

RESEARCH

Comparing Fishery Impacts and Maturation Schedules of Hatchery-Origin vs. Natural-Origin Fish from a Threatened Chinook Salmon Stock

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ABSTRACT

Central Valley Spring-run Chinook (CVSC) are listed as threatened under the California and federal Endangered Species Acts, but how ocean fisheries affect CVSC is not routinely monitored or managed, largely because of data limitations. Most tag data for CVSC are from a hatchery program that may not sufficiently represent

natural-origin fish in ocean and inland fishery recovery data. However, a discontinued tagging program for Butte Creek Wild Spring-run Chinook (BCWSC) provides for estimation of fishery impacts and maturation schedules for a limited set of years, which we compared with estimates for hatchery-origin fish for common years, while extending the hatchery-origin estimates over a wider time-frame. Additional scale-age data from BCWSC allow inferences about more recent maturation rates, conditional on harvest-rate estimates borrowed from other stocks. Overall, CVSC appear to experience low age-3 ocean fishery impact rates, but age-4 impact rates can be comparable to ocean harvest rates estimated for Sacramento River Fall Chinook. Tagging data from the years available indicate that ocean fisheries may reduce spawning run sizes (all ages combined) by 40% to 60% during periods of high fishing effort. Effects of ocean fishing on spawner abundance are weaker in years of reduced fishing or for cohorts displaying earlier maturation. It appears that maturation rates of hatchery-origin CVSC may have increased (i.e., earlier maturation) over the full time-period examined, and there may be indications of increasing maturation rates for BCWSC as well.

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INTRODUCTION

Central Valley Spring-run Chinook (CVSC) salmon occupy the southernmost extent of the native range for *Oncorhynchus tshawytscha* (Healey 1991). Historically, CVSC spawned in the upper headwaters in nearly all streams of the California Central Valley from which natural barriers to migration were absent, with total run sizes that were likely in the hundreds of thousands (Yoshiyama et al. 1998). However, mining activities and construction of impassable dams have eliminated access to about 80% of historical CVSC spawning habitat (Yoshiyama et al. 2001), and the remaining populations have faced or continue to face ongoing negative effects from harvest, habitat degradation, and reduction in genetic integrity (CDFG 1998; Yoshiyama et al. 1998; NMFS 2014).

Population declines and ongoing stresses led to CVSC being listed as threatened under both the California and federal Endangered Species Acts in 1999 (NMFS 2000). Extensive background on CVSC is available in the relevant status-review documents (CDFG 1998; Myers et al. 1998; NMFS 2000, 2011, 2014; Johnson and Lindley 2016), and elsewhere (e.g., CDFG 2004). Currently, only CVSC populations on Butte, Mill, and Deer creeks are considered “independent natural” populations, while there are 19 historically recognized CVSC populations (McElhany et al. 2000; Cordoleani et al. 2020), some of which appear to be persisting as sink populations. Of the remaining populations, Butte Creek Wild spring-run Chinook (BCWSC) has the largest spawning population in most years (Cordoleani et al. 2020). Feather River Fish Hatchery (FRH) spring-run Chinook Salmon (FRHSC) are also included in the federally designated CVSC Evolutionarily Significant Unit (ESU; NMFS 2016) although ESUs do not always include hatchery components (PFMC 2022), and FRHSC were not “considered to be essential for its recovery” (NMFS 2000). Historical practices

at FRH led to substantial introgression of fall-run with nominally spring-run fish (Cramer and Demko 1997; Myers et al. 1998), though recent practices have reduced this (NMFS 2016). For the time-period covered by this paper, FRH was the only hatchery that produced CVSC.

A key challenge in successfully managing and recovering CVSC is understanding the population consequences of fisheries in the broader context of factors that operate throughout the life cycle. Cordoleani et al. (2020) attempted to develop a life-cycle model for CVSC to better understand the effects of natural variability and human activities throughout the CVSC life cycle, but concluded that sufficient data to reliably parameterize the model did not exist. Among the data needs Cordoleani et al. (2020) highlighted were better understanding of ocean fishery impacts and the maturation schedules of CVSC, especially natural-origin fish. Maturation schedules are key to understanding fishery effects both because they affect the cumulative amount of time CVSC are exposed to ocean fisheries, and because the current framework for indirectly managing fishery effects on CVSC depends on active management measures for Sacramento River winter-run Chinook (SRWC), which have a very high age-3 maturation rate (O’Farrell et al. 2012a, Chen et al. 2023) and are protected, in part, by minimum size limits in the fishery that may not similarly protect larger age-4 and older fish (Satterthwaite et al. 2018). Attempts to understand fishing impacts or CVSC maturation schedules have been limited because of the difficulty and cost of aging natural-origin fish, limited tagging of natural-origin fish (e.g., on Butte Creek for brood years 1995–2007, with very limited sample sizes before 1998), and concerns about the representativeness of FRH fish (Satterthwaite et al. 2018). However, the data available in limited years for the BCWSC can provide insight into natural-origin CVSC fishery impacts and maturation schedules, and the representativeness of hatchery fish.

The Biological Opinion and Incidental Take Permit authorizing ocean fishery impacts on CVSC (NMFS 2000) reasoned that constraints on California ocean harvest in the Pacific

Fishery Management Council (PFMC) Salmon Fishery Management Plan (FMP), along with the consultation standard for endangered SRWC, have sufficed to limit harvest effects on CVSC to levels that allowed spawning abundances to increase between 1994 and 2000. Subsequent status reviews have similarly concluded that fishery constraints because of active management of co-occurring stocks have sufficiently protected CVSC (Johnson and Lindley 2016).

In general, ocean harvest opportunity off the coast of California depends on abundance forecasts for Sacramento River fall-run Chinook (SRFC), SRWC, and Klamath River fall-run Chinook (KRFC; PFMC 2022). When forecasted abundances for the respective stocks are low, fishing opportunity is constrained in the times, areas, and fishery sectors where the stocks of concern are most likely to be encountered. Central Valley spring-run Chinook (CVSC) Salmon likely has the most spatial overlap with SRFC and SRWC, and so—to the extent that abundances of the three stocks covary—fishing on CVSC will tend to be restricted when conditions are generally poor for CVSC salmon (Satterthwaite et al. 2018).

However, management of ocean fisheries off the coast of California, and hatchery practices that support the fishery, have changed substantially over time. On the fishery-management side, adoption of “*de minimis*” provisions starting in 2012 allowed some level of fishing on SRFC at low forecasted abundances that previously would have closed fisheries (PFMC 2011), and protections for SRWC have evolved over time as well, shifting from an approach based on recent escapements to one based on forecasted abundance while also modifying the form of the control rule (O’Farrell et al. 2016; SRWC WG 2017).

On the hatchery side, managers of large production hatcheries for SRFC have increasingly turned to trucking hatchery fish downstream to increase their survival in the face of poor river conditions (Sturrock et al. 2019), while hatchery production of SRWC has been increased in years when natural production is expected to be poor

(Meyers 2021). Recently, hatchery managers (for SRFC, SRWC, and FRHSC) have begun recognizing and treating thiamine deficiency in their broodstock (Mantua et al. 2021), which may increase survival of treated fish in some years. While these actions likely increase the abundance of hatchery-origin fish, especially for SRFC and SRWC, they generally do not benefit natural-origin fish still directly exposed to poor river conditions and in most cases not supplemented with thiamine (although FRH does provide some thiamine supplementation to fish taken in at the hatchery during spring that later spawn in natural areas of the Feather River). This raises the concern that fishery management driven by forecasts of hatchery-supplemented SRFC and SRWC abundance may not sufficiently respond to poor conditions for CVSC—especially natural-origin (NMFS 2022)—under recent conditions, or conditions reasonably expected for the future if these practices continue. It therefore becomes important to understand the magnitude of fishery effects on CVSC under a range of conditions, which could inform us about the degree of need to account for CVSC more directly when planning ocean fisheries.

To better understand the potential range of fisheries’ effects on CVSC, we compiled available coded-wire tag (CWT) data for FRHSC and BCWSC to perform cohort reconstructions similar to those performed for SRWC (O’Farrell et al. 2012a) and KRFC (Mohr 2006, unpublished report, see “Note”), and in simplified form for SRFC (O’Farrell et al. 2013). The vast majority of the CWT data (both in terms of years covered, and in tags recovered per year) come from FRHSC. However, FRHSC and BCWSC differ in their within-year return timing (Fisher 1994; Lindley et al. 2004), and they may differ in age structure as well (Grover and Kormos 2009), as has been found for other hatchery–wild comparisons (Hankin and Logan 2010; Chen et al. 2023), with implications for lifetime exposure to fisheries. Although tagging data for BCWSC are not available for more recent years, to make the best use of available information we also analyzed information on the age structure of BCWSC determined from scale analysis of spawners that returned from 2010 to

2016. Taken together, these data allowed us to directly estimate ocean fishery impact rates and maturation rates for both FRHSC and BCWSC for a core set of years, estimate these rates for FRHSC over a wider range of years, and estimate BCWSC maturation rates for some additional years—subject to the assumption that age-specific ocean impact rates on BCWSC covary with impacts on FRHSC or one of the actively managed stocks.

METHODS

Study System

Butte Creek Wild Spring Chinook are the largest natural-origin component of the (CVSC) Evolutionarily Significant Unit (ESU) in most years, and have frequently outnumbered hatchery returns of FRHSC (Azat 2022). Adult fish generally return in the late winter to early spring before holding over the summer and spawning in the fall (Nichols 2022), and in-river fisheries are designed to avoid overlap with this migration.

Juveniles primarily out-migrate the following winter or spring, although some “yearlings” out-migrate the following fall, winter, and spring (Cordoleani et al. 2020). For brood years 1998–2007 (out-migration years 1999–2008), between 16,464 and 400,262 (median 163,992) out-migrating juveniles were captured and marked with adipose fin clips and CWTs. Juveniles were captured using two 8-foot, rotary-screw traps (RSTs) at the Parrott–Phelan Diversion Dam and a fyke trap within the water-diversion canal. All traps were operated as much as possible to maximize the numbers of fish sampled for the CWT program.

Marked and tagged fish were recovered later in systematic surveys of commercial and recreational ocean fisheries, natural spawning areas of Butte Creek (Ward et al. 2003, 2004; McReynolds et al. 2005, 2006, 2007; Garman and McReynolds 2008, 2009), spawning areas elsewhere in the Central Valley, hatcheries, and river fisheries, to the extent they were sufficiently sampled during the relevant return years. Because there were no mark-selective fisheries for Chinook Salmon in California for any of these study years, we assumed equal susceptibility

to fisheries for marked and unmarked fish. Sampling of ocean fisheries aimed to recover CWT from at least 20% of any marked fish landed, as described in O’Farrell et al. (2012a). Coded-wire tags from marked fish on Butte Creek were recovered through a mark–recapture carcass survey conducted weekly through the adult holding period to the end of the spawning season. This mark–recapture survey generated the expansion factor used to convert from the number of tags recovered to the number of tags assumed to have been present in the river but unsampled. Sampling methods for the escapement and river harvest elsewhere in the Central Valley followed a variety of methods. Sampling for—and reporting of—CWT in some parts of the Central Valley was unreliable before the initiation of the constant fractional marking program in out-migration year 2007 (Kormos et al. 2012), but relatively few BCWSC would be expected to stray into poorly sampled areas, and a small number of tags were recovered from elsewhere in the Central Valley (four, compared to 267 from Butte Creek and 119 from ocean fisheries). Although a limited number of BCWSC were tagged in brood years 1995–1997, no more than six tags were recovered from any of these brood years, yielding an insufficient sample size for analysis. The number of tags released each year, along with the numbers of tags recovered, are reported in Appendix A. Note that four tag recoveries excluded for reasons described below in “CWT data acquisition and processing” are not included in the annual totals reported in Appendix A.

Although the tagging program on Butte Creek was discontinued after out-migration year 2008, the California Department of Fish and Wildlife (CDFW) has collected and aged scales from returning BCWSC in most years since 2010 (no scales were collected in 2017). Scales were collected for the duration of the run throughout the entire spawning area to ensure aging assignments reflected any spatial or temporal variation in age structure. Scales were collected from the same location on the fish when possible. Scales were taken from fresh carcasses on the left side of the fish, diagonally down and back from the posterior insertion of the dorsal fin and just

above the lateral line. Each survey collected a minimum of 550 random samples, when possible, although not all scales were read. At the time of writing, we had access to scale ages through return year 2018. The mean annual sample size for BCWSC scales read for 2010–2018 (excluding 2017) was 159 (range 69 to 255).

Feather River Hatchery releases approximately 2 million nominally spring-run Chinook smolts each year for the dual purposes of supplementing harvest and aiding in the conservation and recovery of natural populations (CA HSRG 2012), including reintroduction efforts in the San Joaquin Basin (SJRRP 2017). Maturing FRHSC tend to return later in the year than BCWSC or other natural-origin CVSC (Fisher 1994; Lindley et al. 2004). Tagged fish are recovered in ocean commercial and recreational fisheries, from in-river fisheries (incidentally caught during fisheries targeting Feather River Fall Chinook), in natural spawning areas, and at hatcheries. As noted previously, CWT recovery data for the broader Central Valley may be less reliable before release year 2007, and because FRHSC are released varying distances downstream of the hatchery (CA HSRG 2012), they may be more likely to stray into historically less well-sampled areas (Sturrock et al. 2019). In addition, the COVID-19 epidemic disrupted sampling of ocean fisheries for CWT in early 2020 (PFMC 2021).

