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Life History and Population Dynamics of Chinook Salmon in the Central Valley

By

Emily Katherine Chen

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

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of the

University of California, Berkeley

Committee in charge:

Professor Stephanie M. Carlson, Chair

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Summer 2024

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Abstract

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The complex and seasonal landscape of the California Central Valley produces a mosaic of habitat niches for Chinook salmon (*Oncorhynchus tshawytscha*) to occupy. Diversity in life history enables Chinook salmon to widely distribute across habitats and over time, reducing competition and hedging against environmental disturbances, resulting in overall more abundant and stable populations. Human activity including habitat alteration and resource extraction can eliminate ecological niches available to Chinook salmon and reduce their life history diversity. Maintaining this important element in the face of natural resource demands and climate change requires understanding how human activities influence life history expression and the various life history types. Hatcheries artificially producing salmon to supplement natural populations are pervasive in the Central Valley. Practices during the breeding, rearing, and release process can result in trait divergence between hatchery and natural-origin salmon. Trait differences can result in differential impacts from human activity and potentially bias inferences drawn directly from hatchery fish data for managing the natural or combined population. Throughout the dissertation, I compared the life history of hatchery- and natural-origin fish and evaluated how their distinct traits could influence impact from human activity. For each chapter, I explored how life history shapes population dynamics and affects assessment tools used in managing Chinook salmon. In Chapter 1, I found that natural-origin Sacramento River winter-run Chinook salmon use the basin far more extensively than hatchery-origin fish when migrating to the ocean and have greater habitat needs than what would be suggested from hatchery fish data alone. In Chapter 2, I found winter-run hatchery fish return from the ocean to spawn at earlier and more homogenous ages, which suggests natural-origin fish may be more impacted by ocean fisheries because of their later maturation ages. In Chapter 3, I found trends in maturation schedules for Sacramento River fall-run Chinook

salmon over time have contributed to forecast error in management models used to guide harvest policies. Overall, this dissertation demonstrates that understanding life history diversity and population dynamics can help natural resource managers make well-informed and cost-effective decisions that maintain the integrity and long-term persistence of threatened salmon populations.

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INTRODUCTION

Life history diversity within and across populations results in independent population dynamics that stabilize population complexes (Schindler et al. 2010; Carlson and Satterthwaite 2011). Diversity in life history traits such as habitat selection, migration timing, and maturation schedules contributes to spatial and temporal variation within populations. As a result, individuals distributed across space and time experience different environmental conditions and the population is less vulnerable to catastrophic disturbances and extinction risk (Koski 2009; Greene et al. 2010; Cordoleani et al. 2021). Life history diversity also lowers density in a single habitat at a given instance, reducing intra-specific competition and other density-dependent effects. Populations with diverse life histories are thus able to support greater abundances (Schroeder et al. 2016).

Chinook salmon (*Oncorhynchus tshawytscha*) in the Central Valley of California are an exemplary case of life history radiation. The diverse landscape within the basin and the highly seasonal climate produces a time-varying mosaic of habitat niches for a multitude of life histories to be expressed. In this basin, Chinook salmon populations are classified into four ecotypes: fall, late-fall, winter, and spring, named after the season they return to spawn (Fisher 1994). In addition to returning to spawn at different times of year under different flow conditions, the ecotypes spawn in different parts of the basin and spend different amounts of time in the river before they migrate to the ocean. In the ocean, these ecotypes occupy different regions along the coast and mature at different ages (Satterthwaite et al. 2013). Considerable variation in these characteristics also exists within ecotypes of population. Because of this life history radiation, Chinook salmon are present in the Central Valley year-round, and the basin possesses the greatest abundances of Chinook salmon both historically and currently in the state. Chinook salmon in the Central Valley have been important for the livelihoods, culture, and economics of people living in California for millennia.

Intense past and present land use (i.e., dams, mining, water diversion, agriculture, and flood control) and fisheries have decimated some life histories and depleted Chinook salmon abundance to a fraction of historical abundance overall (Yoshiyama et al. 1998). Supporting Chinook salmon populations in the system requires understanding the impact of natural resource use (e.g., fisheries, water) on the various life histories. Because human activity can selectively impact subsets of the population, such as fisheries impacting older individuals or dams impacting life histories that spawn further upriver, knowing which portion of the population is affected by management decisions is important for avoiding impact on already vulnerable life histories (Yoshiyama et al. 1998; Kendall and Quinn 2013). The loss of life history diversity within a population removes buffering capacity against disturbance and can preclude extirpation. Preserving diversity is important for maintaining viable populations long-term (Adams et al. 2011).

Due to the loss and degradation of habitat, which has dramatically reduced the abundances of wild populations, hatchery-origin Chinook salmon are pervasive in the Central Valley. Multiple hatcheries in the Central Valley together release tens of millions of juvenile salmon each year (Huber and Carlson 2015; Sturrock et al. 2019). Hatchery programs can have different goals, such as producing fish for fisheries (a production hatchery) or producing listed fish for conservation (a conservation hatchery). The objectives of the hatchery program shape the volume of fish produced and hatchery protocols regarding breeding (e.g., broodstock selection, mate pairings), rearing, and release (e.g., release location). While hatchery supplementation can have positive benefits on natural populations by supporting their abundances, especially in years of critically low abundance, hatchery supplementation can have negative impacts on natural populations through increased competition, reduced genetic integrity and fitness, and disease transmission (Brown and Day 2002; Naish et al. 2007). Minimizing adverse impacts requires understanding how hatchery and naturally produced fish differ and where in the environment and at which life stages they may overlap. For the first two Chapters of the dissertation, I focused on comparing the life history differences between natural- and hatchery-origin endangered winter-run Chinook salmon produced as part of a conservation hatchery program at Livingston Stone National Fish Hatchery.

In Chapter 1, I compared differences in juvenile life history traits (e.g., habitat use, migration times, size) between hatchery- and natural-origin winter-run Chinook salmon to evaluate how differences could result in bias in management and protections for this endangered population. Due to their accessibility and abundance, hatchery fish are often used as surrogates for natural-origin fish in monitoring and management (Weitkamp 2010; O'Farrell et al. 2012; Som et al. 2019). However, differences in life history between origin types could result in bias when applying data collected from hatchery fish directly to management of natural-origin fish. Using otoliths collected from returning hatchery and natural-origin spawners, I found that natural-origin fish used the basin far more extensively and that hatchery fish had shorter residence times in the river and more homogenous juvenile life histories. These differences emphasize the extensive habitat needs for natural-origin winter-run Chinook salmon to maintain their life history diversity and the need to consider life history differences between hatchery- and natural-origin fish when using hatchery data as a proxy for natural-origin fish.

Chapter 2 compared the age structure and maturation schedule of hatchery- and natural-origin fish from the same population and evaluated how fishery impacts may differ between origin types because of their age structure. Age structure is a key demographic variable that influences the productivity, survivorship, and stability of the population. Maturation schedules shape the age structure of the population and are determined by the trade-off between higher fecundity but lower survivorship with age (Hutchings 2021). Differences between the maturation schedules of hatchery and natural-origin fish can indicate changes in the trade-off because of hatchery influence. I compared the maturation

rates of natural-origin and hatchery fish using scales and coded-wire tags collected from returning adults and found that compared to natural-born fish, hatchery fish had higher rates of maturing at age three rather than age four. This difference occurred only in males, suggesting mating practices and reproductive success in the hatchery may differ from the wild. Later ages of maturity would suggest the natural-origin component is exposed to more fishing prior to spawning and may be experiencing greater fishery impacts than those reported for hatchery fish (Kendall and Quinn 2013).

Unlike endangered winter-run Chinook salmon, fall-run Chinook salmon are produced in production hatcheries at very high volumes to support fisheries off the coast of California and in the river. As one of the largest populations and an indicator stock for the fisheries, preseason forecasts for this population have large influence on annual fishing regulations off the California and Southern Oregon coast (PFMC 2024). The abundance of fall-run Chinook salmon has been overestimated in the last eight of ten years (PFMC 2023b), indicating changes to the population dynamics may be occurring, specifically in the age structure of population as forecasts are estimated using an age-based model. In Chapter 3, I quantified the maturation schedules of fall-run Chinook salmon over time and evaluated the benefits of incorporating more age structure information into forecast models. I found that maturation rates for the hatchery-origin component have been increasing over time, and years with elevated age-2 maturation rates correspond to years the management model overestimated abundance, suggesting increases in age-2 maturation contributed to forecast error. I conducted closed-loop simulations to evaluate the potential improvements in accuracy from incorporating more age structure information and found little to no improvement in forecasting ability, in large part due to the young age structure of the population and variability in maturation rates across time. Knowing the population structure and how population dynamics are changing is necessary for management planning in the future when the environment is expected to continue to change and become more variable and extreme.

Overall, this dissertation furthered our understanding of Chinook salmon life history in California's Central Valley for the purpose of informing management decisions and improving assessment tools. For each chapter, I described the life history and vital rates of components of the population and evaluated the impact of differences between life histories on assessments and management for the whole population. Each of these Chapters demonstrated that improving our understanding of Chinook salmon life history can help natural resource managers make more informed and effective decisions.

ACKNOWLEDGEMENTS

Chapter 1. Juvenile life history, migration, and habitat use of natural- versus hatchery-origin Chinook salmon

Abstract

Rearing fish in an artificial environment combined with various husbandry decisions can result in divergence of hatchery fish from natural-origin fish. Changes in the behavior, life history, and selective forces on hatchery fish can lead to lowered fitness and loss of life history diversity, reducing the population's overall productivity and resilience. We evaluated the downstream migration behavior, habitat use, and relative growth rates of hatchery and natural-origin juvenile winter-run Chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento River system. Otoliths collected from adult carcasses were analyzed, namely their strontium isotope chemistry and daily increment widths to characterize habitat use, migration timing, and growth. Because of their hatchery rearing period, hatchery fish had much shorter residence times in the river than natural-origin fish. Beyond the reduced duration of river residence, hatchery fish occupied fewer areas of the watershed during ocean outmigration. Despite these differences in outmigration behaviors, adults from both groups reached saltwater at similar sizes and ages as juvenile smolts. Considering differences in habitat use and timing between hatchery and natural-origin fish is critical to avoiding bias when applying data collected from hatchery fish to manage and conserve natural populations.

