winter Chinook cohort reconstruction: analysis of ocean fishery impacts. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-491.

Palmer-Zwahlen, M., and Kormos, B. 2015. Recovery of Coded-Wire Tags from Chinook Salmon in California's Central Valley Escapement, Inland Harvest, and Ocean Harvest in 2012. California Dept. of Fish and Wildlife — Fisheries Administrative Report 2015-04.

Pearcy, W.G., and Schoener, A. 1987. Changes in the marine biota coincident with the 1982–1983 El Niño in the northeastern Subarctic Pacific Ocean. J. Geophys. Res. Oceans, **92**: 14417–14428. doi:10.1029/JC092iC13p14417.

Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. 1st ed. University of Washington Press, Seattle.

Saloniemi, I., Jokikokko, E., Kallio-Nyberg, I., Jutila, E., and Pasanen, P. 2004. Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. ICES J. Mar. Sci. **61**: 782–787. doi:10.1016/j.icesjms.2004.03.032.

Scheuerell, M.D., and Williams, J.G. 2005. Forecasting climate-induced changes in the survival of Snake River spring/summer Chinook salmon (*Oncorhynchus tshawytscha*). Fish. Oceanogr. **14**: 448–457. doi:10.1111/j.1365-2419.2005.00346.x.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. Nature, **465**: 609–612. doi:10.1038/nature09060. PMID:20520713.

Schonher, T., and Nicholson, S.E. 1989. The relationship between California rainfall and ENSO events. J. Clim. **2**: 1258–1269. doi:10.1175/1520-0442(1989)002<1258:TRBCRA>2.0.CO;2.

Schwing, F.B., Bond, N.A., Bograd, S.J., Mitchell, T., Alexander, M.A., and Mantua, N. 2006. Delayed coastal upwelling along the U.S. West Coast in 2005: A historical perspective. Geophys. Res. Lett. **33**. doi:10.1029/2006GL026911.

Sharma, R., Velez-Espino, L.A., Wertheimer, A.C., Mantua, N., and Francis, R.C. 2013. Relating spatial and temporal scales of climate and ocean variability to

survival of Pacific Northwest Chinook salmon (*Oncorhynchus tshawytscha*). Fish. Oceanogr. **22**: 14–31. doi:10.1111/fog.12001.

Skalski, J.R., and Townsend, R.L. 2005. Pacific Northwest hatcheries Smolt-to-Adult Ratio (SAR) estimation using Coded Wire Tags (CWT) data. Technical Report to Bonneville Power Administration, Project No. 1991-051-00, Contract No. 00013690.

Smith, S.G., Muir, W.D., Hockersmith, E.E., Zabel, R.W., Graves, R.J., Ross, C.V., Connor, W.P., and Arnsberg, B.D. 2003. Influence of river conditions on survival and travel time of Snake River subyearling fall chinook salmon. N. Am. J. Fish. Manage. **23**: 939–961. doi:10.1577/M02-039.

Sommer, T.R., Nobriga, M.L., Harrell, W.C., Batham, W., and Kimmerer, W.J. 2001. Floodplain rearing of juvenile chinook salmon: evidence of enhanced growth and survival. Can. J. Fish. Aquat. Sci. **58**(2): 325–333. doi:10.1139/f00-245.

Sturrock, A.M., Wikert, J.D., Heyne, T., Mesick, C., Hubbard, A.E., Hinkelman, T.M., Weber, P.K., Whitman, G.E., Glessner, J.J., and Johnson, R.C. 2015. Reconstructing the migratory behavior and long-term survivorship of juvenile chinook salmon under contrasting hydrologic regimes. PLoS ONE, **10**: e0122380. doi:10.1371/journal.pone.0122380. PMID:25992556.

Wells, B.K., Santora, J.A., Field, J.C., MacFarlane, R.B., Marinovic, B.B., and Sydeman, W.J. 2012. Population dynamics of Chinook salmon *Oncorhynchus tshawytscha* relative to prey availability in the central California coastal region. Mar. Ecol. Prog. Ser. **457**: 125–137. doi:10.3354/meps09727.

Wells, B.K., Santora, J.A., Schroeder, I.D., Mantua, N., Sydeman, W.J., Huff, D.D., and Field, J.C. 2016. Marine ecosystem perspectives on Chinook salmon recruitment: a synthesis of empirical and modeling studies from a California upwelling system. Mar. Ecol. Prog. Ser. **552**: 271–284. doi:10.3354/meps11757.

Wells, B.K., Santora, J.A., Henderson, M.J., Warzybok, P., Jahncke, J., Bradley, R.W., Huff, D.D., Schroeder, I.D., Nelson, P., Field, J.C., and Ainley, D.G. 2017. Environmental conditions and prey-switching by a seabird predator impact juvenile salmon survival. J. Mar. Syst. **174**: 54–63. doi:10.1016/j.jmarsys.2017.05.008.

Whipple, A.A., Grossinger, R.M., Rankin, D., Stanford, B., and Askevold, R.A. 2012. Sacramento–San Joaquin Delta Historical Ecology Investigation: Exploring Pattern and Process. San Francisco Estuary Institute – Aquatic Science Center, Richmond, Calif.

Woodson, L.E., Wells, B.K., Weber, P.K., MacFarlane, R.B., Whitman, G.E., and Johnson, R.C. 2013. Size, growth, and origin-dependent mortality of juvenile Chinook salmon *Oncorhynchus tshawytscha* during early ocean residence. Mar. Ecol. Prog. Ser. **487**: 163–175. doi:10.3354/meps10353.

Yoshiyama, R.M., Gerstung, E.R., Fisher, F.W., and Moyle, P.B. 2001. Historical and present distribution of chinook salmon in the Central Valley drainage of California. *In* Contributions to the Biology of Central Valley Salmonids. *Edited by* R.L. Brown. California Department of Fish and Game, Sacramento, California. pp. 71–176.

Zeug, S.C., Sellheim, K., Watry, C., Wikert, J.D., and Merz, J. 2014. Response of juvenile Chinook salmon to managed flow: lessons learned from a population at the southern extent of their range in North America. Fish. Manage. Ecol. **21**: 155–168. doi:10.1111/fme.12063.