Cohort Reconstruction

We used standard cohort reconstruction methods (Mohr 2006, unpublished report, see “Note”; O’Farrell et al. 2012a, Chen et al. 2023) to estimate abundance-at-age, fishery impact rates, maturation rates, and early life survival for brood year 1998–2007 BCWSC and brood year 1998–2015 FRHSC. We started with 1998 because it was the first year of substantial tagging on Butte Creek (<12,000 tags per year were deployed in brood years 1995–1997). We excluded brood year 2016 FRHSC because of the gap in 2020 ocean fishery sampling that would have missed ocean harvest of age-4 fish from that brood and excluded later brood years because they had not had time to return at all relevant age classes in time for the analysis.

Cohort reconstructions (or virtual population analyses; Pope 1972) work backward from the oldest possible age at return (assumed to be age-5 for CVSC) to reconstruct abundance at each age (Figure 1, Appendix B). Full documentation including equations and code to perform cohort reconstructions for all of the data sets analyzed in this paper are available at <https://doi.org/10.17632/b8ys8kd5vz.1>. To summarize, we assume that all fish which would mature in a particular calendar year leave the ocean on the day before a specified “birth date,” meaning any fish still in the ocean on that birth date will not spawn until the next year, at the earliest. Fish in the ocean are assigned an age equal to the age they would be at the time of return. Thus, we estimate ocean abundance at the start of age-5 as the sum of age-5 escapement, age-5 river harvest, and fishing mortality (including non-landed mortality) of age-5 fish in the ocean; along with an accounting for assumed natural mortality. We tracked ocean fishery impacts and natural mortality monthly. We assumed natural mortality rates equivalent to 20% annually (1.8% monthly) for age-5 fish. We estimated non-landed mortalities from observed harvest via a multi-step process described below.

Once we had an estimate of ocean abundance at the start of age-5, we estimated ocean abundance at the start of age-4 as the sum of fish still in the ocean at the start of age-5, fish spawning at age-4, and natural and fishing mortality during age-4. We estimated the age-4 maturation rate as the age-4 escapement divided by age-4 ocean abundance at the time of return, and calculated age-4 ocean impact rates as the sum of age-4 ocean fishing mortalities divided by reconstructed age-4 ocean abundance immediately after age-3 fish leave the ocean (i.e., on the birthdate). Thus, ocean fishery impact rates describe the proportional reduction in ocean abundance of an age class for a particular cohort because of fishing mortality, and maturation rates are the conditional probability that a fish matures at a particular age, given it lived long enough to have the opportunity to return from the ocean at that age. We used similar calculations to reconstruct ocean abundance and demographic rates for age-3 and age-2 and calculated early life

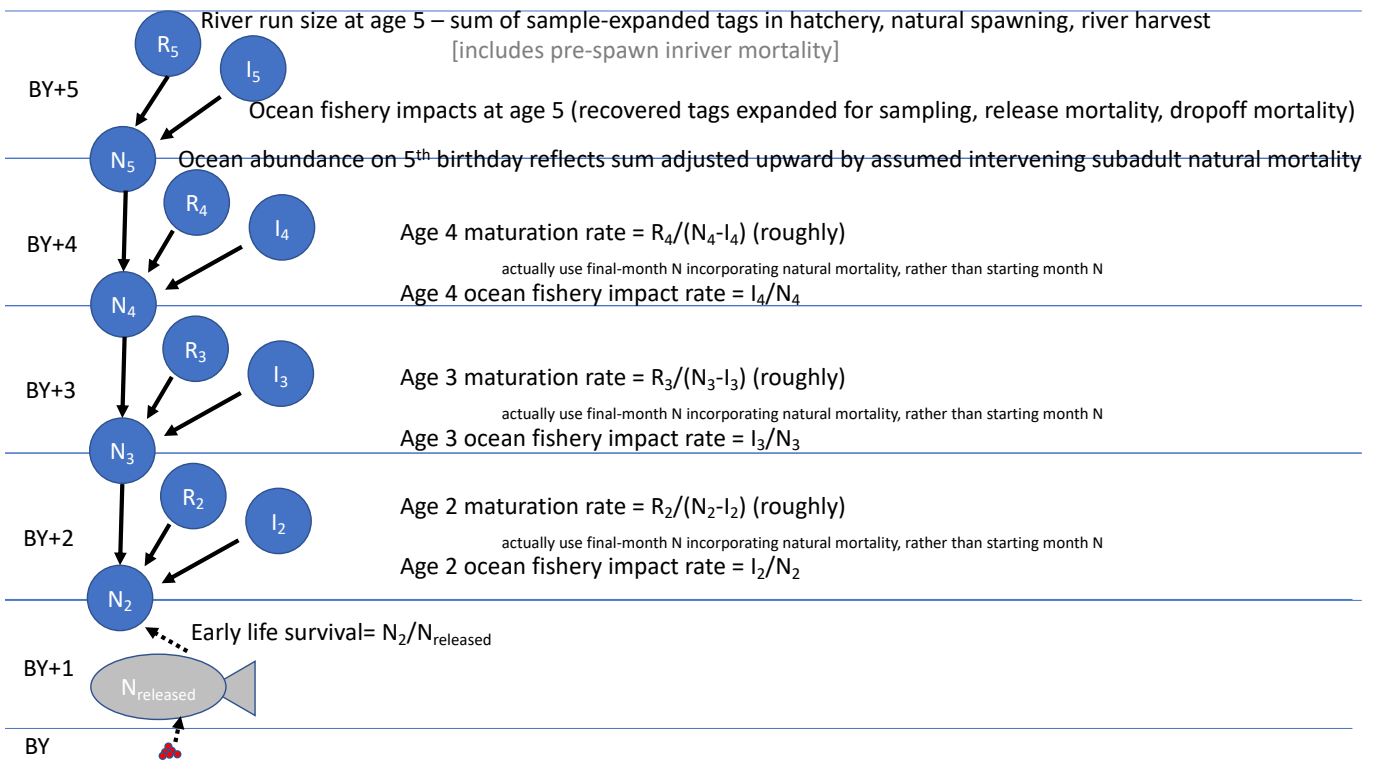


Figure 1 Illustration of the cohort reconstruction process. Assuming a maximum age of 5, we worked backward from estimates of age-5 river run size (R_5) and ocean impacts (I_5)—adjusted upward by assumed intervening natural mortality—to estimate the ocean abundance at the start of ocean age-5 (N_5). We continued to add river run size and ocean impacts at younger ages to reconstruct ocean abundance at younger ages. River run size includes spawners in natural areas and hatcheries, river harvest, and pre-spawn mortality. Ocean impacts include landed harvest, release mortality, and drop-off mortality. For readability, we show annual time-steps in the figure, but ocean impacts and ocean abundance are calculated monthly, and the adjustment for natural mortality depends on the time elapsed between the birth date and the month of ocean impacts.

survival by dividing estimated ocean abundance at the start of age-2 by the number of tagged fish released. Thus, early life survival reflects survival from the time when tagged fish are released to the beginning of ocean age-2. Following assumptions for California fall-run cohort reconstructions (Mohr 2006, unpublished report, see “Note”), we assumed monthly mortality rates of 5.6% (equivalent to 50% annually) between the start of age-2 and the August 2 years after the brood year, and 1.8% (equivalent to 20% annually) thereafter. Finally, we calculated spawner reduction rates for each cohort by dividing the estimated total escapement by the escapement that would be expected to have occurred in the absence of fishing mortality. Thus, the spawner reduction rate describes the overall reduction in escapement attributable to the combined effects

of ocean and river fisheries (when present), integrated across the full life cycle of a cohort.

We estimated escapement at age of a particular brood year based on the number of CWTs from that brood year recovered from spawners in that brood year, expanded by the sampling fraction associated with each tag recovery (O’Farrell et al. 2012a), summed across recoveries in all relevant natural areas and hatcheries. We estimated river harvest based on recoveries in creel surveys, expanded by their estimated sampling rates (O’Farrell et al. 2012a). We estimated monthly ocean fishery mortality separately for commercial and recreational sectors each month, and then summed the two sectors. We estimated ocean fishery mortalities based on tag recoveries expanded by the sampling rate, and then further expanded to account for assumed

drop-off mortality (mortality of fish that contact a hook but are not taken onto a fishing vessel; O'Farrell et al. 2012a) and release mortality of sublegal-sized fish. We estimated the number of sublegal-sized fish that corresponded to each fish in the landed harvest on a sector-, month-, and area-specific basis, based on a model of size-at-age for CVSC and the size limit in effect in the fishery stratum under consideration, assuming that fish lengths are normally distributed, and fish of all lengths are equally likely to be captured (O'Farrell et al. 2012a). (The model of size-at-take for CVSC was taken from Satterthwaite et al. 2018 with linear extrapolation to ages [in months] earlier than the minimum age reported there and assumed asymptotic length at the maximum length reported there for older fish.) We assumed that release mortality rates varied as a function of fishing practices, using time-, area-, and sector-specific values provided by CDFW that are also used in management models applied annually for KRFC and SRWC (see code in online supplement for specific values).

After expanding for sampling for FRHSC, we expanded tag recoveries (and corresponding non-landed mortalities) in spawning areas, hatcheries, river fisheries, and ocean fisheries based on the tagging rate reported for each release group (Mohr 2006, unpublished report, see "Note"; O'Farrell et al. 2012a). For hatchery-origin fish with multiple release groups that differed in tagging rates, this weights the contribution of each release group toward the composite estimate based on the number of fish rather than the number of tags. Because the fraction of BCWSC tagged is unknown, we did not expand BCWSC tag recoveries for tagging rates and the BCWSC cohort reconstruction reflects tagged fish only.

For BCWSC, we assumed a birthdate of April 1, meaning that March was the last month maturing fish remained in the ocean. This is 1 month earlier than the value assumed by Grover et al. (2004); however, local experts at CDFW suggested that an even earlier date might be appropriate. Since ocean fisheries are generally closed before April, we did not explore even earlier birthdates for BCWSC, because it would not change the age

assigned to many harvested fish. Some BCWSC harvested in the ocean in April or May might still have returned that year, but it seems likely based on local knowledge of return timing that most fish still in the ocean then were on a trajectory to remain at least 1 more year. For FRHSC, we assumed a baseline birthdate of June 1, based on descriptions of return timing (Fisher 1994; Palmer-Zwahlen et al. 2006), discussions with local biologists, and the timing of a drop in mean ocean size-at-age (Satterthwaite et al. 2018, their Figure 4), all of which point to a later incidence of larger fish of a cohort maturing and departing the ocean. In addition, we explored sensitivity to alternative FRHSC birthdate assumptions of April 1 and July 1. No single birthdate approximation can accommodate the range of within-year variation in individual return time and across-year variation expected in median return timing, and so inevitably some ocean harvest age assignments will be incorrect.

For comparison, we obtained annual early life survival, maturation rate, and ocean impact rate estimates for SRWC from annual cohort reconstructions performed for that stock (O'Farrell et al. 2012a and unpublished analyses summarized in PFMC 2023a), along with ocean harvest rate estimates for SRFC obtained by dividing annual ocean harvest estimates by the annual index of ocean abundance (the Sacramento Index; SI) for SRFC (Table II-1 in PMFC 2023a).

Scale Age Analyses

CDFW staff estimated ages for BCWSC by counting winter annuli on scales (Bhatia 1932). An experienced individual reader performed the aging and took sex and length into consideration only after the initial evaluation of age. Only 14 read BCWSC scales were from tagged fish of known age, so we could not evaluate BCWSC scale reading error directly. However, each year a total of 320 to 476 (median = 391) CVSC scales from tagged fish of known age were read, although almost all of these were FRHSC. Although reading error may differ between hatchery- and natural-origin fish, especially given the phenological differences between BCWSC

and FRHSC, this allowed for the construction of validation matrices for potential adjustment of age compositions estimated from BCWSC scales (Kimura and Chikuni 1987).

We estimated the age composition of BCWSC for each year with scale data available, and then estimated total escapement at age by multiplying these proportions by total escapement of BCWSC reported by Azat (2022). The escapement reported in Azat (2022) includes fish that died before spawning, which seems appropriate for the purpose of determining the number of fish that entered the river. Assuming an age-4 ocean impact rate h (which we explored borrowing from FRHSC or SRFC estimates), we estimated age-3 BCWSC maturation rates for a particular brood year as the age-3 escapement estimated for that brood year divided by the sum of the age-3 escapement and the age-4 escapement of that brood divided both by $(1-h)$ to expand for harvest and by 0.8 to account for assumed natural mortality. This does not account for the within-year timing of harvest and natural mortality as in the cohort reconstructions, and this approach yields only a coarse approximation, given the borrowing of harvest rates from other stocks. It also assumes 100% maturation at age-4, but there were no age-5 scales within our BCWSC samples.