1. INTRODUCTION

While hatcheries are intended to support and, in some cases, replace lost natural production (e.g., dam mitigation, Maynard and Trial 2014), hatchery fish can differ from naturally produced fish due to broodstock selection, artificial rearing environments and release logistics (Brown and Day 2002). Environmental conditions in the wild shape the behavior (e.g., predator avoidance, social dominance), life history (e.g., age at maturity), and ultimately selection on natural populations, which can be dramatically altered in a hatchery (Berejikian et al. 2001; Yamamoto and Reinhardt 2003; Shearer et al. 2006). Wild Pacific salmon and trout can exhibit complex variation in their life history expression, including the timing and pathway of migrations. This diversity in movement can augment growth and/or survival if habitats outside of their natal habitat exhibit differing levels of food, predator and conspecific densities and water quality (Koski 2009; Schroeder et al. 2016). Off-channel habitats, tributaries, floodplains, and estuaries can serve as important non-natal habitats for fish to grow in prior to entering the ocean (Ebersole et al. 2006; Jeffres et al. 2020; Rossi et al. *in review*). This life history diversity spreads risk across the landscape and can increase overall population productivity (Greene et al. 2010).

Chinook salmon in hatcheries are limited to the rearing conditions of the hatchery prior to their release. A handful of studies has explored how migratory tactics and habitat use differ between hatchery and wild fish, typically reporting that hatchery fish migrate more quickly and use a subset of available habitats as compared to wild fish (Levings et al. 1986; del Real et al. 2012). Hatchery programs can release fish at sizes and times that deviate from natural life histories to increase survivorship and minimize interactions with natural populations (Huber and Carlson 2015; del Real et al. 2012; Huber et al. 2024). Differences in behavior, life history, and survival between hatchery and natural-origin fish have the potential to lead to different population dynamics that could reduce long term ecological resilience (Sturrock et al. 2019).

Due to their abundance and accessibility, hatchery salmon are often used as surrogates of wild fish to infer the conditions experienced by their wild counterparts. Prior to release, large numbers of hatchery fish can be implanted with tags to estimate reach-specific and lifetime survival rates to provide insights into the in-river and ocean conditions wild fish may be experiencing. Indeed, tagged hatchery fish often serve as proxies for wild fish in management and research (Weitkamp 2010; Fujiwara et al. 2011; O'Farrell et al. 2012; Som et al. 2019). However, the influence of the hatchery environment and release methods on the behavior and life history of hatchery fish raises questions about whether they are reliable surrogates for natural-origin fish. Understanding the potential biases when using hatchery fish as a proxy is critical to accurately interpreting management models and making informed decisions for the natural population.

The California Central Valley, which includes the Sacramento River and San Joaquin River drainages, comprises a large fraction of the state and has been highly altered by human activities (Yoshiyama et al. 1998). The watershed hosts four distinct runs of Chinook salmon (*Oncorhynchus tshawytscha*), historically supporting high total abundances through diverse life histories. Today, most major rivers in the system are

blocked by large impassable dams that block access to the majority of suitable spawning and rearing habitat (Lindley et al. 2006) and alter downstream flow regimes (Brown and Bauer 2010), resulting in the loss and reduction of many salmonid populations. Outmigrating juvenile salmon experience elevated mortality in the heavily altered Sacramento-San Joaquin Delta due to habitat degradation, major water diversion projects (e.g., Kimmerer 2008), and the introduction of non-native predators (Michel et al. 2020). In recent years, biotelemetry studies on hatchery fish implanted with acoustic tags have allowed for a higher-resolution understanding of migration survival and movement. However, most of these studies have focused on larger, smolt-size hatchery fish of at least 80 mm, because they are large enough to be implanted with a tag without a tag burden that impacts their health or behavior (Perry et al. 2010; Buchanan et al. 2018; Hassrick et al. 2022).

Otolith ("earstone") chemistry represents another approach for evaluating fish movement, utilizing natural tags from the ambient water to provide insight into the early life stages of fish that are too small to physically tag. Otoliths are internal calcified structures that are frequently used to understand the age and life history of fish because they typically grow isometrically to body length, and growth rings are deposited both daily (Neilson and Geen 1982) and annually (Campana & Thorrold 2001). As they grow, otoliths incorporate ions from the surrounding environment, making it possible to determine the habitat used by an individual during a specific period of life (Campana and Thorrold 2001; Claiborne and Campbell 2016). Within the Sacramento Basin, some tributaries have unique geologic composition and strontium isotope ratios (87Sr/86Sr) resulting in an ^{87}Sr/^{86}Sr "isoscape" that makes it possible to assess natal-origin and movement between regions of the watershed (Barnett-Johnson et al. 2008; Phillis et al. 2018). The strontium concentration and isotope ratio also differ between marine and freshwater, making it possible to identify when the fish had entered the ocean (Miller et al. 2010).

Winter-run Chinook salmon in the Sacramento River are currently listed as endangered under the federal and California Endangered Species Acts (Good et al. 2005). Their designated critical habitat includes the Sacramento mainstem, the westward margin of the Delta, and the northern half of the San Francisco Bay (Federal Register 1993). Conserving the population requires relying on information on their habitat use needs and how aspects of the riverscape influence their growth and survival, and ultimately their reproductive success (Johnson et al. 2017). Previous work using otolith isotope chemistry revealed that natural-origin winter-run Chinook salmon are the most nomadic of all Central Valley salmon runs, making extensive use of the watershed and often rearing in habitats outside of the designated critical habitat (Phillis et al. 2018; Morais et al. *in review*). Another recent study using acoustic-tagged hatchery fish evaluated how the residence time of winter-run hatchery fish varies with spring flows in the upper Sacramento River (Hassrick et al. 2022), but it is unclear whether these residence times and flow sensitivities also apply to natural-origin fish that initiate downstream migration months earlier than hatchery fish. Using data collected from hatchery fish for managing the natural-origin population could potentially bias assessments and lead to less effective actions if managers do not account for differences.

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In this study, we provide a much-needed comparison of the outmigration behaviors of hatchery and natural-origin winter-run Chinook salmon. We did this by reconstructing the freshwater life history of hatchery and natural-origin fish through microstructural and chemical analyses of otoliths collected from returning adults. Specifically, we compared 1) juvenile habitat use, 2) residence time in the system, and 3) size-at-age and relative growth of juveniles. Our approach allowed us to directly compare the early life history and migration patterns of hatchery and natural-origin fish and determine the conditions and life stages when hatchery fish provide good surrogates for natural-origin winter-run Chinook salmon.

2. MATERIALS & METHODS

2.1 Study Site and Population

Winter-run Chinook salmon were historically comprised of multiple populations that spawned in the upper Sacramento River and its tributaries, on the land of the Wintu, Yana, Achomawi, and Atsugewi peoples (University of California 1995; Good et al. 2005). Establishment of major water and flood control projects, including reservoirs, diversions, and levees, has dramatically impacted habitat conditions for Sacramento River winter-run Chinook salmon (Yoshiyama et al. 1998). Construction of Shasta and Keswick dam blocked access to historic spawning and rearing habitats, and currently, the vast majority of natural-origin winter-run Chinook salmon spawn as a single population below Keswick Dam. Efforts are underway to reintroduce winter-run Chinook salmon to historic habitats such as Battle Creek and the McCloud River in order to expand and diversify the ESU (Evolutionary Significant Unit) and restore winter-run Chinook salmon in their historical range (ICF International 2016, NMFS 2016; Federal Register 2023).

Winter-run Chinook salmon spawn from May to July, and fry typically emerge in August and September (Jennings and Hendrix 2020). In most years, the majority of juveniles migrate past Red Bluff Diversion Dam in the upper Sacramento River in October and peak migration through the lower Sacramento River past Knights Landing occurs anytime between November and March depending on the timing of high flow events during the wet season (del Rosario et al. 2013; Bellido-Leiva et al. 2021). Based on trawl surveys, smolts typically exit the legal Delta near Chipps Island in March and April (del Rosario et al. 2013). In the ocean, winter-run Chinook salmon tend to remain off the California coast, and are primarily encountered by recreational and commercial fisheries in the Monterey and San Francisco areas south of Point Arena (Satterthwaite et al. 2015). Winter-run Chinook salmon rear for one to three years at sea, and adults reenter the watershed from November onwards to spawn as two-, three-, and four-year-olds (Killam 2021; Chen et al. 2023).

The winter-run Chinook salmon hatchery program at Livingston Stone National Fish Hatchery was established in 1997 and has the overarching purpose to sustain and recover the population (Good et al. 2005). A key objective of this conservation hatchery is to maintain stock integrity and minimize harmful genetic and ecological interactions with

natural-origin fish (USFWS 2016). To do this, the hatchery program uses natural-origin fish as broodstock whenever possible and selects individuals for inclusion in the broodstock with traits (e.g., run timing and size) that are representative of the entire run. Juvenile fish are released in the upper Sacramento River during high flow events in February after most natural-origin fish have initiated their downstream migration. Hatchery winter-run fish implanted with acoustic tags spend about 30 days rearing and migrating in the mainstem Sacramento River, although this can vary among individuals and across years (Hassrick et al. 2022). The proportion of hatchery to natural-origin fish on the spawning grounds has usually been less than 30 percent, but the proportion was over 80 percent in 2017 and 2018 due to large hatchery cohorts in 2014 and 2015 during a multi-year drought when survival of natural-origin fish was exceptionally low (Meyers 2021). Production of hatchery fish has increased over time, including a 50 percent increase in 2022, due to low returns of natural-origin fish (NMFS 2023a).

2.2 Sample Collection and Analysis

We analyzed sagittal otoliths collected from adult carcasses during spawning ground surveys on the Sacramento River by the United States Fish and Wildlife Service and California Department of Fish and Wildlife and from the Livingston Stone National Fish Hatchery (Table I-1). Winter-run Chinook salmon spawn from May to July when no other runs are spawning, eliminating the possibility of other runs in our samples. As the hatchery adipose clips all hatchery fish prior to release, a sample was considered hatchery origin if the adipose fin of the adult carcass was clipped. A sample was considered natural origin if the adipose fin was present, although misclips and adipose fin regeneration may occur (Kinziger et al. 2022). For this analysis, otoliths from natural-origin fish returning to spawn from 2007-2009 and 2015-2019 (n = 970) were compared to hatchery-origin otoliths from 2008-2009 and 2015-2019 (n = 263), but primarily 2015, 2018, and 2019 due to the larger sample sizes available in those years (Table I-1). Otoliths were thin sectioned in the sagittal plane by rough polishing both sides until the core and early increments were exposed using 600 and 1500 grit wet/dry sandpaper. A final smooth polish was achieved using 3- and 1-micron Al_2O_3 lapping films (Barnett-Johnson et al. 2007).

Table I-1 Summary of hydrology and sample sizes in years included in the analysis. Otolith chemistry informed habitat use at size, while the addition of daily increment analysis on a subset of samples informed residence times and relative growth rates.

Escape Year	Brood Year*	Migrant Year*	Start Flow[a]	Peak Flow[b]	Mean Flow[c]	Year Type[d]	Otolith chemistry		with increment analysis		Previously reported in
							Natural	Hatchery	Natural	Hatchery	
2007	2004	2005	Dec 8	40645	8263	AN	29	0	0	0	Phillis et al. 2018
2008	2005	2006	Dec 2	88950	20929	W	90	1	0	0	Phillis et al. 2018
2009	2006	2007	Dec 13	28946	7970	D	67	5	0	0	Phillis et al. 2018
2015	2012	2013	Nov 30	37441	7957	D	305	58	0	0	Morais et al. *in review*
2016	2013	2014	Mar 4	19604	5804	C	186	3	0	0	Morais et al. *in review*
2017	2014	2015	Dec 4	63646	7020	C	27	3	0	0	Morais et al. *in review*
2018	2015	2016	Dec 21	44458	9518	BN	128	108	83	37	This manuscript
2019	2016	2017	Nov 20	93096	23784	W	138	85	78	33	This manuscript

*The brood year and outmigration year assume all individuals returned age 3 (Chen et al. 2023).

[a] Start Flow is the first date from Sept 1 when daily mean flow exceeds 15,000cfs at Bend Bridge gauge station (California Department of Water Resources 2023).

[b] Peak Flow is the highest recorded mean daily flow (in cfs) at Bend Bridge gauge station from Sept 1 to Mar 31.

[c] Mean Flow is the mean daily flow at Bend Bridge gauge station from Sept 1 to Mar 31 each year.

[d] Sacramento Valley Water Year Classification according to California Department of Water Resources for Oct 1 of Brood year to Oct 1 of Migrant Year (W = Wet; AN = Above Normal; BN: Below Normal; D = Dry; C = Critical) (California Department of Water Resources 2023).

Otolith ^{87}Sr/^{86}Sr and total strontium voltage were measured using a multiple collection laser ablation inductively coupled mass spectrometry (MC-LA-ICPMS) at the UC Davis Interdisciplinary Center for Plasma Mass Spectrometry following established protocols (Barnett-Johnson et al. 2007; Sturrock et al. 2015). The strontium measurements were sampled with a spot transect starting from the core and extending 800 microns towards the dorsal edge, far enough to include the entire natal portion of the otolith and past the transition into ocean residence. Each spot was 40 microns in diameter and pulsed at 10 Hz for 20 seconds with a fluence of ~4-6 J/cm2. Instrument bias and drift were monitored by periodically measuring the ocean residence portion within the sampled otoliths which have a known ^{87}Sr/^{86}Sr global marine value of 0.70918. Analyzed otoliths were later imaged in 100x magnification with a Q-Imaging digital camera (MicroPublisher 6 CCD) and the distance of each spot (i.e., otolith radius) was measured from the most dorsal-posterior primordia along a standardized transect in Image-Pro Premier. We interpolated the isotope ratio between measurements by assuming a linear relationship between each point.

2.3 Habitat Use Reconstructions

We characterized habitat use of individual fish by assigning sections of the otolith transect to parts of the watershed or the ocean based on measured ^{87}Sr/^{86}Sr values and the logical progression of downstream migration. Individuals were characterized into a juvenile life history based on their habitat use. For the isoscape, we used ^{87}Sr/^{86}Sr ranges established in Phillis et al. (2018), which were based on a series of water and juvenile otolith sample collections, to assign a habitat to every section of the otolith (Table I-2). We assumed all natural-origin fish were born in the Sacramento River, even though early ^{87}Sr/^{86}Sr values were sometimes higher because fish were still receiving nutrients from the maternally derived yolk sac, which has marine-derived nutrients, and thus an elevated isotopic ratio.

Table I-2. ^{87}Sr/^{86}Sr for the ocean and regions of the Sacramento River watershed, sorted based on ^{87}Sr/^{86}Sr range. The American River and Estuary/Ocean were further distinguished using strontium voltage, a proxy for strontium concentration (see below and Supplement Material of Phillis et al. 2018).

Region	^{87}Sr/^{86}Sr range
Lassen tributaries	< 0.70467
Sacramento River	0.70467 – 0.70600
Delta or Feather River	0.70600 – 0.7082
American River	> 0.7082
Estuary/Ocean	> 0.7082

Sections of the otolith transect with $^{87}Sr/^{86}Sr$ values below the range of the Sacramento River mainstem were considered to indicate periods of non-natal rearing in tributaries in the Lassen volcanic region, including Mill, Deer, Battle, Mud, Dye, Toomes and Antelope Creeks (Morais et al. *in review*). These creeks have overlapping $^{87}Sr/^{86}Sr$ values all below the Sacramento River mainstem $^{87}Sr/^{86}Sr$ range, and measurements in this range were collectively grouped as the "Lassen tributaries". The Feather River and Delta have similar $^{87}Sr/^{86}Sr$ values and were not distinguished separately, although fish that rear in the Feather River may sometimes show a subsequent decrease in $^{87}Sr/^{86}Sr$ as they reenter the Sacramento River. The Delta is on the migration route to the ocean and most fish show periods of being in the Delta. Fish can stop and reside in the Delta, and we considered a span of measurements greater than 120 μm (approximately 40 days) in this range to be an indicator of residing in the Delta or Feather River. Fish with sections spanning less than 120 μm in this range were considered to have only used the Delta as a migratory corridor.

One challenge to using $^{87}Sr/^{86}Sr$ to infer habitat use in the Sacramento River Basin is that the lower end of the American River $^{87}Sr/^{86}Sr$ range overlaps with the $^{87}Sr/^{86}Sr$ range of the estuary and ocean. To distinguish whether $^{87}Sr/^{86}Sr > 0.7082$ reflects the American River or the estuary and ocean, we inferred the otolith strontium concentration from strontium voltage. Concentrations of strontium in freshwaters of the Sacramento Basin, including the American River, are multiple orders of magnitude lower than in marine waters (Weber 2002; Phillis et al. 2011). Therefore, $^{87}Sr/^{86}Sr$ values that exceed 0.7082 but do not have a corresponding increase in strontium voltage were assumed to be from the American River (Phillis et al. 2018). We identified the transition point to brackish water in the strontium voltage profile, identifying a single transition point through breakpoint analysis. A breakpoint analysis for each sample is robust to the variation of strontium voltage values observed across samples. A breakpoint is identified that divides the strontium voltage profile into two lines of different slopes while minimizing residuals (Zeileis et al. 2022). Sections of the otolith transect with $^{87}Sr/^{86}Sr > 0.7082$ were considered periods of rearing in the American River if they occurred prior to the breakpoint in the strontium voltage profile.

While winter-run Chinook salmon were rearing in the hatchery, $^{87}Sr/^{86}Sr$ was generally higher than $^{87}Sr/^{86}Sr$ values of the Sacramento River mainstem where the hatchery is located because of their marine-derived diet, often overlapping with the $^{87}Sr/^{86}Sr$ range of the Delta (Weber 2002; Barnett-Johnson et al. 2008). We identified when a hatchery fish was released into the upper Sacramento River when $^{87}Sr/^{86}Sr$ was first within the range of the Sacramento mainstem's $^{87}Sr/^{86}Sr$ values. In many instances, hatchery fish migrated downstream quickly and no rearing in the mainstem was detected, making it difficult to distinguish Delta rearing from hatchery rearing without mainstem $^{87}Sr/^{86}Sr$ values separating the two stages. Consequently, we excluded these samples (n = 41) when estimating residence time and growth in the hatchery and Delta for hatchery-origin fish. Finally, the $^{87}Sr/^{86}Sr$ value of water within the Delta does not exceed 0.7082, so measurements greater than 0.7082 not categorized as the American River were considered to reflect rearing in the estuary and ocean. We refer to this as "ocean entry", although this may include rearing in the San Francisco Estuary.

2.4 Residence time

Residence time in each habitat was estimated for a subset of otoliths from 2018 and 2019 that were imaged and had their microstructure analyzed. The specific samples analyzed and included in the residence time analyses were chosen based on the visibility of daily increments. Next, we imaged the otoliths at 200x magnification using a Canon Rebel XS camera and program EOS Utility 2 (Version 2.14) and marked and measured them using ImageJ (Version 1.53). Following the same transect as $^{87}Sr/^{86}Sr$ measurements, we measured the widths of increments from the dorsal-posterior primordia towards the dorsal side of the otolith. We measured at least the first 200 increments starting from the exogenous feeding check to evaluate the age and size of fish within the individual's first 200 days from exogenous feeding (Barnett-Johnson et al. 2007). To evaluate the residence time in each habitat, we totaled the number of increments present within each section of the otolith assigned to a particular habitat (Neilson and Geen 1982). We summarized and compared the residence time in each habitat for natural- and hatchery-origin fish.

2.5 Size, age, and relative growth

The size and age at which fish transitioned to a new habitat was estimated by measuring the otolith radius and counting the number of increments present between the exogenous feeding check and the first increment within the new habitat's $^{87}Sr/^{86}Sr$ range (Claiborne and Campbell 2016). To test whether the size and age at ocean entry differed between origin types and among years, we compared the otolith radius and age at ocean entry in hatchery and natural-origin fish across years using two-way ANOVAs after evaluating the data for normality and homoscedasticity. Because of limited hatchery-origin microstructure samples prior to 2018, we only compared samples from 2018 and 2019 when there were sufficient and comparable sample sizes in the two-way ANOVA for ocean entry age.

We used daily increment widths to assess whether habitat, life history type, origin, and/or escapement year affected juvenile salmon growth. Juvenile salmon growth rates vary ontogenetically (Coleman et al. 2022), and the samples in this study exhibited a nonlinear relationship between increment width and age. We fit a generalized additive mixed-effects model (GAMM) using a smoothing function for distance from center using the R package "mgcv" (Wood 2023). Because increment measurements within each sample are non-independent, we included a random intercept effect for each sample and specified an autocorrelation structure of order 1 (Coleman et al. 2022). Habitat, life history, origin, and escapement year were included as covariates in the full model, and nested versions of the full model were compared using Akaike's information criterion scores (Burnham and Anderson 2002). We checked models for lack of residual autocorrelation and checked the residuals for normality and homoscedasticity.