Uncertainty and Sensitivity Analyses

Cohort reconstruction models used in Pacific salmon management generally do not account for uncertainty (Mohr 2006, unpublished report, see “Note”; O’Farrell et al. 2012a; PSC 2022, but see Allen et al. 2017). We accounted for this through bootstrapping exercises where we recalculated total estimated tags present in a harvest or escapement sampling stratum (both sampled and unsampled) by using a negative binomial distribution. This bootstrapping drew the expected number of “failures” to sample a tag that corresponded to an observed number of “successes” in sampling tags with a specified sampling rate or probability of success (Satterthwaite et al. 2013, Chen et al. 2023), using 1,000 bootstrap replicates. We applied the bootstrapping at the level of each tag recovery based on its reported sampling

fraction, confirming that the mean and variance that resulted from this approach was equivalent to the mean and variance from pooling all tag recoveries within a sampling stratum. However, we note that this method does not account for the number of tags that might have gone unsampled in a sampling stratum with zero tag recoveries.

In addition to sampling uncertainty, cohort reconstruction outputs suffer confounding effects of adult (i.e., after the start of age-2) natural mortality assumptions typically required for statistical identifiability (Allen et al. 2017), assumptions about non-landed mortality of fish contacted but not retained in the harvest, and uncertainty in how many fish are contacted but not retained. Allen et al. (2017) explored the sensitivity of key cohort reconstruction outputs to errors in the assumed adult natural mortality rates and the consequences of assuming constant adult natural mortality rates if they actually vary and found that errors were generally small so long as true adult natural mortality rates are low to moderate (≤ 0.4), so we did not consider uncertainty in natural mortality further. Uncertainty in non-landed mortality depends, in part, on release mortality rates (for which we assumed CDFW’s assumptions provided the best available science) and also on (1) uncertainty about the true mean and standard deviation in size-at-age, (2) the extent to which this varies from year to year, (3) the extent to which individual lengths follow a normal distribution, and (4) whether fish of all lengths within a cohort are equally susceptible to being caught. We were unable to adequately address all these uncertainties, but to quantify the sensitivity of age-specific impact rate estimate and spawner reduction rates to non-landed mortality assumptions, we recalculated these rates when assuming drop-off and release mortality rates were both equal to zero, then assessed sensitivity to non-landed mortality assumptions by comparing these estimates to the baseline estimates that accounted for non-landed mortality.

For the BCWSC scale analyses, we explored the sensitivity to borrowing age-4 impact rate

estimates from FRHSC or assuming they were equal to the ocean harvest rates estimated for SRFC (PFMC 2023a). We considered use of the SRFC ocean harvest rate estimates as our baseline approach since this quantity is routinely calculated and reported (PFMC 2023a), whereas FRHSC impact rates are not. Feather River Hatchery Spring-run Chinook differ from BCWSC in their return timing, which may limit the correspondence across populations in age-specific impact rates. We used the SRFC ocean harvest rate estimated for the management year 3 years after the brood year in question, which would overlap with the period in which BCWSC are considered age-4 for most of the time that ocean fisheries tend to open. We also explored the sensitivity to using age compositions estimated directly from the raw scale readings vs. adjusted age compositions after the Kimura–Chikuni (1987) algorithm was applied, with the validation matrix either derived yearly or by pooling all years' validated scale readings together. We note, however, that the validation matrices for this adjustment were almost entirely informed by FRHSC scales, and that our simulations based on artificial data sets constructed from subsets of the validation reads suggest that the Kimura–Chikuni (1987) adjustment may not improve estimates of age composition even when the validation matrices are representative (Appendix C). We did not account for the sample sizes of scales read each year since these numbers were generally large (>100), nor did we account for uncertainty in annual escapement since that uncertainty is not reported in Azat (2022).

CWT Data Acquisition and Processing

We queried the Regional Mark Information System (RMIS) database (www.rmipc.org) for all tagged releases of spring-run Chinook salmon from Butte Creek in brood years 1998–2007 and from Feather River Hatchery in brood years 1998–2015, then queried the RMIS recovery database for all recoveries of those tag codes. Our analysis included all recoveries in fishery codes 10 (ocean troll), 40 (ocean recreational), 46 (river fisheries), 50 (hatcheries), and 54 (spawning areas); for the FRHSC reconstructions, we excluded tag recoveries from other fishery codes or that

lacked reported expansion factors. Out of 89,307 FRHSC tag recoveries, 2,067 were from juvenile out-migrant trapping studies downstream (codes 73 and 75), leaving 87,240 adult tag recoveries. Among these recoveries, we excluded 473 recoveries from treaty troll, aboriginal, sport, and estuary fisheries north of Cape Falcon, Oregon (codes 15, 18, 21, 39, 41, 42, and 45), 481 freshwater recoveries classified as “other” (code 59), and 144 recoveries from bycatch in trawl fisheries (codes 80, 85, 800, 802, and 803). Among the remaining 86,142 adult tag recoveries, 109 were missing a sampling expansion factor, which we did not attempt to impute.

For BCWSC, there were 383 reported tag recoveries for these brood years, all of adults. We excluded one recovery from trawl bycatch. Among the remaining tags, we reclassified one from fishery 41 (ocean sport–charter) to 40 (ocean sport) and consulted internal CDFW records to resolve status for three recoveries classified as “other” (code 59). One was from a poached fish confiscated by a warden, which we reclassified as in-river harvest (code 46); one was a pre-spawn mortality found opportunistically downstream of the sampling area (which we reclassified as fishery 54–spawning grounds); and one was of unknown provenance and excluded from the analysis. To provide an estimated expansion factor for these reclassified tag recoveries, since they did not come from a sampling program with a known sampling rate, we assumed a sample expansion factor of 1.0. In addition, three tag recoveries from fishery code 54 (spawning grounds) were missing expansion factors. Consulting internal CDFW records revealed that two were recovered in spawning areas outside designed surveys, so we included them in our analysis with expansion factors of 1.0, whereas the third was an opportunistic recovery by a private party from within the sampled area, so we excluded it to avoid double-counting.

We repeated the analysis with the tag reclassified from fishery 41 to fishery 40 excluded, and deemed the change to have minimal effect (changing the spawner reduction rate and age-4 impact rate estimates for its brood year by less

than 1%). The poached fish was counted toward the spawner reduction rate for its brood year but excluding it would change the calculated spawner reduction rate by very little (40.2% versus 40.6%) and minimally affected other vital rate estimates for that brood year.

Data and Code Availability

Data and code to reproduce all of the results in this paper are available at <https://doi.org/10.17632/b8ys8kd5vz.1>. We have tried to make the cohort reconstruction code and its documentation applicable to other CWT data sets readers may be interested in, but we offer no warranty on its performance when applied to other data sets and scenarios we have not tested, and users employ the code at their own risk.

RESULTS

Butte Creek Wild Spring Chinook Demographic Rates

Age-3 ocean fishery impact rate (hereafter impact rate) estimates for BCWSC were low, below 20% for brood years 1998–2003 and 2005–2007 (Figure 2A). Age-4 impact rates were higher (Figure 2A), with point estimates above 50% in all brood years that experienced open fisheries except 2004. Fisheries were closed in 2008–2009 (Carlson and Satterthwaite 2011), corresponding mainly to brood years 2005 and 2006 for age-4, and the very high estimate for brood year 2007 reflects a single age-4 tag recovery in ocean fisheries with none recovered in freshwater; thus, no confidence interval could be computed for it. Age-2 maturation rate estimates were consistently low (Figure 2B), with no observations of age-2 spawners among the CWTs recovered for 8 out of 10 brood years. Age-3 maturation rate estimates were moderate (Figure 2B), with point estimates below 0.6 and upper bounds of confidence intervals below 0.7 in all but two brood years. The two brood years with point estimates above 0.6 were based on limited tag recoveries and had the largest uncertainty intervals. It was difficult to estimate age-4 maturation rates because of the lack of recoveries after age-4, so estimates were 1.0 for all but two brood years, and we do not report age-4 maturation rate estimates, though they are available in the online code supplement.

For 1998 and 2001 brood years where age-5 fish were recovered, confidence intervals were very wide.

Feather River Hatchery Spring Chinook Demographic Rates

Because of the much larger sample sizes, the bootstrapped confidence intervals that accounted for sampling-related uncertainty for FRHSC were relatively tight, especially at younger ages where the most tags were recovered (Appendix D). Age-specific ocean fishery impact rates estimated for FRHSC were sensitive to the birth date assumption (Figure 3A), while estimates of maturation rates (Figure 3B), spawner reduction rates (Figure 3C), and early life survivals (Figure 3D) were much less sensitive to the birthday assumption. Assuming a birthday earlier in the year tended to decrease the age-3 impact rate estimate and increase the age-4 estimate, resulting in estimates more like those obtained for BCWSC (Figure 2). The one exception to this pattern—a higher age-3 impact rate estimate for brood year 2014 when assuming an earlier birthday—reflects impacts on fish that were otherwise classified as age-2 and were associated with many assumed release mortalities as a result of their small size. Figure 3 only shows estimates for brood years 2006–2015, which follow improvements to CWT sampling and reporting associated with the constant fractional marking program that may make them more robust than estimates for earlier years. In the later figures, we only present FRHSC estimates that corresponded to a June 1 birthday assumption, to increase legibility.

Comparison of Demographic Rates Across Stocks and Through Time

When considering a longer time-period and both BCWSC and FRHSC (Figure 4), demographic rate estimates vary by time-period and to some extent by origin, although there are limited periods of sufficient data to provide direct within-year comparisons. Age-3 ocean impact rates on both FRHSC and BCWSC tended to be low (<20%, though note the sensitivity to birth date assumptions displayed in Figure 2A, and the uncertain effect of non-landed mortalities as

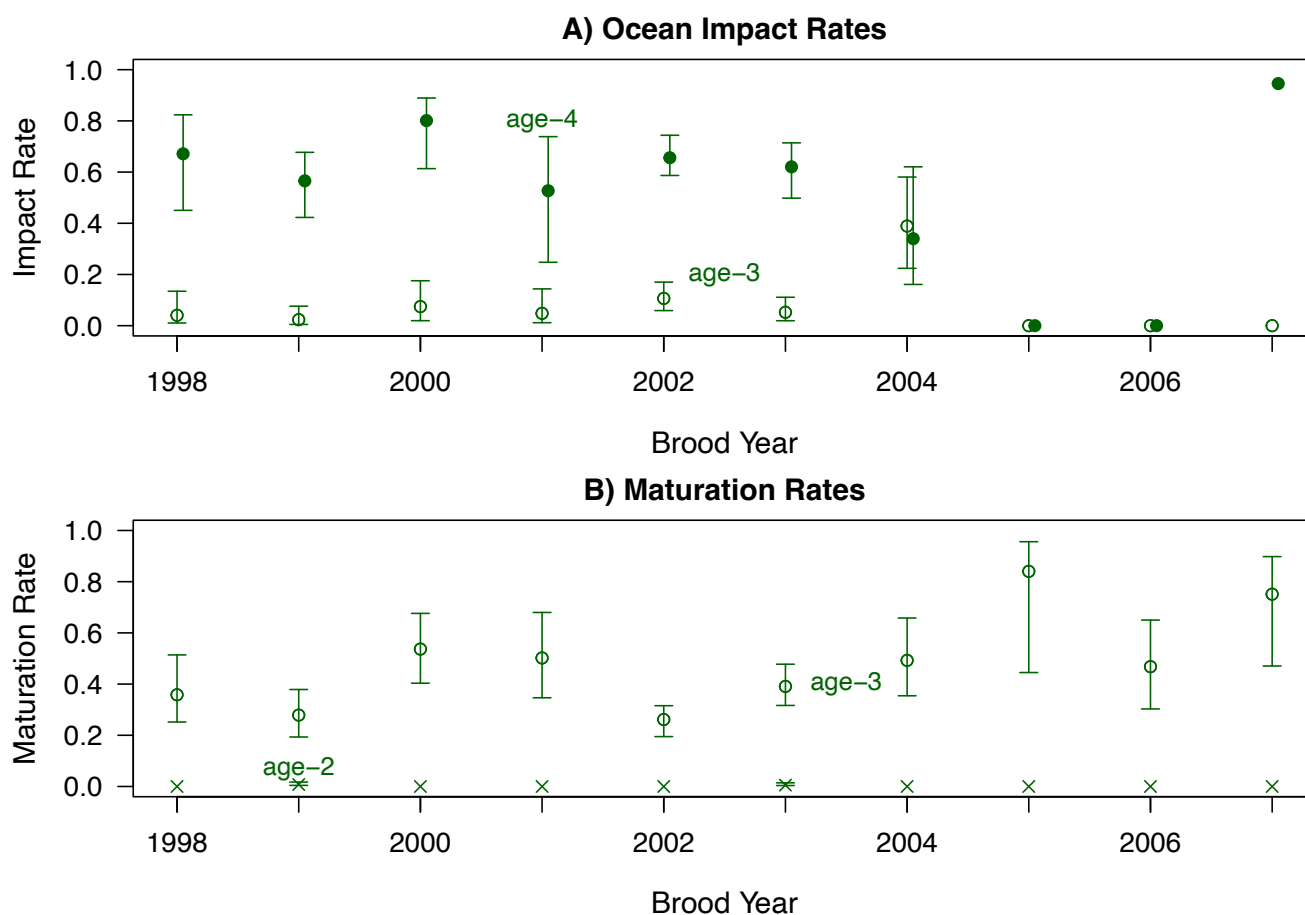


Figure 2 Demographic rates estimated from coded-wire tags for Butte Creek Wild Spring Chinook Salmon (BCWSC). *Point estimates* are from deterministic cohort reconstructions; *error bars* are approximate 95% confidence intervals that resulted from bootstrapping to account for sampling uncertainty. Note that the bootstraps do not account for the possibility of unobserved tag recoveries in sampling strata where none were observed; thus, estimates at 0 or 1 do not have appropriate uncertainty bounds. Confidence intervals also do not account for uncertainty in non-landed fishing mortality or adult natural mortality. *Crosses* indicate age-2, *open circles* indicate age-3, and *filled circles* indicate age-4. Age-4 maturation rates are not shown as a result of estimates being pinned at 1.0 for most brood years, with wide confidence intervals in the only brood years (1998 and 2001) with estimates less than 1.0.

discussed further below) and often comparable to or lower than estimates for SRWC of the same brood year (Figure 4A). Age-4 impact rate estimates were highly variable across years but could reach as high as 60% to 80% in years of high fishing intensity and were often comparable to ocean harvest rate estimates for SRFC, although FRHSC age-4 impact rate estimates (the only CVSC estimates available for more recent brood years) were lower than SRFC ocean harvest estimates for brood years 2012–2015 (Figure 4A). Correlations among stocks in year-specific impact-rate estimates tended to be modest to poor (Table 1),

especially after excluding brood years 2005–2007, which overlapped with a fishery closure (Table 2).

Age-2 maturation rate estimates for BCWSC were consistently very low for years with data, while FRHSC age-2 maturation rate estimates were also low but somewhat higher than BCWSC (Figure 4B). Apart from brood year 2008, age-3 maturation rates for both stocks were otherwise always lower than corresponding estimates for SRWC, but there was some indication of increasing age-3 maturation rates through time (Figure 4B). There was no consistent pattern in yearly differences between BCWSC and FRHSC in age-3 maturation

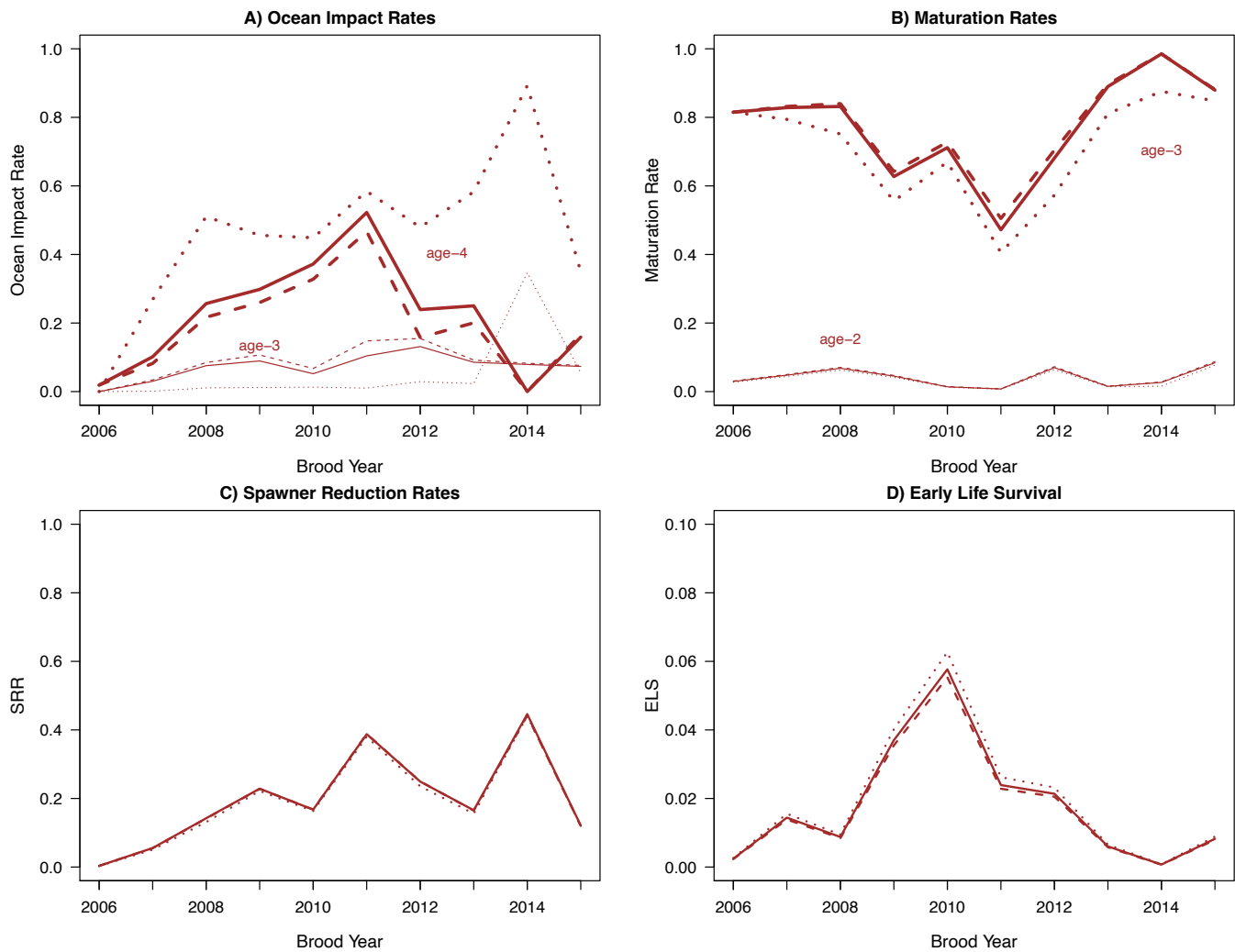


Figure 3 Demographic rates estimated for Feather River Hatchery Spring Chinook (FRHSC), brood years 2006–2015 (following initiation of the constant fractional marking and improved sampling and reporting of freshwater CWT recoveries throughout the Central Valley). The *solid lines* show results that assume a June 1 birthday (i.e., maturing FRHSC depart the ocean at the end of May), the *wide-dashed lines* show results that assume a July 1 birthday, and the *closely dotted lines* show results that assume an April 1 birthday.

rates, although the earlier brood years with the best data for BCWSC displayed lower maturation rates than the later brood years with the best data for FRHSC. The annual correlation between age-3 maturation rate estimates for BCWSC and FRHSC was 0.54 for brood years 1998–2007, and 0.68 between BCWSC and SRWC for brood years 2001–2007. Maturation rate estimates at age-4 (not shown) were generally high, but difficult to estimate precisely because of small sample sizes.

BCWSC age-3 maturation rate estimates from scales were minimally affected by the Kimura–Chikuni adjustment for brood years 2008–2011, but substantially increased by the adjustment for brood years 2007 and 2012 (Figure 4B; Table 3), with a larger effect of annual validation matrices in place of a single pooled validation matrix. Application of the Kimura–Chikuni adjustment to a simulated data set led to worse estimates (Appendix C), and the validation matrix was almost entirely informed by hatchery-origin fish. Using FRHSC age-4 impact-rate estimates in place

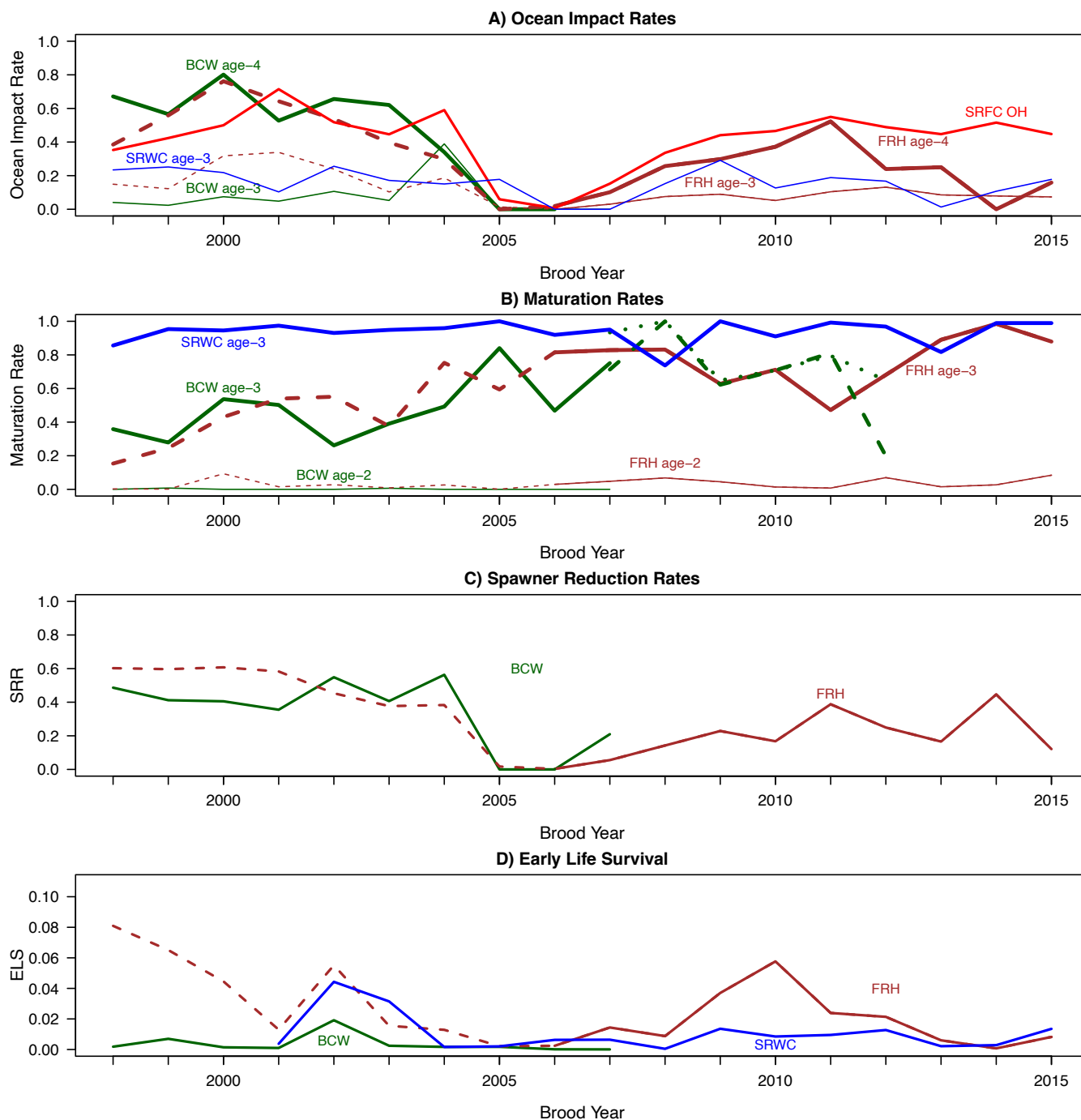


Figure 4 Demographic rates estimated for Butte Creek Wild Spring Chinook (BCW, *green*, April 1 birth date), Feather River Hatchery Spring Chinook (FRH, *brown*, June 1 birth date), Sacramento River Winter Chinook (SRWC, *blue*, March 1 birth date), along with the Sacramento River Fall Chinook ocean harvest rate estimates (SRFC OH, *red*, September 1 birthday) for brood years 1998–2015 as available. *Solid lines* represent the brood years that correspond to more reliable data sets for each stock (for FRH, following implementation of the constant fractional marking program; for BCW, based on tagged fish rather than scale readings and borrowed ocean impact rates). For BCW in **panel B**, maturation rate estimates based on scales are shown with *dashed lines* and were based on assuming age-4 ocean impact rates equal to the SRFC ocean harvest rate. *Wide dash spacing* reflects application of the Kimura–Chikuni adjustment, *narrow dash spacing* reflects no adjustment. We did not plot the brood year 2007 age-4 impact rate estimate for BCWSC since it is based on only one tag recovery.

Table 1 Correlation among Butte Creek Wild (BCW) Spring Chinook, Feather River Hatchery (FRH) Spring Chinook, Sacramento River Winter Chinook (SRWC), and Sacramento River Fall Chinook (SRFC) stocks in brood-year-specific ocean-impact rate estimates (i_3 = age-3 impact rate, i_4 = age-4 impact rate), ocean harvest (OH) rate estimates, and spawner reduction rate (SRR) estimates, for all brood years with data from tagged BCWSC. Note that the strongest within-brood year correlations are expected for the same age classes, although differing birth dates preclude complete pairing. FRHSC estimates correspond to a June 1 birth date assumption. The SRFC ocean harvest rate index is for the fishery management year 3 years after the brood year.