3. RESULTS

3.1 Habitat Use

Examination of otolith ^{87}Sr/^{86}Sr patterns across sources revealed that natural-origin fish used the basin much more extensively than hatchery fish did following release (Figure I-1). Importantly, a mean of 48.4 percent of returning natural-origin fish across years used non-natal tributaries as juveniles. In particular, 21.0 percent (sd = 8.0 percent) reared in tributaries within the Lassen volcanic region (e.g., Battle Creek, Deer Creek, Mill Creek) while 13.2 percent (sd = 8.0 percent) of fish showed evidence of rearing in the American River (Figure I-2). Another 14.2 percent (sd = 4.8 percent) of natural-origin fish reared in the Feather River or Delta for an extended period of time (at least ~ 40 days). Overall, large proportions of natural-origin winter-run fish reared in non-natal habitats every year (Figure I-2), including years with different hydrologies (summarized in Table I-1).
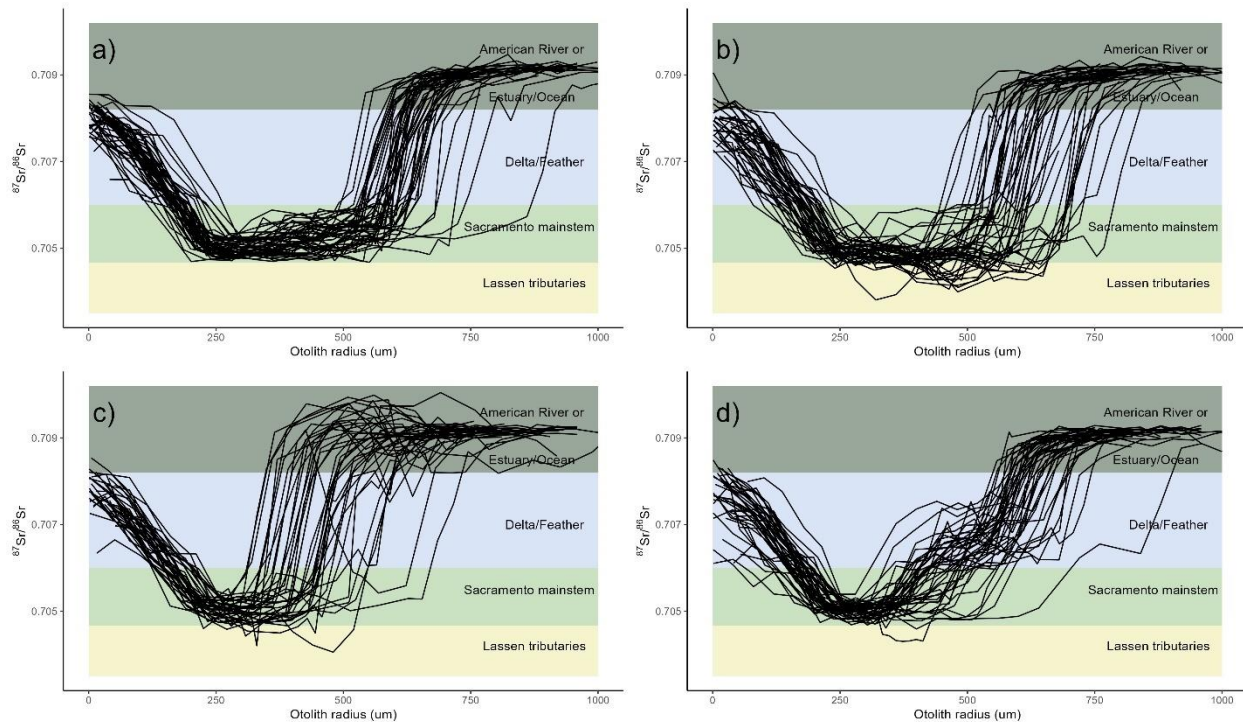
Figure I-1. Strontium isotopic ratio profiles of natural-origin fish with a) Sacramento River mainstem rearing only, b) non-natal rearing in Lassen region tributaries, c) non-natal rearing in the American River rearing, and d) non-natal rearing in the Feather River or Delta. Fifty samples were randomly selected among analyzed samples for each type for this example.
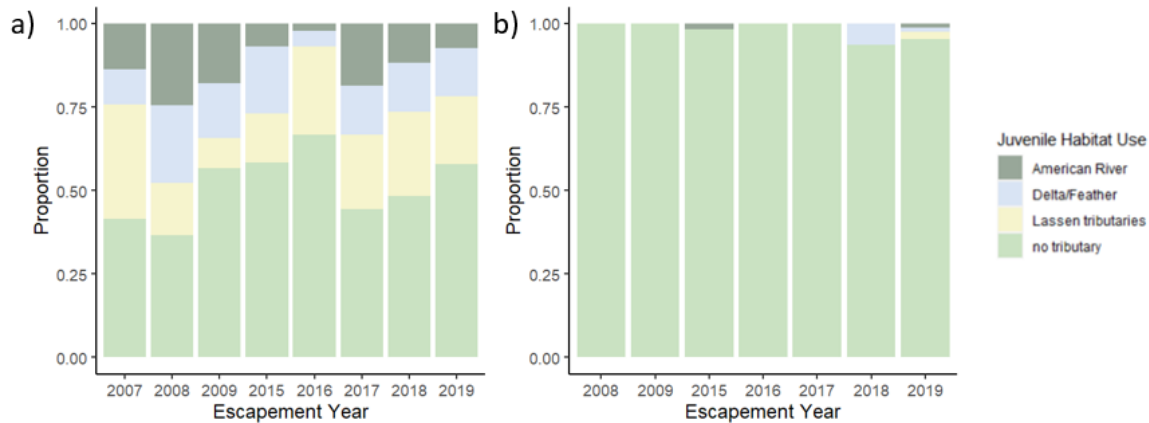
Figure I-2. Juvenile habitat use of returning a) natural-origin and b) hatchery-origin winter-run Chinook salmon by escapement year.

In contrast, of the 263 hatchery-origin otoliths analyzed, only twelve samples (~5 percent) showed evidence of non-natal rearing (Figure I-2). Even though hatchery fish migrate through the Delta, they did not rear for extended periods like natural-origin fish. Because of the resolution of the strontium isotope transect measurements, we may not detect the Sacramento River mainstem signature if fish were only in the mainstem for a short period of time prior to ocean entry. This occurred in approximately 30 percent of hatchery fish samples and was highly variable across years (range: 0 – 69 percent) (Appendix A Figure A-1).

3.2 Residence time, size, age, and relative growth

We quantified the residence time, size, age, and relative growth of returning natural- and hatchery-origin adults (Table I-1). Hatchery fish spent a mean of 118 days (sd = 31 days) after emergence rearing in the hatchery. For hatchery fish in which we were able to detect the transition from the hatchery to the Sacramento River mainstem, the mean otolith radius at which we detected the mainstem's $^{87}Sr/^{86}Sr$ range was 486 μm. Hatchery fish reared for a much shorter time in the Sacramento mainstem once they were released compared to natural-origin fish. The mean duration hatchery fish were detected in the Sacramento River mainstem, including samples with no mainstem rearing detected, was 11 days (sd = 16 days) compared to natural-origin fish which were detected in the mainstem for an average of 129 days (sd = 37 days) from exogenous feeding (Figure I-3). Faster-migrating hatchery fish without any measurements within the mainstem's $^{87}Sr/^{86}Sr$ range were excluded from our estimates of residence time in the hatchery and the Delta because we were unable to distinguish hatchery and Delta rearing, which may bias mean residence times if these fish reared in the hatchery or Delta for longer or shorter periods.

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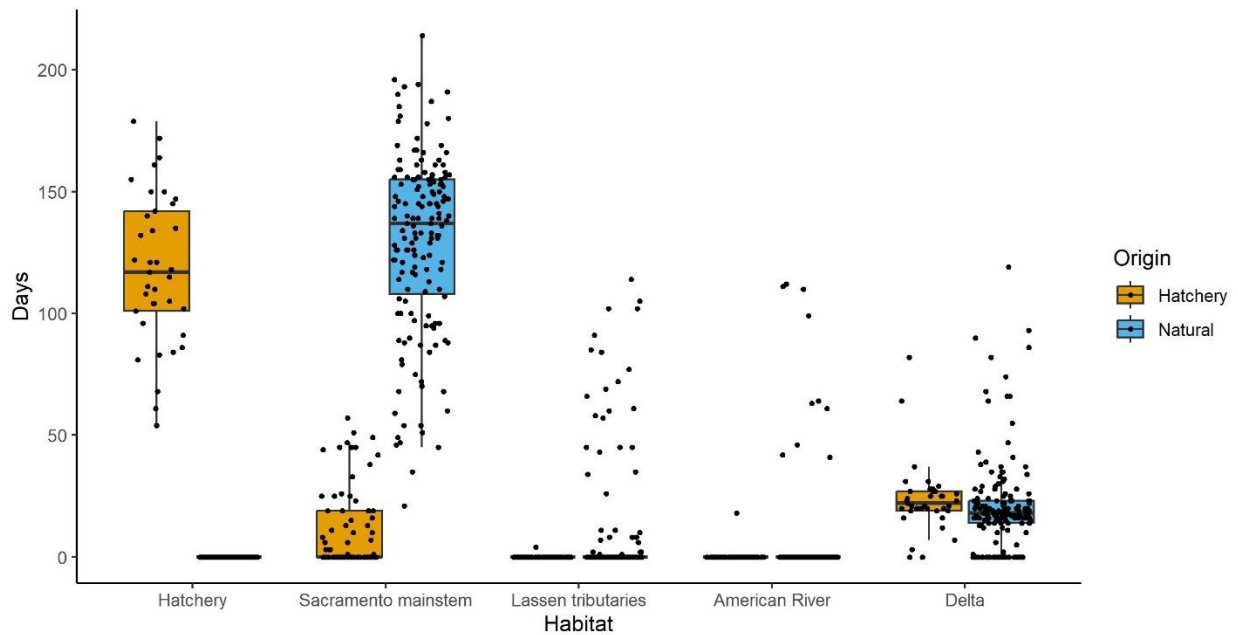
Figure I-3. Number of daily increments counted in hatchery versus natural-origin winter-run Chinook salmon otoliths in each habitat. Bold lines indicate the median and boxes indicate the interquartile range. Hatchery samples in which there was no Sacramento mainstem ^{87}Sr/^{86}Sr values detected were excluded from estimating residence time in the hatchery and Delta.