	FRH i_3	FRH i_4	FRH SRR	SRWC i_3	SRFC OH
BCW i_3	0.33	0.14	0.22	0.17	0.52
BCW i_4	0.43	0.56	0.51	0.20	0.43
BCW SRR	0.67	0.71	0.81	0.62	0.83

Table 2 Correlation among Butte Creek Wild (BCW) Spring Chinook, Feather River Hatchery (FRH) Spring Chinook, Sacramento River Winter Chinook (SRWC), and Sacramento River Fall Chinook (SRFC) stocks in brood-year-specific, ocean impact rate estimates (i_3 = age-3 impact rate, i_4 = age-4 impact rate), ocean harvest (OH) rate estimates, and spawner reduction rate (SRR) estimates, *excluding brood years 2005–2007 as a result of the fishery closure for management years 2008–2009*. FRH estimates correspond to a June 1 birth date assumption. The SRFC ocean harvest rate index is for the fishery management year 3 years after the brood year.

	FRH i_3	FRH i_4	FRH SRR	SRWC i_3	SRFC OH
BCW i_3	-0.01	-0.52	-0.60	-0.32	0.35
BCW i_4	0.20	0.61	0.49	0.54	-0.46
BCW SRR	-0.25	-0.60	-0.50	0.32	-0.15

of SRFC ocean harvest rate estimates had minimal effects, although using FRHSC age-4 impact rates calculated assuming a June 1 birth date could increase the maturation rate estimates by a few percent (Appendix E).

Spawner reduction rates reached as high as 40% to 60% for both BCWSC and FRHSC for years of high fishing intensity (Figure 4C), although spawner reduction rates for the most recent brood years included (only available for FRHSC) have not been as high. Note that the FRHSC spawner reduction rate calculated for brood year 2014 is relatively

Table 3 Butte Creek Wild Spring Chinook (BCWSC) age-3 maturation-rate estimates from scale data, assuming age-4 ocean impact rates are equivalent to Sacramento River Fall Chinook (SRFC) ocean harvest rates (OH) from the management year 3 years after the brood year. Calculations are based on annual escapement-at-age proportions estimated directly from raw scale ages, or after applying the Kimura-Chikuni (1987) adjustment for age reading error, based on pooled or annual validation matrices.

Brood year	SRFC OH, no adjustment	SRFC OH, pooled KC	SRFC OH, annual KC
2007	0.71	0.93	1.00
2008	1.00	1.00	1.00
2009	0.62	0.65	0.65
2010	0.71	0.71	0.71
2011	0.81	0.79	0.78
2012	0.20	0.65	0.99

high despite low age-3 and age-4 impact rates: this reflects a high age-2 impact-rate estimate that corresponds to the recovery of age-2 tags associated with a very large expansion to account for the small proportion of legal-sized fish and the assumption that many fish were contacted and released for each young fish retained to sample. Over the full time-period with BCWSC CWT data, BCWSC spawner reduction rates were correlated with FRHSC spawner reduction rate estimates ($r=0.81$) or SRFC ocean harvest rate estimates ($r=0.83$), but this largely reflects the effect of the fishery closure. Correlations dropped to -0.50 or -0.15, respectively, with the closure years excluded (Table 2).

Early life survival rate estimates were highly variable across years (Figure 4D), and often substantially lower for BCWSC than FRHSC for years when both stocks had data. BCWSC early life survival estimates were more correlated with those from SRWC ($r=0.82$) than FRHSC ($r=0.46$).

The proportion of estimated age-specific ocean-impact rates attributable to non-landed mortality varied considerably across years and by age (Figure 5A). The proportion of estimated age-3 impact rates attributable to non-landed mortality ranged from 3% to 59% for BCWSC and from 4% to 30% for FRHSC (Figure 5A). In contrast, the proportion of estimated age-4 impact

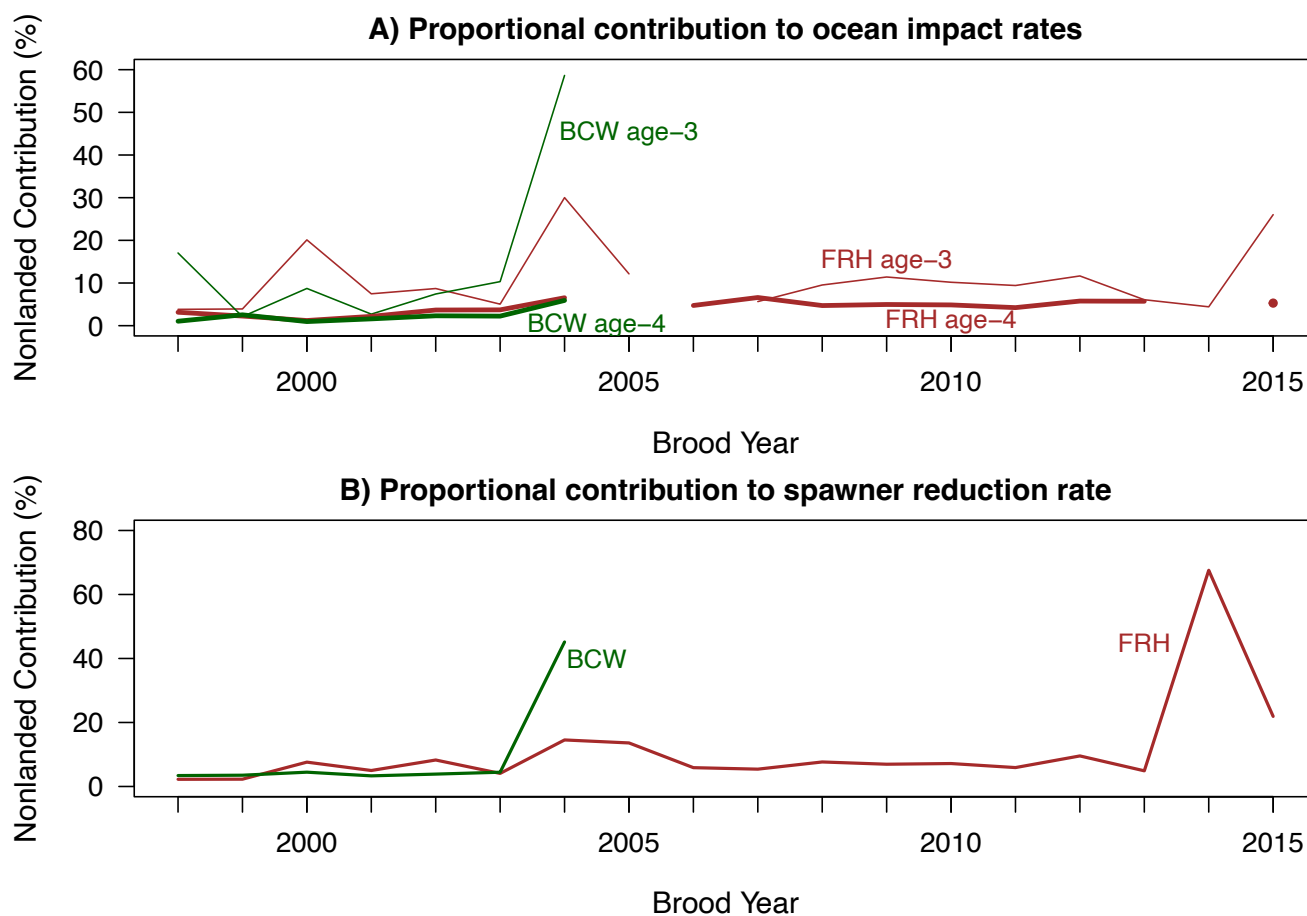


Figure 5 Proportion of estimated age-specific ocean impact rates (A) or spawner reduction rates (B) attributed to non-landed (release and drop-off) mortality for Butte Creek Wild (BCW) or Feather River Hatchery (FRH) Spring-run Chinook.

rates attributable to non-landed mortality was consistently less than 7% (Figure 5A) for both BCWSC and FRHSC, and primarily reflects drop-off (assumed equal to 5%) rather than release mortality. The proportion of the estimated spawner reduction rate attributable to non-landed mortality was also highly variable, ranging from 3% to 45% for BCWSC and from 2% to 68% for FRHSC (Figure 5B). The high contribution of non-landed mortality to the spawner reduction rate for brood year 2004 BCWSC reflects a high contribution of non-landed mortalities to age-3 impact rates for that brood year (Figure 5A); whereas, the high contribution to spawner reduction rates for brood year 2014 FRHSC comes from the unusual recovery of age-2 fish in the ocean harvest at a time when they were modeled to be very small, which expanded to

a large number of assumed sublegal releases and mortalities. Landed ocean harvest of age-2 BCWSC was never observed in the data set for this study but was observed in 12 of 19 brood years for FRHSC. No estimates of the non-landed contributions are possible for impact rates estimated as zero, or for BCWSC brood year 2007, because there was no landed age-3 harvest observed and no age-4 escapement observed.

DISCUSSION

Butte Creek Wild Spring Chinook Demographic Rates and Fishery Effects

Aside from a gray literature publication that reports estimates for 2 brood years (Glover et al. 2004), this study constitutes the first publication we know of that reports BCWSC

demographic rates and fishery effects. In the past, managers have expressed skepticism about the utility of BCWSC tag data for cohort reconstruction because of limited sample sizes (Grover et al. 2004; Satterthwaite et al. 2018). Our bootstrapping exercise demonstrates that there is considerable uncertainty in annual vital rate estimates attributable to sampling effects, and that tag recoveries are likely inadequate to support the types of highly stratified models that managers may desire to craft time- and area-specific regulations which target precise harvest rates (O'Farrell et al. 2015). However, despite the uncertainty in year-specific estimates, we can robustly conclude that age-3 impact rates for BCWSC are usually low (<20%) and comparable to or less than those for age-3 SRWC, that age-4 impact rates can be relatively high (>50%) in years of high fishing intensity (comparable to ocean harvest rates of SRFC, and that age-3 maturation rates are generally modest (<60%) for brood years 1998–2007 and lower than those estimated for SRWC. These conclusions depend on assumptions about non-landed fishing mortality and natural mortality that nearly all cohort reconstructions share, regardless of sample size.

The vast majority of tagged BCWSC were young of the year rather than “yearlings” that have reared for an extended period in freshwater, with the only yearlings included in this study being from brood year 1998. The rotary screw trap (and to a lesser extent, the diversion fyke trap) used to capture fish for tagging is biased toward capturing smaller fish, because larger yearlings can often avoid it. Yearlings may have different survival, maturation, and susceptibility to the fishery (Grover et al. 2004; Hankin and Logan 2010; Cordoleani et al. 2021) but are not represented in our estimates for brood years after 1998 and may not be represented in the brood year 1998 estimates in proportion to their relative abundance. Although fish that may have emigrated as yearlings may have been present in the scale data, they were not identified as such or analyzed separately.

Feather River Hatchery Spring Chinook Demographic Rates and Fishery Effects

In the past, the only published estimates of demographic rates for FRHSC we know of were limited to a few brood years reported in the gray literature (Cramer and Demko 1997; Palmer–Zwahlen et al. 2006). Fisheries managers have expressed skepticism about the utility of further analyses of fishery effects via FRHSC tags because of concerns about the completeness of sampling and reporting of freshwater recoveries before brood year 2006 (Baker and Morhardt 2001; Kormos et al. 2012), and fears that life-history differences between FRHSC and the rest of the CVSC ESU may make them unrepresentative (Grover et al. 2004; Satterthwaite et al. 2018). It is unclear how incomplete tag recovery data may have affected our demographic rate estimates for FRHSC brood years before 2006 (when the constant fractional marking program was initiated; Buttars 2010); and varying rates of offsite releases and resultant straying (Sturrock et al. 2019) may also affect the reliability of escapement data from earlier years. For brood years 2006–2011, estimated FRHSC age-4 impact-rate estimates seemed to scale with the SRFC ocean harvest rate similarly to how they had for brood years 1998–2005; but for brood years 2012–2015, the FRHSC age-4 impact rate seemed smaller in comparison to the SRFC ocean harvest rate (though ocean tag recoveries for brood year 2014 were very limited as a result of low early life survival). This could reflect sampling (or reporting) biased toward ocean recoveries over freshwater recoveries in earlier years, which would tend to over-estimate ocean impact rates. However, the breakpoint does not coincide cleanly with the initiation of the constant fractional marking program and associated changes in sampling programs. Additionally, age-4 impact-rate estimates for these brood years were much higher when assuming an earlier birthdate, so this could just be a consequence of what time of year fishing was most intense in different study years.

In terms of representativeness, correlations in annual impact rate estimates between FRHSC and BCWSC were generally poor, especially

when excluding years of fishery closure where impact rates were inevitably equal to zero for both stocks. Even including the years of fishery closures, correlations were generally below 0.5, a level deemed insufficient when potential proxies for threatened California Coastal Chinook were considered (O'Farrell et al. 2012b). This low level of correlation might be an inevitable consequence of the sampling error associated with the small number of BCWSC tag recoveries. Our analysis also pooled together all FRHSC releases, but certain release types (e.g., timing and location) may represent wild fish better than others. In addition, age-specific impact-rate estimates for FRHSC were highly sensitive to the assumed time of year that maturing fish leave the ocean, and this is not equivalent between FRHSC and BCWSC or other natural populations (Lindley et al. 2004). Variation in the timing of ocean departure will interact with annual variation in the timing of fishing effort to influence how ocean fisheries affect different stocks. Therefore, even if the correlations estimated here are somewhat reduced by sampling error or pooling together less representative release types, there is little reason to expect FRHSC to be a good proxy for BCWSC in terms of maturation rates or age- and year-specific fishery-impact rates. However, estimates based on FRHSC tags seem to track periods of generally high or low spawner reduction rates.

Return Timing / Birth Date Assumption

As noted for FRHSC, the assumed time of year that maturing fish leave the ocean can substantially affect age-specific impact-rate estimates, although estimates of maturation rates and spawner reduction rates were less affected by this assumption. Differences between stocks (or among years within a single stock) can also have biological consequences. Earlier ocean departure leads to lower age-3 impact rates for BCWSC compared to FRHSC, and therefore if maturation rates were similar between the stocks, BCWSC would face less exposure to the fishery. BCWSC may also derive some benefit from fishing effort being reduced around their time of peak return when they may be highly aggregated and most susceptible to being caught. Later-returning

spring-run stocks such as FRHSC as well as natural-origin fish from Mill and Deer creeks may not receive similar protection, however. Thus, other independent natural populations of CVSC would not receive as much protection from the seasonal fishery restrictions as BCWSC do.

Not all returning spawners leave the ocean simultaneously, and this limits the ability to estimate age-specific impact rates for FRHSC, given that they return during months when the ocean fishery is typically active, unlike SRWC that typically return during the winter closure of the fishery. This concern applies to a lesser extent to BCWSC, which seem to have largely but not entirely left the ocean before fisheries start up in late spring, and to SRFC, which have mostly left the ocean before fisheries wind down in the fall.

Caveats

As with almost all published cohort reconstructions (but see Allen et al. 2017), the demographic rates estimated here are conditional on assumed, constant values of adult natural mortality in the ocean. Given the limited number of tag recoveries for BCWSC and the limited number of FRHSC broods with complete data after the constant fractional marking was initiated—along with the relatively low contribution of age-4 spawners in recent years—it is doubtful there would be sufficient data from overlapping cohorts to apply the methods of Allen et al. (2017) to estimate adult natural mortality for FRHSC, and certainly not for BCWSC.

Estimated impact rates also depend on assumptions about non-landed mortalities. This reflects both assumptions about the per-capita release and drop-off mortality rates and assumptions about how many sublegal-sized fish are contacted for each legal-sized fish observed in the harvest. The sublegal-sized fish calculations depend on the assumption that size-at-age is normally distributed and constant across years, which may not be true. Satterthwaite et al. (2012) offers methods for estimating annual variation in size-at-age, but still depends on the assumption of normality, and requires larger sample sizes than are available for BCWSC. Additionally, in

sampling strata where no tags are recovered from fish sampled in the retained harvest, we could not account for the possibility that tagged fish were in the unsampled part of the harvest, or among the sublegal releases.

Consistent with the uncertainty about non-landed impacts, the proportion of total modeled impacts attributed to non-landed mortality was highly variable across years. Variation in the proportion of age-3 impacts and spawner reduction rates attributable to non-landed mortality at least partially reflects differences in the timing of fishing effort within the year (i.e., more sublegal releases per retained fish earlier in the year when fish are smaller), relative effort in commercial vs. recreational fisheries (which differ in their size limits), and/or changes in size limits across years. Indeed, peaks in the proportion of impacts attributable to non-landed mortality often occurred in the same years for BCWSC and FRHSC, suggesting a shared effect of annual fishing practices or other year-specific factors. However, the high degree of variation also raises concerns that non-landed mortalities may often be completely missed in sampling strata where few fish are of legal size. The large impact-rate estimates that sometimes result from large expansion factors may seem implausibly large, but this suggests that many strata are being assigned zero impacts when this may be equally implausible. Thus, suspiciously large values may still be appropriate to include in sums or averages, unless or until suitable methods are developed for inferring likely non-landed but unobserved impacts in strata where retention of contacted fish is unlikely (Satterthwaite et al. 2013; Martin et al. 2015). That age-2 ocean harvest was never observed for BCWSC but observed in most years for FRHSC likely reflects the much larger sample sizes for FRHSC, making it more likely to observe rare events rather than a true invulnerability of age-2 BCWSC to fisheries—although a later birthdate assumption for FRHSC expands the temporal window in which nominally age-2 harvest can occur.

Although our bootstrapping was intended to capture the effects of sampling uncertainty,

the number of BCWSC CWT recovered for brood years 2005–2007 was very limited (Appendix A). Since ocean fisheries for Chinook off California and most of Oregon were closed for 2008–2009 and constrained in 2010 (PFMC 2023b), the lack of ocean tag recoveries for these brood years is largely expected, and the estimates of low to zero impact rates on these broods (except age-4 of BY 2007, where the high impact rate is consistent with the fishery reopening) seem robust. However, even after accounting for sampling uncertainty, we may be underestimating the true uncertainty in the probability of maturation as a result of the limited number of tagged fish from which this rate could be estimated.

Comparison to Actively Managed Stocks

Age-3 ocean fishery impact rates on CVSC seemed comparable to but generally lower than age-3 ocean impact rates for SRWC. This may partially reflect the effect of size limits and where recreational ocean fisheries are most intense. At age-3, CVSC are smaller than SRWC and less likely to be retained in the fishery during the summer when fishing intensity is highest. Especially early in the year, age-3 fish from these stocks are small (Satterthwaite et al. 2018, their Table 1) and unlikely to be retained in commercial fisheries with high minimum size limits; thus, estimated age-3 impacts (and rarely observed age-2 impacts) are largely restricted to the recreational fishery. CVSC seem to be more spread out along the California and Oregon coast than SRWC, which seem to be highly concentrated in central California (Satterthwaite et al. 2013, 2018) where more recreational fishing effort occurs (PFMC 2023b).

Age-4 ocean fishery impact rates on CVSC seemed generally comparable to ocean harvest rate estimates for SRFC, an indicator stock for ocean fisheries and a large contributor to ocean catch (PFMC 2022). The age-4 impact rate for FRHSC seemed lower relative to SRFC for brood years 2012–2015, but estimated age-4 impact rates for those brood years were much higher if it were assumed that maturing FRHSC left the ocean at the end of March rather than at the end of May,

suggesting this may just be a consequence of when fishing effort was concentrated for those years.

Age-3 maturation rates for CVSC, especially BCWSC, were consistently lower than those estimated for SRWC. As a result, age-4 fishery impact rates tended to be consequential and result in a spawner reduction rate substantially higher than the age-3 impact rate, with the spawner reduction rate generally of the same magnitude as the SRFC ocean harvest rate.

Early life-survival for BCWSC (but not FRHSC) seemed to covary with the early life survival estimated for SRWC. Thus, predictive models of SRWC juvenile survival may have some ability to predict cohort strength for BCWSC (Satterthwaite et al. 2018), although ideally the effects of parent spawner abundance would be accounted for as well.

Conservation and Fishery Considerations

For tagged BCWSC brood years, and early brood years of FRHSC, the combination of modest age-3 maturation rates and relatively high age-4 ocean impact rates leads to spawner reduction rates on the order of 40% to 60% for all ages combined in years of high fishing intensity. It is uncertain how much of a conservation concern a spawner reduction rate of this magnitude poses for CVSC in the absence of a well-parameterized life-cycle model (Cordoleani et al. 2020). This is higher than the spawner reduction rates allowed for some other ESA-listed Chinook Salmon, but lower than the rate allowable for others, at least under certain conditions (PFMC 2022). Plans for CVSC reintroduction to the San Joaquin basin (SJRRP 2017) anticipated spawner reduction rates on the order of 50% and did not see this as incompatible with successful reintroduction. Grover et al. (2004) estimated spawner reduction rates for the 1998 and 1999 CVSC brood years of 36% and 42%, respectively, compared to our estimates of 49% and 41% (with differences driven by different models of size-at-age and proportion legal, release mortality assumptions, birthday assumptions, and possibly intervening updates to the tag recoveries or expansion rates

reported in RMIS). They noted that impact rates may have been substantially higher in earlier years. Grover et al. (2004) further pointed out that CVSC populations had generally increased in the 1990s and early 2000s in the face of those rates, given environmental conditions at that time, but stated that reductions in impact rates would be warranted if then-recent trends in recovery were reversed.

There is some indication that maturation rates for CVSC may be higher in more recent brood years, although CWT sample sizes for brood years 2005–2007 are very limited, and the scale-derived BCWSC estimates for recent brood years depend on assumptions about ocean harvest rates, and the last brood year with an age-3 maturation rate estimate available again estimated a low rate. To the extent that age-3 maturation rates have increased or are increasing, this would reduce the importance of age-4 impacts to the overall spawner reduction rate, and potentially reduce conservation concerns relative to the ocean fishery. However, reduced age-structure diversity would reduce the resilience of the CVSC population (Greene et al. 2010), especially if later maturity is linked with the yearling life history shown to be increasingly important under drought conditions (Cordoleani et al. 2021). Thus, reduced age-structure diversity might raise overall conservation concern for CVSC, with unclear net effects on the level of fishing impacts that corresponded to acceptable overall risk.

Although spawner reduction rates for CVSC could be on the order of 40% to 60% in years of high fishing intensity, they were considerably lower in years when fishing was restricted. Under the current fishery-management regime, fishing in areas that affect CVSC are not directly informed by anticipated CVSC abundance. Instead, allowable impact rates on SRFC, SRWC, and KRFC are adjusted based on forecasts for those stocks, with forecasts of SRFC and SRWC likely of the highest relevance to the areas of the most overlap with CVSC (Satterthwaite et al. 2018). Thus, reductions in fishery effects on CVSC are likely in years of low forecasted abundance for SRWC and SRFC. Historically, correlations among these

stocks in their abundance have been modest to low ($r=0.3-0.6$; Satterthwaite et al. 2018) and these correlations may be even weaker in the future as a result of (1) changes in hatchery practices that truck an increasing fraction of SRFC downstream in response to drought conditions (Sturrock et al. 2019), (2) increased hatchery production of SRWC (Meyers 2021), and (3) attempts to treat thiamine deficiency in hatchery fish from all three stocks (Mantua et al. 2021).

CONCLUSIONS

Using existing data sources, we were able to gain substantial insights into the demographics and susceptibility to fisheries of CVSC, particularly the core natural BCWSC population. However, our estimates were limited in their precision because of small sample sizes and limited in their temporal coverage. We have identified the potential for spawner reduction rates on the order of 40% to 60% given historically observed levels of age-3 maturation rates and age-4 ocean impact rates but have also identified some indications that these rates may be changing over time. Thus, contemporary information on CVSC maturation rates and fishery impact rates would be highly valuable. Given the return timing and other life-history differences between FRHSC and BCWSC (and presumably the rest of the ESU), information on natural-origin CVSC would be particularly valuable. Thus, maintaining the collection and aging of scales from BCWSC has considerable merit, as does extending these analyses to other tributaries as well. At minimum, this would allow ongoing monitoring of spawner age structure.

Converting spawner age structure information into understanding of maturation rates would require further information on ocean harvest impacts, as well. Ideally, ocean harvest of natural-origin CVSC would be estimated directly, for each of the independent natural populations. This might be possible for Butte Creek through restarting the BCWSC tagging program, although larger sample sizes would be needed for confident year-specific estimates, which may not be feasible. Alternatively, scale collection could provide age-structure information for any

natural population that was sufficiently sampled, and this could be used to infer maturation rates conditional on assumed or borrowed ocean impact rates. Although age-specific impact rates for FRHSC may not fully represent the rest of the ESU, tagging at FRHSC is ongoing and should provide adequate sample sizes for impact rate estimation via proxy—perhaps using a return timing assumption appropriate for BCWSC or the other core populations rather than one tuned to FRHSC. While the use of a proxy for impact rates would introduce uncertainty, the maturation rates estimated from scales did not seem highly sensitive to the harvest rate proxy used. That said, adjustments for scale aging error could be more consequential, but we have limited information on how accurately natural-origin CVSC can be aged from scales. Alternatively, or additionally, information on ocean harvest of natural-origin CVSC could be obtained through genetic sampling (e.g., Satterthwaite et al. 2015). To date, comprehensive estimates of CVSC ocean harvest via genetics have not been possible because of the limited spatial and temporal coverage of genetic sampling, but this might be possible in the future. Sampling efficiency for natural-origin fish might be improved if all hatchery-origin fish were marked and/or tagged such that genetic sampling could focus on unmarked/untagged fish with the assumption that they are natural-origin, while information on hatchery-origin fish could be obtained from subsampling tags in the marked/tagged fish. However, such a change would be costly and would need to be implemented carefully to avoid interfering with existing sampling strategies for other stocks, especially SRWC (Mohr et al. 2017).

Incorporating genetic information into cohort reconstructions would require that age estimates for genetically-sampled fish—and the stock resolution used for harvest estimates—would need to match the resolution used for age-specific escapement (i.e., ESU-wide harvest would need to be compared to ESU-wide escapement, not escapement on a single tributary, unless that tributary could be separately identified genetically [Meek et al. 2020]). Genetic sampling extended to sublegal releases would address

another major uncertainty in the current cohort reconstructions, where estimates of non-landed mortality are heavily driven by assumptions about unobserved processes.

In addition to ongoing and expanded data collection, continued work on life-cycle modeling of CVSC—including estimates of spawner–recruitment relationships—is key to putting ocean-impact rate and spawner reduction rates into a broader context and determining the levels of impact consistent with the ongoing viability and recovery of this threatened stock.