       Fish that reared in non-natal tributaries higher in the watershed and closer to the spawning grounds (i.e., the Lassen tributaries) were smaller (mean otolith radius for natural-origin fish = 369 μm) when they entered these habitats than fish that reared in the American River further downstream (mean otolith radius for natural-origin fish = 406 μm). The two hatchery individuals that were considered to have reared in one of the Lassen tributaries were first detected in this isotopic range at 399 μm and 473 μm, whereas the two hatchery individuals that were considered to have reared in the American River were first detected at 484 μm and 608 μm – sizes larger than when natural-origin fish first used these tributaries. For natural-origin fish that we categorized as having reared in Lassen tributaries, we estimated they reared in these tributaries for an average of 42 days (sd = 37 days) based on the number of daily increments within the appropriate strontium isotopic range. For natural-origin fish that we detected having reared in the American River, we estimated their mean rearing time to be 79 days (sd = 29 days), although this may be biased high because the ^{87}Sr/^{86}Sr range of the American River is considerably higher and fish that are in the American River for short periods may have an intermediate ^{87}Sr/^{86}Sr value below the American River's ^{87}Sr/^{86}Sr range due to signal averaging.

Based on their otolith radius, hatchery fish had similar size distributions at ocean entry to natural-origin fish (Figure I-4). The otolith radius of natural-origin fish upon ocean entry was 625 µm (sd = 68.9 µm) while the mean otolith radius for hatchery fish was 617 µm (sd = 65.2 µm) (ANOVA: F = 1.19, p > .05). Ocean entry size differed across years (ANOVA: F = 2.67, p = 0.009) but the difference in mean radius between the year with the largest otolith radius (652 µm in 2007) and the smallest radius (612 µm in 2009) was 38 µm, less than the overall standard deviation of ocean entry size across all samples (69 µm).
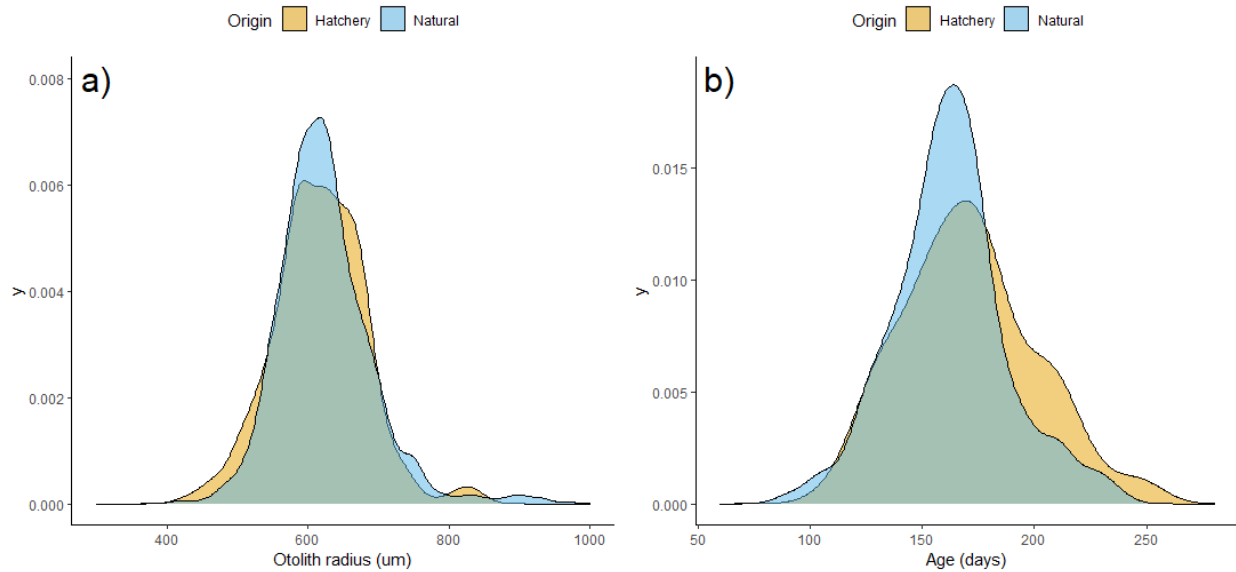
Figure I-4. a) Otolith radius (proxy for size) and b) age at ocean entry for hatchery and natural-origin winter-run Chinook salmon.

The ocean entry age differed between sources and across years (ANOVA: origin – F = 5.09, p < .05; year – F = 14.79, p < .001), but differences in hatchery versus natal-origin fish's mean ages were on the order of approximately two weeks. Hatchery fish were on average 171 days old (sd = 30 days) since exogenous feeding when they entered the ocean while natural-origin fish were on average 163 days old (sd = 25 days) (Figure I-4). Both hatchery and natural-origin fish reared in the basin for around two weeks longer in outmigration year 2017 (wet) than 2016 (below normal) assuming fish returned at age 3 (Table I-1). (natural: 156 days in 2018 versus 170 days in 2019; hatchery: 165 days in 2018 versus 178 days in 2019).

The GAMM with the most parsimonious fit selected to model juvenile salmon growth included habitat, origin, and escapement year as covariates but not life history type (Appendix A Table A-1). Based on daily increment widths, hatchery fish had lower growth rates than natural-origin fish at all life stages regardless of habitat (Figure I-5; Figure I-6). Rearing in the Lassen tributaries was associated with significantly lower relative growth (p < .01) than rearing in mainstem Sacramento River, and rearing in the estuary/ocean was

associated with higher daily growth rates (p < .001) (Appendix A Table A-2). Higher growth was also observed in 2019 adults than in 2018 (p < .001) (Figure I-5; Appendix A Table A-2).
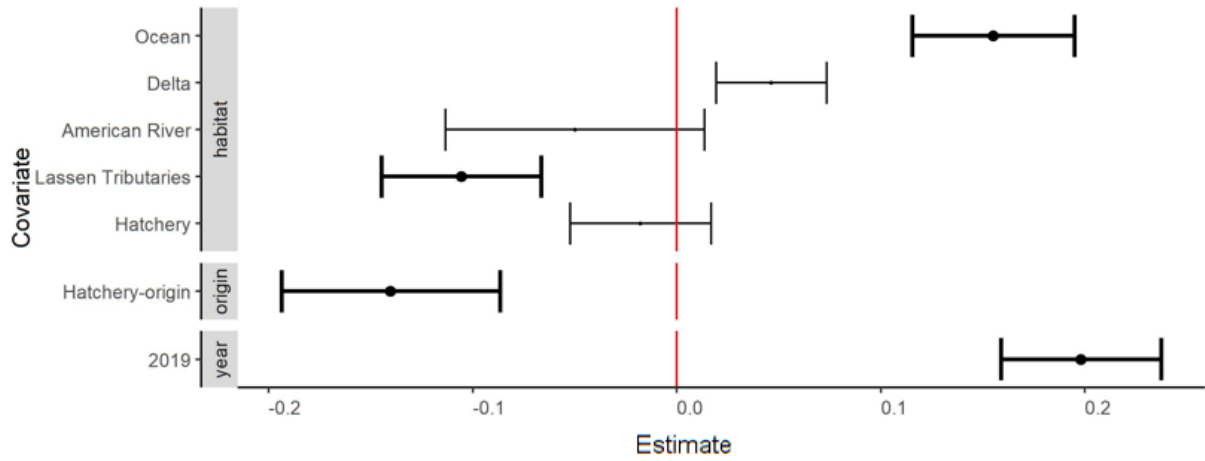
Figure I-5 Coefficient estimates for selected GAMM predicting otolith daily increment widths (μm) (error bars indicate standard error). Estimates reflect differences from baseline – habitat: Sacramento River, origin: natural, and year: 2018. Coefficient estimates with p < 0.05 are bolded.
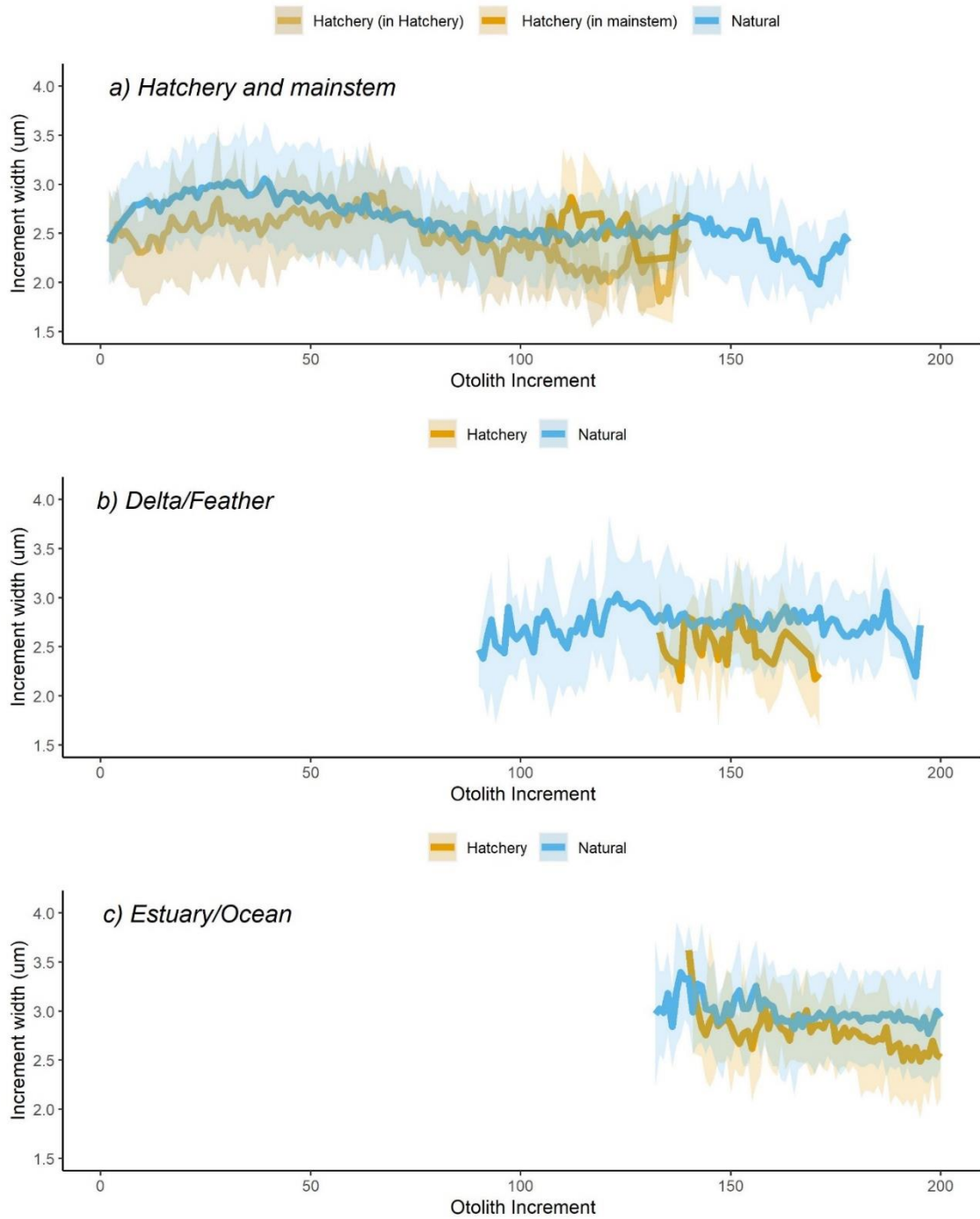
Figure I-6 Otolith daily increment widths for natural-origin (blue) and hatchery-origin (brown) individuals while in the a) Hatchery and Sacramento River mainstem, b) Delta/Feather, and c) the San Francisco estuary or ocean. Lines indicate the mean increment widths and are plotted when there were at least 10 individuals per habitat at the increment while shading indicates the interquartile range.