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REFERENCES

- Allen SD, Satterthwaite WH, Hankin DG, Cole DJ, Mohr MS. 2017. Temporally varying natural mortality: sensitivity of a virtual population analysis and an exploration of alternatives. *Fish Res.* [accessed 2023 May 22];185:185–197. <http://doi.org/10.1016/j.fishres.2016.09.002>
- Azat J 2022. GrandTab 2022.07.20. California Central Valley Chinook population database report. [accessed 2023 May 22]. Sacramento (CA): California Department of Fish and Wildlife. Available from: <https://www.calfish.org/ProgramsData/Species/CDFWANadromousResourceAssessment.aspx>
- Baker PF, Morhardt, JE. 2001. Survival of Chinook Salmon smolts in the Sacramento–San Joaquin Delta and Pacific Ocean. [accessed 2023 May 22]. In: Brown RL, editor. Contributions to the biology of Central Valley salmonids. Vol. 2. Fish Bulletin 179. Sacramento (CA): California Department of Fish and Game. p. 163–182. <https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=3589>
- Bhatia D. 1932. Factors involved in the production of annual zones on the scales of rainbow trout (*Salmo irideus*) II. *J Exp Biol.* [accessed 2023 May 22];9:6–11. <https://doi.org/10.1242/jeb.9.1.6>
- Buttars B. 2010. Constant fractional marking/tagging program for Central Valley fall-run Chinook Salmon, 2010 marking season. [accessed 2023 May 22]. Red Bluff (CA): Pacific States Marine Fisheries Commission. Available from: https://www.calfish.org/Portals/2/Programs/CentralValley/CFM/docs/2010_CFM_Report.pdf
- [CA HSRG] California Hatchery Scientific Review Group. 2012. California hatchery review report. [accessed 2023 May 22]. Prepared for the US Fish and Wildlife Service and Pacific States Marine Fisheries Commission. 100 p. Available from: <https://swfsc-publications.fisheries.noaa.gov/publications/CR/2012/2012California.pdf>
- Carlson SM, Satterthwaite WH. 2011. Weakened portfolio effect in a collapsed salmon population complex. *Can J Fish Aquat Sci.* [accessed 2023 May 22];68(9):1579–1589. <https://doi.org/10.1139/F2011-084>
- [CDFG] California Department of Fish and Game. 1998. Report to the Fish and Game Commission: a status review of the spring-run Chinook Salmon (*Oncorhynchus tshawytscha*) in the Sacramento drainage. [accessed 2023 May 22]. Candidate Species Status Report 98-01. Available from: https://www.waterboards.ca.gov/waterrights/water_issues/programs/bay_delta/deltaflow/docs/exhibits/nmfs/spprt_docs/nmfs_exh4_dfg_report_98_1.pdf
- [CDFG] California Department of Fish and Game. 2004. Spring-run Chinook Salmon: 2002–2003 biennial report. Prepared for the Fish and Game Commission. [accessed 2023 May 22]. Habitat Conservation Division Native Anadromous Fish and Watershed Branch. Available from: <https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=3502>
- Chen EK, Satterthwaite WH, Kormos BJ, Johnson RC, Phillis CC, Carlson SM. 2023. Age structure of natural versus hatchery-supplemented endangered Chinook Salmon and implications for fisheries management in California. *Mar Ecol Prog Ser.* [accessed 2023 Nov 23];723:37–55. <https://doi.org/10.3354/meps14446>

- Cordoleani F, Satterthwaite WH, Daniels ME, Johnson MR. 2020. Using life cycle models to identify monitoring gaps for Central Valley spring-run Chinook Salmon. *San Franc Estuary Watershed Sci.* [accessed 2023 May 22];18(4):3.
<https://doi.org/10.15447/sfews.2020v18iss4art3>
- Cordoleani F, Phillis CC, Sturrock AM, FitzGerald AM, Malkassian A, Whitman GE, Weber PK, Johnson RC. 2021. Threatened salmon rely on a rare life history strategy in a warming landscape. *Nat Clim Change.* [accessed 2023 May 22];11:982–988.
<https://doi.org/10.1038/s41558-021-01186-4>
- Cramer SP, Demko DB. 1997. The status of late-fall and spring Chinook Salmon in the Sacramento River basin regarding the Endangered Species Act. [accessed 2023 May 22]. Gresham (OR): Special report submitted to National Marine Fisheries Service on behalf of the Association of California Water Agencies and California Urban Water Agencies. Available from: <https://www.cuwa.org/publications-archive/g2a6zx7mwhdzt7lrbs64ztkaccw76d>
- Federal Register. 1999. Endangered and threatened species; threatened status for two Chinook Salmon Evolutionarily Significant Units (ESUs) in California. *Federal Regist.* [accessed 2023 May 22];64(79):50394–50415. Available from: <https://www.federalregister.gov/documents/1999/09/16/99-24051/endangered-and-threatened-species-threatened-status-for-two-chinook-salmon-evolutionarily>
- Fisher FW. 1994. Past and present status of Central Valley Chinook Salmon. *Cons Bio.* [accessed 2023 May 22];8(3):870–873.
<https://doi.org/10.1046/j.1523-1739.1994.08030863-5.x>
- Garman CE, McReynolds TR. 2008. Butte and Big Chico Creeks spring-run Chinook Salmon, *Oncorhynchus tshawytscha* life history investigation, 2006–2007. [accessed 2023 May 22] Rancho Cordova (CA): California Department of Fish and Game, Inland Fisheries Report No. 2008-1. 44 p. Available from: <https://www.calfish.org/ProgramsData/ConservationandManagement/CentralValleyMonitoring/SacramentoValleyTributaryMonitoring/ButteCreek.aspx>
- Garman CE, McReynolds TR. 2009. Butte and Big Chico Creeks spring-run Chinook Salmon, *Oncorhynchus tshawytscha* life history investigation, 2007–2008. [accessed 2023 May 22]. Rancho Cordova (CA): California Department of Fish and Game, Inland Fisheries Report No. 2009-1. 39 p. Available from: <https://www.calfish.org/ProgramsData/ConservationandManagement/CentralValleyMonitoring/SacramentoValleyTributaryMonitoring/ButteCreek.aspx>
- Greene CM, Hall JE, Guibault KR, Quinn TP. 2010. Improved viability of populations with diverse life-history portfolios. *Biol Lett.* [accessed 2023 May 22];6:382–386.
<https://doi.org/10.1098/rsbl.2009.0780>
- Grover A, Kormos B. 2009. The 2006 Central Valley Chinook age-specific run size estimates. [accessed]. Santa Rosa (CA): Scale Aging Program, California Department of Fish and Game. [Find better URL or DOI and update accession date or give total no. of pages in the hard copy.]
- Grover A, Low A, Ward P, Smith J, Mohr M, Viele D, Tracy C. 2004. Recommendations for developing fishery management plan conservation objectives for Sacramento winter Chinook and Sacramento River spring Chinook. [accessed 2023 May 22]. Interagency Workgroup Progress Report to the Pacific Fishery Management Council. Available from: <https://www.pcouncil.org/documents/2004/12/c-salmon-management-march-2004.pdf/#page=100>
- Hankin DG, Logan E. 2010. A preliminary analysis of Chinook Salmon coded-wire tag recovery data from Iron Gate, Trinity River and Cole Rivers hatcheries, brood years 1978–2004. [accessed 2023 May 22]. Arcata (CA): Prepared under contract for The Hoopa Valley Tribal Council and the Arcata Office, US Fish and Wildlife Service, via the Humboldt State University Sponsored Programs Foundation. Financial support provided by the US Bureau of Reclamation, Klamath Basin Area Office. Available from: <https://www.trrp.net/DataPort/doc.php?id=1467>
- Healey MC. 1991. Life history of Chinook Salmon (*Oncorhynchus tshawytscha*). In: Groot C, Margolis L, editors. *Pacific Salmon: life histories*. Vancouver (BC): University of British Columbia Press. p. 311–394.

- Johnson RC, Lindley ST. 2016. Central Valley recovery domain. In: Williams TH, Spence BC, Boughton DA, Johnson RC, Crozier LG, Mantua NJ, O'Farrell MR, Lindley ST, editors. Viability assessment for Pacific Salmon and steelhead listed under the Endangered Species Act: southwest. [accessed 2023 May 22]. NOAA Technical Memorandum NMFS-SWFSC-564. p. 83–108. Available from: <https://repository.library.noaa.gov/view/noaa/12013>
- Kimura DK, Chikuni S. 1987. Mixtures of empirical distributions: an iterative application of the age-length key. *Biometrics* [accessed 2023 May 22];43:23–35. <https://doi.org/10.2307/2531945>
- Kormos B, Palmer-Zwahlen M, Low A. 2012. Recovery of coded-wire tags from Chinook Salmon in California's Central Valley escapement and ocean harvest in 2010. *Cal. Depart. Fish and Game Fisheries Branch Admin. Rep.* 2012–02. [accessed 2023 May 22]. Available from: <https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=162355>
- Lindley ST, Schick RS, May BP, Anderson JJ, Greene S, Hanson C, Low A, McEwan D, MacFarlane RB, Swanson C, et al. 2004. Population structure of threatened and endangered Chinook Salmon ESUs in California's Central Valley basin. [accessed 2023 May 22]. US Department of Commerce. NOAA Tech. Memo. NOAA-TM-NMFS- SWFSC-360. Available from: <https://repository.library.noaa.gov/view/noaa/3391>
- Mantua N, Johnson R, Field J, Lindley S, Williams T, Togdham A, Fanguie N, Jeffres C, Bell H, Cocherell D, et al. 2021. Mechanisms, impacts, and mitigation for thiamine deficiency and early life stage mortality in California's Central Valley Chinook salmon. *North Pacific Anadromous Fish Commission Technical Report* [accessed 2023 May 22];17:92–93. Available from: https://npafc.org/wp-content/uploads/technical-reports/Tech-Report-17-DOI/28_Mantua-et-al.pdf
- Martin SL, Stohs SM, Moore JE. 2015. Bayesian inference and assessment for rare-event bycatch in marine fisheries: a drift gillnet case study. *Ecol App.* [accessed 2023 May 22];25:416–429. <https://doi.org/10.1890/14-0059.1>
- McElhany P, Ruckelshaus MH, Ford MJ, Wainwright TC, Bjorkstedt EP. 2000. Viable salmonid populations and the conservation of evolutionarily significant units. Seattle (WA): US Dept. of Commerce. NOAA Tech. Memo. NMFS-NWFSC-42. [accessed 2023 May 22]. 174 p. Available from: <https://repository.library.noaa.gov/view/noaa/3139>
- McReynolds TR, Garman CE, Ward PD, Schommer MC. 2005. Butte Creek and Big Chico creeks spring-run Chinook Salmon, *Oncorhynchus tshawytscha*, life history investigation, 2003–2004. [accessed 2023 May 22]. Rancho Cordova (CA): California Department of Fish and Game. Inland Fisheries Administrative Report No. 2005-1. 46 p. Available from: <https://www.calfish.org/ProgramsData/ConservationandManagement/CentralValleyMonitoring/SacramentoValleyTributaryMonitoring/ButteCreek.aspx>
- McReynolds TR, Garman CE, Ward PD, Plemons SL. 2006. Butte Creek and Big Chico creeks spring-run Chinook Salmon, *Oncorhynchus tshawytscha*, life history investigation, 2004–2005. [accessed 2023 May 22]. Rancho Cordova (CA): California Department of Fish and Game. Inland Fisheries Administrative Report No. 2006-4. 37 p. Available from: <https://www.calfish.org/ProgramsData/ConservationandManagement/CentralValleyMonitoring/SacramentoValleyTributaryMonitoring/ButteCreek.aspx>
- McReynolds TR, Garman CE, Ward PD, Plemons, SL. 2007. Butte Creek and Big Chico Creeks spring-run Chinook Salmon, *Oncorhynchus tshawytscha*, life history investigation, 2005–2006. [accessed 2023 May 22]. Rancho Cordova (CA): California Department of Fish and Game. Inland Fisheries Report No. 2007-2. 43 p. Available from: <https://www.calfish.org/ProgramsData/ConservationandManagement/CentralValleyMonitoring/SacramentoValleyTributaryMonitoring/ButteCreek.aspx>
- Meek MH, Stephens MR, Goodbla A, May B, Baerwald MR. 2020. Identifying hidden biocomplexity and genomic diversity in Chinook Salmon, an imperiled species with a history of anthropogenic influence. *Can J Fish Aquat Sci.* [accessed 2023 May 22];77:534–547. <https://doi.org/10.1139/cjfas-2019-0171>
- Meyers EM. 2021. Protecting a displaced species in an altered river: a case study of the endangered Sacramento River winter-run Chinook Salmon. *California Fish and Wildlife* [accessed 2023 May 22];Special CESA Issue:172–188. <https://doi.org/10.51492/cfwj.cesasi.8>