4. DISCUSSION

Migratory species often display a range of migration strategies, allowing populations to exploit the shifting habitat mosaic and enhance use of the range of growth opportunities available across the landscape (Cordoleani et al. 2022). Similar to Phillis et al. (2018) and Morais et al. (*in review*), we found large spatial variation in juvenile rearing patterns of winter-run Chinook salmon in the Sacramento River system, including considerable evidence of natural-origin fish moving into and rearing in non-natal tributaries and the Delta. Among natural-origin fish, nearly half of adults returning to spawn showed evidence of having reared for an appreciable length of time in a non-natal habitat during their outmigration. Rearing in non-natal habitats reduces the population's density in a single habitat and dampens the effect of environmental perturbations in individual habitats. Many of the non-natal habitats used by winter-run are outside of the Endangered Species Act's critical habitat designation (Federal Registrar 1993). In contrast, hatchery fish limited to rearing in the hatchery for the first part of their life moved quickly through the system to the ocean after release, using the system primarily as a migratory corridor.

Compared to natural-origin fish, we found simple migratory behavior among hatchery releases. Hatchery produced winter-run Chinook juveniles were at liberty in the river for much shorter periods (mean = 11 days) prior to entering the ocean compared to their natural-origin counterparts (mean = 129 days). Releasing all individuals within a short span of time condenses migration timing and aggregates downstream movement, potentially resulting in a more homogenous response of hatchery fish to the environment and reduced stability in downstream survival across years (Sturrock et al. 2019). However, releasing fish over a narrow range of dates may also have a benefit in terms of predator swamping. In general, hatchery fish are released at a size and stage more ready for ocean rearing, thus it is not too surprising that they migrate downstream faster than natural-origin fish. Many hatchery fish (~30 percent) migrated downstream so quickly (within ~ two weeks) that we did not detect a mainstem isotopic signature in the otolith. Unlike natural-origin fish, hatchery fish generally stay within and are protected by the critical habitat designation (Federal Registrar 1993). Hatchery fish are larger upon release than when natural-origin fish go into non-natal tributaries, suggesting they may not require extended rearing in the basin and might explain why non-natal rearing was not frequently observed in hatchery fish. Although a majority of hatchery fish only reared in the river for a short period, there was a large range of migration rates and some fish were observed rearing in the basin for extensive periods, including some tributary rearing. Hatchery fish overall had slower growth across habitats than natural-origin fish, potentially because of reduced natural fitness and foraging ability, which can lead to low survival post release (Ersbak and Haase 1983; Brown and Laland 2005). In the years of our study that overlap with Hassrick et al. (2022), there were similar year to year patterns in migration rate in the studies (i.e., hatchery fish had a lower migration speed during the wet year of 2017 versus the below normal year of 2016). The hatchery residence times we measured in the mainstem using otoliths (averaging 6 days in migrant year 2016 and 16 days in migrant year 2017) were shorter than residence times estimated through acoustic tags in Hassrick et al. (2022) (averaging 13 days in 2016 and 48 days in 2017). This is likely because hatchery fish were

not categorized as being in the Sacramento River until their otolith chemistry had entered the $^{87}Sr/^{86}Sr$ range of the Sacramento mainstem. Given measurements typically integrate around two weeks, regions of the otolith when fish were transitioning from the hatchery to the mainstem isotopic range were classified as hatchery residence, so estimates of mainstem rearing in hatchery-origin fish may be underestimated by up to two weeks. However, the residence time difference was greater than two weeks between acoustic-tagged fish and otolith reconstructions from returning fish in 2017, suggesting higher overall survival among the fish that moved out of the system faster.

Although hatchery fish reared in the river for much shorter periods and exhibited lower diversity in habitat use, returning hatchery-origin fish entered the ocean a similar size and age as returning natural-origin fish. Similar ocean entry timing and size, key predictors for early ocean survival, among hatchery and natural-origin fish suggest possibly similar early ocean survival rates (Woodson et al. 2013; Satterthwaite et al. 2014). Natural-origin juveniles were typically 4 – 6 months post-exogenous feeding when they exited the Delta and entered the estuary, which corresponds to approximately January – April if fish emerge in mid-September (Jennings and Hendrix 2020; Torres et al. unpublished), while hatchery juveniles were slightly older when they entered the estuary. These date estimates are similar to when natural- and hatchery-origin winter-run fish are captured by trawl sampling in the estuary at Chipps Island. Fish the size of natural-origin winter-run Chinook salmon are captured from December to April, peaking in March (del Rosario et al. 2013), while hatchery fish are captured soon after their release in February to April (RMPC 2020). Returning hatchery fish had similar standard deviations in their ocean entry age and size as natural-origin fish, which was surprising given hatchery fish all rear under the same conditions and are all released within the span of a few weeks. Overall, this suggests that hatchery practices have not greatly altered the size or timing at ocean arrival, though the paths the fish take to arrive at those sizes and timings differ greatly. It is also important to note that our results only reflect surviving fish so the actual variation in ocean entry may differ between hatchery and natural-origin fish. The similarity in size and timing at ocean entry observed here could also partly reflect strong selection during early ocean residence (Woodson et al. 2013; Satterthwaite et al. 2014).

Data collected continuously across years are invaluable to understanding how populations respond to variation in annual conditions. For Chinook salmon in the Central Valley, egg-to-fry and downstream survival rates vary across years and are positively related to flow and its related parameters (Henderson et al. 2019; Hassrick et al. 2022). We expected hydrological conditions to shift the habitat mosaic in the basin across time, changing the productivity and importance of habitats in years with different rainfall patterns (Coleman et al. 2022; Cordoleani et al. 2022). For example, drier conditions are expected to reduce habitat availability and quality and potentially disconnect small tributaries and off-channel habitats (Bellido-Leiva et al. 2021; Moidu et al. 2023). While greater flows in the mainstem tend to result in a higher occurrence of non-natal rearing (Morais et al. *in review*), we still found evidence of considerable non-natal rearing in all years. Surprisingly, we found growth rates in non-natal tributaries tended to be lower than in the mainstem, despite evidence of potential growth benefits in other studies (Maslin et

al. 1996) and growth benefits being a primary hypothesis for why salmon use these habitats (Phillis et al. 2018; Morais et al. *in review*). While, on average, tributary rearers were overall slower growing than mainstem rearers, the effect of life history type was not significant. The high contribution rates of tributary rearing life histories to the spawning population suggests other advantages to rearing in these tributaries may exist. Considerable spatial diversity and contribution of non-natal rearing life histories warrant closer investigation into how non-natal habitat use differs across years with different escapement sizes and hydrologies. With environmental conditions expected to become more variable and extreme with climate change, understanding how a population's use of the habitat mosaic contributes to a diverse portfolio of life histories is critical to supporting their habitat needs.

Currently much of the habitat supporting spatial diversity of winter-run Chinook salmon is outside of the critical habitat designated in 1993 under the Endangered Species Act. Otolith chemistry studies (i.e., Phillis et al. 2018, Morais et al. *in review*, and here) and field sampling (i.e., Maslin et al. 1996) documenting habitat use throughout the basin since then suggest the need for an updated designation to better support the diversity of migratory strategies within natural-origin winter-run Chinook salmon. While there is overlap between winter-run Chinook salmon habitat use and the critical habitat designated for other listed species (e.g., spring-run Chinook salmon, steelhead (*Oncorhynchus mykiss*), Delta smelt (*Hypomesus transpacificus*)), protections and flow releases intended for these species may not be as effective or match temporally with the habitat needs for winter-run Chinook salmon. Explicitly considering the presence of winter-run Chinook salmon in habitats beyond the migratory corridor during habitat management (e.g., restoration and flow management) is needed to promote and enable the contribution of multiple life histories for productivity and resilience.

Information from hatchery-origin fish is often used for managing natural-origin populations because data from natural-origin fish can be difficult to attain, particularly for endangered species such as Sacramento River winter-run Chinook salmon. However, hatchery-origin fish may not be representative of natural-origin fish because of differences in life history due to the hatchery selection, rearing, and release processes. This bias should be considered and quantified whenever possible. In management and conservation models for Sacramento River winter-run Chinook salmon (e.g., Juvenile Production Estimate described in O'Farrell et al. (2018), Life Cycle Model described in Hendrix et al. (2017)), smolt survival rates from acoustically tagged hatchery fish are used to calculate smolt abundance of natural-origin fish reaching the lower river. Because hatchery fish generally spend much shorter durations in the river, we expect their downstream survival rate to be considerably higher than for natural-origin fish, and therefore to potentially overestimate natural-origin survival and number of smolts. Hatchery-origin juveniles were estimated to have much higher juvenile survival, which includes in-river rearing, than their wild counterparts in Winship et al. (2014), and this is partly attributed to different durations in river. One practical solution is to normalize survival rates to a rate per day as a lower end estimate of survival, however this still does not account for other potential influences on survival, such as size and time of year. Hatchery fish migrate downstream in the spring while natural-origin fish generally migrate through the same reaches the previous fall and

winter, which can have very different flow conditions that affect turbidity (and therefore visibility to predators), flow velocity, and predator abundance and lead to further differences in downstream survival of hatchery versus natural-origin fish (Matern et al. 2002; Henderson et al. 2019). When possible, hatchery fish with life histories most similar to that of the natural-origin fish should be used to estimate natural-origin parameters of interest.

Our study compared the juvenile life history patterns of hatchery and natural-origin fish with the goal of evaluating the suitability of applying measurements and results obtained from one group to the other. However, there are aspects of otolith analysis that make their estimates not directly comparable to other methods. Otoliths are collected only from adults that have survived to spawn and therefore reflect the life history and habitat use of successful individuals, which may differ from sampling the early life stages of that same cohort in situ. Sampling juvenile life history while fish are juveniles would likely reveal a far broader spectrum of life histories and habitat use patterns (Sturrock et al. 2020). Measurements of otolith chemistry in this study were generally performed at 40 micron resolution, encompassing approximately 10-20 daily increments depending on increment width. Rearing in a habitat for short periods may not have been detected depending on when rearing occurred relative to where point isotopic measurements were taken. Additionally, some tributaries and intermittent streams have isotopic signatures in the same range as the mainstem Sacramento River (e.g., Butte, Red Bank, and Dibble Creek; Morais et al. *in review*). Consequently, any non-natal rearing in these tributaries would not be detected with this method, even though winter-run sized fish have been found in these tributaries (Maslin et al. 1996). Moreover, the upper and lower Sacramento River have similar strontium isotope chemistry, so it is not possible to distinguish upper-river rearing from lower-river rearing to understand the distribution of winter-run Chinook within the Sacramento River mainstem. These limitations generally result in underestimating the true variation in juvenile life history patterns in winter-run Chinook salmon.

In response to the increasing frequency of drought conditions in California and the possibility of high in-river egg mortality, hatchery production and densities have increased three-fold within Livingston Stone since 2014, including a 50 percent increase in production in 2022 from 2021 (NMFS 2023a; Johnson et al. 2023). Increasing densities can slow physiological development (Schreck et al. 1985) and alter behavior (Cogliati et al. 2023) in juvenile Chinook salmon but does not definitively lead to differences in post-release survival (Banks and LaMotte 2002; Brockmark et al. 2007; Olson and Paiya 2013). When mechanisms for shaping behavior and life history are not well understood, mimicking natural conditions to the greatest extent possible lowers negative hatchery effects. Studying whether increased densities affect juveniles in-hatchery and the juvenile life history and survival post-release will be necessary to achieve production of winter-run Chinook salmon that meets conservations goals (USFWS 2016). Identifying sources of divergence between hatchery and naturally produced fish and developing practices to avoid artificial selection is key to conservation programs having long-term benefits to the populations they support.

5. ACKNOWLEDGEMENTS

Chapter 2. Age structure of natural versus hatchery-origin endangered Chinook salmon and implications for fisheries management in California

Abstract

Maturation schedules shape a population's age structure and influence productivity and exposure to fishing. Fish cultivated and raised in artificial environments like hatcheries may mature at different ages compared to their natural-origin counterparts. We evaluated whether endangered Sacramento River winter-run Chinook salmon (*Oncorhynchus tshawytscha*) produced in a conservation hatchery had different maturation schedules compared to natural-origin fish, and how any differences affected their exposure to, and impact from, the ocean salmon fishery. Using coded-wire tags collected from hatchery fish in the ocean and in-river fisheries and on the spawning grounds, and scales collected from natural-origin spawner carcasses, we reconstructed the life history of hatchery and natural-origin cohorts from 2002-2015 brood years. Hatchery fish had similar age-2 maturation rates but higher age-3 maturation rates compared to natural-origin fish, resulting in fewer age-4 individuals and an overall more truncated age structure. Because natural-origin winter-run Chinook salmon were more likely to remain at sea until age-4, they were exposed to fishing for an additional year and experienced greater reduction in escapement. Compared to natural-origin males, hatchery-origin males were much less likely to return at an older age, possibly because sexual selection that is occurring on the spawning grounds is not occurring to the same extent in the hatchery. Identifying how reproductive maturation differs across sources, sex, and life histories is critical to understanding how fisheries can disproportionately impact subsets of a population and affect its long-term population dynamics and sustainability.

1. INTRODUCTION

Hatcheries are established for many reasons, such as to support fisheries or to aid in conservation of a threatened or endangered population (Mobrand et al. 2005). Producing fish in hatcheries increases the abundance of stocks but can threaten the long-term viability of self-sustaining wild populations (Naish et al. 2007; McMillan et al. 2023). Practices during hatchery production such as selection of brood stock, cultivation of fry, and release logistics (e.g., size, timing, Huber and Carlson 2015), can select for or result in skewed phenotypic expression, leading to divergence between the hatchery and natural-origin individuals in the population (Brown and Day 2002). For example, differences in the diet composition and foraging behavior between hatchery and natural-origin juveniles can select for physiological and behavioral traits at the hatchery that are maladaptive in the wild (Blouin et al. 2021). Trait differences are especially concerning if the trait is heritable, and hatchery and natural-origin fish interbreed.

Differences in the maturation schedules of hatchery and natural-origin fish are of major concern for the long-term persistence of the combined population (Vainikka et al. 2010). Age at maturity influences an individual's fecundity, survival to spawning, and exposure to harvest (Hutchings 2021). For example, fish that mature earlier typically have smaller body sizes and lower fecundity. However, early maturation increases survival to adulthood because fish are exposed to mortality for shorter durations. Maturation rates shape the population age structure, a key demographic variable influencing the interannual stability and resilience of salmon stocks (e.g., Schindler et al. 2010). In general, populations with more age classes are able to withstand more frequent recruitment failures (Hsieh et al. 2010). Natural and anthropogenic changes to the environment, such as shifts in ocean productivity or increased natural and fishing mortality, can shift drivers of selection and the age structure of the population (Ohlberger et al. 2018; Oke et al. 2020). Among salmonids, age at maturity is diverse and influenced by genetics and the individual's environment, particularly growth conditions (Spangenberg et al. 2015). Unnaturally high rates of precocious maturation occur in some hatchery populations, such as in some Atlantic salmon (Piggins and Mills 1985) and spring-run Chinook salmon populations (Larsen et al. 2019; Winsor et al. 2021) and thereby truncate a population's age structure. Knowing the maturation schedules and, consequently the age structure, of hatchery and natural-origin fish is critical to understanding how their dynamics may differ and consequences for population productivity.

Identifying differences between hatchery and natural-origin fish is also key for managing water and fisheries. Data collected from tagged hatchery fish inform survival of smolts during outmigration (Rechisky et al. 2013; Henderson et al. 2019), distribution of adults in the ocean (Weitkamp 2010, Shelton et al. 2019), survival to adulthood (Kilduff et al. 2015, Harstad et al. 2018), and maturation and age structure (O'Farrell et al. 2012; Satterthwaite et al. 2017). A key assumption in Pacific salmon stock management when relying upon coded-wire tag recovery data is that hatchery fish are representative of their associated natural-origin counterparts (PFMC 2023a). However, differences in life history between hatchery and natural-origin fish can create bias when applying hatchery-origin

parameters to the entire population. Concerns about differences have been an impetus for incorporating genetics and scale aging to more fully assess natural populations (Satterthwaite et al. 2015; Klamath River Technical Advisory Team 2022). Knowing when it is appropriate to use data from hatchery fish as a proxy for wild fish is critical to the accuracy of management models and making informed decisions for the natural population.

Within the endangered Sacramento River winter-run Chinook salmon population, tagged hatchery fish are currently used as a proxy for natural-origin fish in models that influence the management and conservation of the whole population. Maturation rates estimated for the hatchery-origin fish are used in life cycle models developed to inform freshwater management (Zeug et al. 2012; Hendrix et al. 2017) and in analyses of fishery impacts on population viability for the combined population (Winship et al. 2013, 2014). The maturation rate of hatchery fish at the end of age 3 is very high (mean 94 percent in O'Farrell et al. 2012), and age-4 hatchery fish are rare in the fishery and on the spawning grounds. Additionally, the majority of spawners prior to the establishment of the hatchery were age-3 fish, suggesting age-4 fish are also uncommon in the naturally produced population (Hallock and Fisher 1985). Consequently, assessments and management of fishing impact for the combined population are focused on impact at age 3 prior to spawning, when sufficient data are available and when most fish have yet to mature. Several ocean salmon fishery restrictions in California are designed to avoid impact on smaller age-3 fish, e.g., through use of minimum size limits and seasonal restrictions in areas where winter-run Chinook salmon are concentrated (O'Farrell and Satterthwaite 2015).

Knowing how the maturation schedules of hatchery and natural-origin fish differ is key to accurately interpreting assessments that use hatchery fish data to inform models for the natural-origin population. In this study, we compared sex-specific maturation schedules and age structure of hatchery versus natural-origin Sacramento River winter-run Chinook salmon and explored how differences in age structure influence assessments of the fishery's impact on this endangered population. Our first objective was to reconstruct hatchery and natural-origin cohorts from 2002-2015 and estimate sex-specific maturation schedules. Our second objective was to evaluate whether differences in age structure have the potential to contribute to differences in the impact of fishing on hatchery versus natural-origin escapement.

2. MATERIALS & METHODS

2.1 Study system

Sacramento River winter-run Chinook salmon are one of four runs of Chinook salmon in California's Central Valley and their unique life history occurs nowhere else across the range of Chinook salmon (Healey 1991). Adults return to the river in the winter and spawn in the upper reaches of the Sacramento Basin in the summer. Natural-origin juveniles hatch and rear in the early fall and outmigrate from the upper Sacramento River from

October to April. Juvenile winter-run Chinook salmon reach the lower river and Delta in December and exit freshwater from March to May (del Rosario et al. 2013).

Construction of dams blocked passage of winter-run Chinook salmon to their historical spawning areas, so fish have been restricted to spawning in mainstem habitats downstream of Shasta and Keswick dams for decades. The population was listed as endangered under the U.S. Endangered Species Act in 1994 due to continually declining abundances and high variability in recruitment (NMFS 2016). Winter-run Chinook salmon are propagated at the Livingston Stone National Fish Hatchery on the Sacramento River, California to support conservation of the population (Good et al. 2005). Adults captured at Keswick dam are selected for broodstock randomly with respect to size and throughout the season at a rate based on the expected distribution of spawner run timing. Like other conservation hatchery programs, this program genotypes adults to ensure they belong to the population of interest and uses numerous parent combinations in the broodstock to maximize genetic diversity (USFWS 2016). Juveniles are typically released in February in the upper river near the Red Bluff Diversion Dam. The hatchery program has historically produced far fewer fish than what is produced naturally to manage gene flow and because their primary objective is not production for harvest but rather conservation (Johnson et al. 2017). Although the proportion of hatchery to natural-origin fish on the spawning grounds is usually less than 30 percent, the proportion peaked at over 80 percent in 2017 and 2018 due to large hatchery cohorts in 2014 and 2015 during a multi-year drought and very low survival of natural-origin fish from those brood years (Meyers 2021).