- Mohr MS, Satterthwaite WH, Hankin DG, Bisson PA, Grimes CB, Hamelberg S, Hillemeier DC, Lindley ST, Low A, Palmer-Zwahlen ML, et al. 2017. Evaluation of alternative marking/tagging systems for hatchery produced California fall-run Chinook salmon. [accessed 2023 May 22]. NOAA Tech Memo NMFS-SWFSC-571. Available from: <https://repository.library.noaa.gov/view/noaa/14328>
- Myers JM, Kope RG, Bryant GJ, Teel D, Lierheimer LJ, Wainwright TC, Grant WS, Waknitz FW, Neely K, Lindley ST, et al. 1998. Status review of Chinook Salmon from Washington, Idaho, Oregon, and California. [accessed 2023 May 22]. NOAA Tech Memo NMFS-NWFSC-35. Available from: https://www.nwfsc.noaa.gov/assets/25/7190_07042012_124647_Myers.et.al.1998-rev.pdf
- Nichols J. 2022. Butte Creek Spring-run Chinook Salmon Adult Monitoring Annual Report 2021. [accessed 2023 May 22]. California Department of Fish and Wildlife Report. Available from: http://www.buttecreek.org/documents/2021_Butte_Creek_SRCS_Adult_Monitoring_Report_CDFW_05262022.pdf
- [NMFS] National Marine Fisheries Service. 2000. Biological opinion and incidental take statement: effects of the Pacific Coast Salmon Plan on California Central Valley spring-run Chinook, and California coastal Chinook Salmon. [accessed 2023 May 22]. [unknown]: NMFS, Southwest Region, Protected Resources Division. Available from: <https://media.fisheries.noaa.gov/2021-12/2000-biop-oceanfisheries-chinook-cv-spring-ca-coastal.pdf>
- [NMFS] National Marine Fisheries Service. 2011. Central Valley recovery domain 5-year review: summary and evaluation of Central Valley spring-run Chinook Salmon ESU. [accessed 2023 May 22]. Long Beach (CA): National Marine Fisheries Service, Southwest Region. Available from: http://www.nmfs.noaa.gov/pr/pdfs/species/centralvalley_springrunchinook_5yearreview.pdf
- [NMFS] National Marine Fisheries Service. 2014. Recovery plan for the evolutionarily significant units of Sacramento River winter-run Chinook Salmon and Central Valley spring-run Chinook Salmon and the distinct population segment of California Central Valley Steelhead. [accessed 2023 May 22]. Sacramento (CA): NMFS California Central Valley Area Office. 1561 p. Available from: https://media.fisheries.noaa.gov/dam-migration/central_valley_salmonids_recovery_plan-accessible.pdf
- [NMFS] National Marine Fisheries Service. 2016. Central Valley recovery domain 5-year review: summary and evaluation of Central Valley spring-run Chinook Salmon ESU. [accessed 2023 May 22]. Long Beach (CA): National Marine Fisheries Service, Southwest Region. Available from: <https://www.fisheries.noaa.gov/resource/document/5-year-review-summary-and-evaluation-central-valley-spring-run-chinook-salmon>
- [NMFS] National Marine Fisheries Service. 2022. National Marine Fisheries Service Report, Fisheries Science Center Activities. [accessed 2023 May 22]. Available from: <https://www.pcouncil.org/documents/2022/03/d-1-a-supplemental-nmfs-report-1.pdf/>
- O'Farrell MR, Mohr MS, Grover AM, Satterthwaite WH. 2012a. Sacramento River winter Chinook cohort reconstruction: analysis of ocean fishery impacts. [accessed 2023 May 22]. NOAA Technical Memorandum NMFS-SWFSC-491. 74 p. Available from: <https://repository.library.noaa.gov/view/noaa/4474>
- O'Farrell MR, Satterthwaite WH, Spence BC. 2012b. California Coastal Chinook Salmon: status, data, and feasibility of alternative fishery management strategies. [accessed 2023 Sep 13]. US Department of Commerce, NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-494. 34 p. Available from: <https://repository.library.noaa.gov/view/noaa/4365>
- O'Farrell MR, Mohr MS, Palmer-Zwahlen ML, Grover AM. 2013. The Sacramento Index (SI). [accessed 2023 May 22]. US Department of Commerce, NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-512. 41 p. Available from: <https://repository.library.noaa.gov/view/noaa/4449>

- O'Farrell M, Palmer-Zwahlen M, Simon J, Kormos B. 2015. An evaluation of the proposed increases in spatial stratification for California salmon fisheries. Report to Pacific Fishery Management Council. [accessed 2023 May 22]. 23 p. Available from: <https://www.pcouncil.org/documents/2015/11/agenda-item-d-2-attachment-4-2.pdf/>
- O'Farrell M, Hendrix N, and Mohr M. 2016. An evaluation of preseason abundance forecasts for Sacramento River winter Chinook salmon. Report prepared for the 2016 Salmon Methodology Review. Pacific Fishery Management Council, Portland, Oregon. [accessed 2023 May 22]. 35 p. Available from: <https://www.pcouncil.org/documents/2016/11/agenda-item-d-2-attachment-1-an-evaluation-of-preseason-abundance-forecasts.pdf/>
- Palmer-Zwahlen ML, Grover AM, Duran JA. 2006. Feather River Chinook cohort reconstruction brood years 1998 and 1999 fall and spring runs. Santa Rosa (CA): California Department of Fish and Game, Marine Region, Ocean Salmon Project Technical Report. [accessed 2023 May 22] Available from: <https://web.archive.org/web/20201021125617/http://cahatcheryreview.com/wp-content/uploads/2012/08/FRH-fall-chinook-cohort-reconstruction-report-July-04.pdf>
- [PFMC] Pacific Fishery Management Council. 2011. Final Environmental Assessment and initial regulatory impact review for Pacific Coast Salmon Plan Amendment 16: classifying stocks, revising status determination criteria, establishing annual catch limits and accountability measures, and *de minimis* fishing provisions. (Document prepared by The Ad Hoc Salmon Amendment Committee for the Pacific Fishery Management Council and National Marine Fisheries Service). [accessed 2023 May 22]. Portland (OR): PFMC. Regulatory Identifier 0648-BA55. 525 p. Available from: <https://www.pcouncil.org/documents/2011/12/salmon-fmp-amendment-16-environmental-assessment-and-regulatory-impact-review.pdf/>
- [PFMC] Pacific Fishery Management Council. 2021. Preseason report I: stock abundance analysis and environmental assessment part 1 for 2021 ocean salmon fishery regulations. (Document prepared for the Council and its advisory entities.) [accessed 2023 May 22]. Portland (OR): PFMC. Regulation identifier number. 0648-BJ97.142 p. Available from: <https://www.pcouncil.org/documents/2021/03/2021-preseason-report-i.pdf/>
- [PFMC] Pacific Fishery Management Council. 2022. Pacific Coast Salmon Fishery Management Plan for commercial and recreational salmon fisheries off the coasts of Washington, Oregon, and California as amended through Amendment 23. [accessed 2023 May 22]. Portland (OR). 92 p. Available from: <https://www.pcouncil.org/documents/2022/12/pacific-coast-salmon-fmp.pdf/>
- [PFMC] Pacific Fishery Management Council. 2023a. Preseason report I: stock abundance analysis and environmental assessment part 1 for 2023 ocean salmon fishery regulations. (Document prepared for the Council and its advisory entities.) [accessed 2023 May 22]. Portland (OR): PFMC. Regulation identifier number 0648-bl66. 146 p. Available from: <https://www.pcouncil.org/documents/2023/03/supplemental-preseason-report-i-stock-abundance-analysis-and-environmental-assessment-part-1-for-2023-ocean-salmon-fishery-regulations-electronic-only.pdf/>
- [PFMC] Pacific Fishery Management Council. 2023b. Review of 2022 ocean salmon fisheries: stock assessment and fishery evaluation document for the Pacific Coast Salmon Fishery Management Plan (Document prepared for the Council and its advisory entities.) [accessed 2023 May 22]. Portland (OR) PFMC. 368 p. Available from: <https://www.pcouncil.org/documents/2023/02/review-of-2022-ocean-salmon-fisheries.pdf/>
- Pope JG. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. ICNAF Res. Bull. 9:65–74.
- [PSC] Pacific Salmon Commission Coded Wire Tag Workgroup. 2008. An action plan in response to coded wire tag (CWT) expert panel recommendations. [accessed 2023 May 22]. PSC Technical Report No. 25. Available from: <https://www.psc.org/download/33/psc-technical-reports/2042/psctr25.pdf>

- [PSC] Pacific Salmon Commission Chinook Technical Committee. 2022. 2021 exploitation rate analysis and model calibration, volume 1. [accessed 2023 May 22]. PSC TCCHINOOK (2022)-03. Available from: <https://www.psc.org/download/35/chinook-technical-committee/14594/tcchinook-22-03.pdf>
- Satterthwaite WH, Mohr MS, O'Farrell MR, Wells BK. 2012. A Bayesian hierarchical model of size-at-age in ocean-harvested stocks—quantifying effects of climate and temporal variability. *Can J Fish Aquat Sci.* [accessed 2023 May 22];69(5):942–954. <https://doi.org/10.1139/F2012-036>
- Satterthwaite WH, Mohr MS, O'Farrell MR, Wells BK. 2013. A comparison of temporal patterns in the ocean spatial distribution of California's Central Valley Chinook Salmon runs. *Can J Fish Aquat Sci.* [accessed 2023 May 22];70(4):574–584. <https://doi.org/10.1139/cjfas-2012-0395>
- Satterthwaite WH, Ciancio J, Crandall E, Palmer-Zwahlen ML, Grover AM, O'Farrell MR, Anderson EC, Mohr MS, Garza JC. 2015. Stock composition and ocean spatial distribution inference from California recreational Chinook Salmon fisheries using genetic stock identification. *Fish Res.* [accessed 2023 May 22];170:166–178. <https://doi.org/10.1016/j.fishres.2015.06.001>
- Satterthwaite WH, Cordoleani F, O'Farrell MR, Kormos B, Mohr MS. 2018. Central Valley spring-run Chinook Salmon and ocean fisheries: data availability and management possibilities. *San Franc Estuary Watershed Sci.* [accessed 2023 May 22];16(1). <https://doi.org/10.15447/sfew.2018v16iss1/art4>
- [SJRRP] San Joaquin River Restoration Program. 2017. Fisheries framework: spring-run and fall-run Chinook Salmon. [accessed 2023 May 22]. Available from: http://www.restoresjr.net/?wpfb_dl=1055
- [SRWC WG] Ad Hoc Sacramento River Winter Chinook Work Group. 2017. Evaluation of Sacramento River winter Chinook Salmon control rules: updated management strategy evaluation analysis. [accessed 2023 May 22]. Available from: https://www.pcouncil.org/documents/2017/09/f2a_srwcr_rpt1_sept2017bb.pdf
- Sturrock AM, Satterthwaite WH, Yoshida KM, Huber ER, Sturrock HJW, Nusslé S, Carlson SM. 2019. Eight decades of hatchery salmon releases in the California Central Valley: factors influencing straying and resilience. *Fisheries* [accessed 2023 May 22];44:433–444. <https://doi.org/10.1002/fsh.10267>
- Ward PD, McReynolds TR, Garman CE. 2003. Butte and Big Chico creeks spring-run Chinook Salmon, *Oncorhynchus tshawytscha*, life history investigation, 2001–2002. [accessed 2023 May 22]. Rancho Cordova (CA): California Department of Fish and Game, Inland Fisheries. 53 p. Available from: <https://www.calfish.org/ProgramsData/ConservationandManagement/CentralValleyMonitoring/SacramentoValleyTributaryMonitoring/ButteCreek.aspx>
- Ward PD, McReynolds TR, Garman CE. 2004. Butte and Big Chico creeks spring-run Chinook Salmon, *Oncorhynchus tshawytscha*, life history investigation, 2002–2003. [accessed 2023 May 22]. Rancho Cordova (CA): California Department of Fish and Game, Inland Fisheries Administrative Report No. 2004-6, 2004. 43 p. Available from: <https://www.calfish.org/ProgramsData/ConservationandManagement/CentralValleyMonitoring/SacramentoValleyTributaryMonitoring/ButteCreek.aspx>
- Yoshiyama RM, Fisher FW, Moyle PB. 1998. Historical abundance and decline of Chinook Salmon in the Central Valley region of California. *North Am J Fish Management.* [accessed 2023 May 22];18(3):487–521. [https://doi.org/10.1577/1548-8675\(1998\)018<0487:HAAD OC>2.0.CO;2](https://doi.org/10.1577/1548-8675(1998)018<0487:HAAD OC>2.0.CO;2)
- Yoshiyama RM. 2001. Yoshiyama RM, Gerstung ER, Fisher FW, Moyle PB. 2001. Historical and present distribution of Chinook Salmon in the Central Valley of California. *California Department of Fish and Game Fish Bulletin.* [accessed 2023 May 22];179:71–176. Available from: https://www.researchgate.net/publication/242536414_Historical_and_Present_Distribution_of_Chinook_Salmon_in_the_Central_Valley_Drainage_of_California

NOTE

Mohr MS. 2006. Klamath River fall Chinook assessment: overview. Unpublished report. Santa Cruz (CA): National Marine Fisheries Service. Available from: Michael R. O'Farrell, National Marine Fisheries Service, 110 McAllister Way, Santa Cruz, CA 95060, USA.