2.2 Hatchery-origin age structure

2.2.1 Data

Nearly all (95%) winter-run hatchery Chinook salmon have their adipose fin clipped and are implanted with a coded-wire tag (CWT) prior to release. Used extensively for salmonids on the Pacific coast, CWTs are batch tags identifying a fish's release group (e.g., stock, brood year, origin) (Johnson 1990). Data on the release and recovery of coded-wire tagged Pacific salmonids are uploaded to the Regional Mark Information System (RMIS) database provided by the Regional Mark Processing Center (RMPC 2020). To match the data available for natural-origin cohorts below, we queried the RMIS database for batches of winter-run Chinook salmon released from Livingston Stone National Fish Hatchery 2002-2015. For tag recoveries, we queried the RMIS database for recoveries of winter-run Chinook salmon coded-wire tags on the spawning grounds, in the commercial ocean salmon fishery, recreational ocean and in-river salmon fisheries, and at hatcheries from 2003-2019. Analysis data and code for all components are available on github: https://rb.gy/7qhn7 and Dryad: https://doi.org/10.6078/D16T59.

2.2.2 Cohort reconstruction

Every year on March 1 ($t = 3$), we assume ocean fish enter the river to spawn or advance an age class. By convention (Prager and Mohr 2001; O'Farrell et al. 2012; Cordoleani et al. 2020), ocean ages refer to the age corresponding to a fish's next opportunity to spawn, thus fish are effectively indexed as age-1 upon hatching. The maturation rate m at age a is the proportion of fish that mature M to the total number of fish N.

$$m_a = M_a / N_{a.t=3} \qquad (1)$$

In all other months t, M equals zero. On rare occasions, age-1 males return to spawn a few months after their release. We did not estimate an age-1 maturation rate because they rear in the ocean for little to no time, and their recovery rate is likely variable and biased low because of their small size. Fish returning to spawn (M) may: 1) be captured in the in-river fishery (rare), 2) be taken to the hatchery, or 3) enter the natural spawning grounds. For each of these outcomes, CWTs are recovered at a sampling fraction of Θ. We estimated the number of unrecovered tags for every recovered tag by sampling the number of unrecovered tags k 1000 times from a negative binomial distribution,

$$k \sim NB(1, \Theta) \qquad (2)$$

where "success" is each recovery and probability of success is the sampling fraction Θ for each outcome (river fishery, spawning grounds, and hatcheries) (Michielsens et al. 2006). After estimating the total number of tagged fish for each recovered tag, we multiplied this value by the inverse of the tag's batch tagging frequency to account for untagged hatchery fish (O'Farrell et al. 2012). We then summed hatchery fish in all recovery locations to estimate the total mature fish (M) every run year.

To estimate total ocean abundance N from ages 2–5 and quantify fishing impact, we reconstructed the total number of fish for each cohort on a monthly timestep using cohort analysis methods beginning from the final year each cohort was encountered and working backwards to age 2 (Pope 1974). Abundance at the start of the timestep equals the abundance from the following timestep and any mortalities from natural causes in the ocean v, spawning, and fishing that occurred that period.

$$N_{a.t} = \frac{N_{a+1.t+1}}{1-v} + M_{a.t} + I_{a.t} \qquad (3)$$

We used annual natural mortality rates commonly used for Pacific salmon, 0.5 at age 2 and 0.2 at age 3 and age 4, for v (Klamath River Technical Advisory Team 1986; O'Farrell et al. 2012). Mortality impacts from commercial and recreational ocean fisheries (rate = i, number = I) includes retained harvest F, release mortality R, and drop-off mortality D.

$$i = \frac{I}{N} \qquad (4)$$

$$I = F + R + D$$

Similar to in-river fisheries harvest and escapement to the spawning grounds and the hatchery, ocean harvest was estimated from recovered tags. When tags were recovered, unrecovered tags were estimated from recovered tags and reported sampling fractions by drawing from a negative binomial distribution 1000 times (Eq. 2). The total number of tags was expanded based on the tagging frequency of every recovered tag to estimate F.

Fish under the size limit that were captured and released experienced a release mortality rate of r, which was assumed and varied by the fishery type g, region b, and time. Release mortality was 0.26 for commercial fisheries for all regions and times and ranged between 0.14 and 0.39 for recreational fisheries depending on fishing techniques in the region and time (Salmon Technical Team 2000; O'Farrell et al. 2012).

$$R_{a.t} = \left(\frac{F_{a.t}}{h_{g.b.a.t}} - F_{a.t} \right) \times r_{g.b.t} \qquad (5)$$

The proportion of fish encountered that are of legal size h varied as a function of the size limit for the fishery type in the region and the size distribution of the cohort at the time. Size at age was estimated in Appendix A of O'Farrell et al. (2012) from CWT recoveries during 1993-2007 harvest years and static across years.

Furthermore, we accounted for mortality of fish that were hooked but not captured by applying a fixed drop off mortality rate d (0.05) to the estimated number of individuals that encountered fishing (Salmon Technical Team 2000).

$$D_{a.t} = \frac{F_{a.t}}{h_{g.b.a.t}} \times d \qquad (6)$$

2.3 Natural-origin age structure

2.3.1 Data

We obtained in-river escapement estimates and number of adults taken to the hatchery from GrandTab, managed by the California Department of Fish and Wildlife (CDFW), for 2005-2018, when natural-origin age composition data was available (Azat 2022). Reported escapement includes that of both natural and hatchery-origin spawners to the spawning grounds. We subtracted hatchery-origin fish from in-river escapement and fish taken to the hatchery to estimate natural-origin escapement to the spawning grounds and hatchery.

Scales were collected from carcasses on the spawning grounds throughout the 2005-2018 spawning season and analyzed by CDFW. Fish with intact adipose fins were considered to be of natural origin, although adipose regeneration and misclips can possibly result in including hatchery fish in the sample (Kinziger et al. 2022). Natural-origin scale samples were selected to reflect the spatial and temporal distribution of each run. Scale samples were read by an individual experienced reader, and individual ages were determined from scales by counting winter annuli (Gilbert 1912). Sex and length were taken into consideration only after the initial evaluation of age by the reader. Samples from hatchery-origin fish were also analyzed to assess aging error and develop a confusion

matrix. Coded-wire tags from hatchery-origin fish were read and used to compare known age to the age determined based on scales from the same individual.

2.3.2 Cohort reconstruction

We used parallel methods to estimate maturation for natural-origin cohorts, replacing hatchery-origin escapement at age with natural-origin escapement at age. Escapement of natural-origin fish includes fish returning to spawn on the spawning grounds and at the hatchery. We calculated the age distribution of the natural-origin run based on the composition of read natural-origin scales. We estimated the age distribution from the aged scales with or without an algorithm described in Kimura and Chikuni (1987) to account for bias caused by scale aging error. The confusion matrix was composed of winter-run hatchery Chinook salmon with read age from scales and known age from their coded-wire tags. To assess uncertainty in the age composition of read samples, we resampled the age composition derived from scale samples with replacement 1000 times prior to applying the adjustment for aging error.

Data on the impact of ocean and in-river fisheries for natural-origin fish were very limited, so we assumed natural-origin fish experience fishing impacts at the same rates as hatchery fish. We applied cohort-specific impact rates ($i_{a.t}$) estimated from hatchery cohorts at age a and time t to natural-origin cohorts at each timestep. In some years, coded-wire tags from age-4 fish were never recovered in ocean fisheries either because the fisheries were closed (i.e., 2008 and 2009) or because of low age-4 abundance (e.g., 2007, 2012, 2014 when few age-4 hatchery fish from recovered on the spawning grounds the following year). This resulted in an estimated age-4 impact rate of zero in those years.

Because of sparse CWT data from age-4 fish, we tested sharing information from cohorts in the ocean experiencing fishing during the same year (i.e., age-3 fish from one cohort and age-4 fish from the previous cohort). We assumed age-3 and age-4 fish are caught by the fishery at the same rate and in the same regions and fisheries but have different retention rates because of their size. To estimate the number of age-3 and age-4 fish caught by fisheries, we divided harvest of hatchery age-3 and age-4 fish by the proportion of fish caught that are of legal size at those ages. We summed age-3 and age-4 catches and divided catches by the sum of hatchery age-3 and age-4 reconstructed abundance to estimate the general catch rate c in the ocean during period t.

$$c_t = \frac{\sum_{a=3}^4 \frac{F_{a.t}}{h_{a.t}}}{\sum_{a=3}^4 N_{a.t}} \tag{7}$$

From the catch rate c_t, we estimated the age-specific impact rate $i^*_{a.t}$, which includes harvest, release mortality, and drop mortality, to reconstruct natural-origin cohorts.

$$i^*_{a.t} = c_t \times h_{g.b.a.t} + c_t(1 - h_{g.b.a.t}) \times r_{g.b.a.t} + c_t \times d \tag{8}$$

2.4 Sex-specific maturation schedules

In addition to reconstructing cohorts of hatchery and natural-origin fish, we separately reconstructed the life history of males and female fish of each origin. The female to male ratio in recovered coded-wire tags and scales from carcasses is biased high because females tend to remain near their redd and are less likely to drift downstream (Murdoch et al. 2009; USFWS 2023). To reduce this sampling bias, we estimated the abundance of males and females by proportioning the total return by the sex ratio of individuals recovered from carcass surveys plus fish taken to the hatchery (CDFW 2020). For hatchery-origin cohorts, we used the age composition from recovered coded-wire tags of each sex to estimate the sex-specific age composition. To estimate sex-specific hatchery-origin maturation rates, we reconstructed their ocean abundance using impact rates ($i_{a.t}$) estimated in the non-sex-specific hatchery-origin cohort reconstruction. Similarly, we used the age composition of males and females from recovered and analyzed scale samples to estimate the age composition of natural-origin males and females and then reconstructed their abundance to estimate sex-specific natural-origin maturation rates.

2.5 Fishery Exposure

We evaluated whether differences in age structure between the hatchery and natural-origin populations can lead to differences in their fishing impact and bias assessments of fishery impact. To quantify fishing impact, we estimated the would-be escapement and age composition of hatchery and natural-origin fish from 2005-2018 in the absence of fishing. Starting from the reconstructed abundance before cohorts began to experience fishing (i.e., start of age-3), we estimated their would-be ocean abundance, N', of 2002-2015 cohorts through time by applying only natural mortality to their estimated ocean abundance.

$$N'_{a+1} = N'_a \times v \tag{9}$$

We applied the origin- and cohort-specific maturation schedule (m_a) to estimate the age-specific number of hatchery and natural-origin spawners every year in the absence of fishing mortality, M'.

$$M'_a = N'_{a.t=3} \times m_a \tag{10}$$

To assess the fishery impact on the population, we calculated the spawner reduction rate (SRR), i.e., the proportion of escapement reduced by fishing.

$$SRR = 1 - \frac{M}{M'} \tag{11}$$

We calculated the SRRs for the hatchery and natural-origin populations. Additionally, we calculated sex- and origin-specific SRRs using reconstructed abundances and maturation schedules estimated in the sex- and origin-specific cohort reconstructions.

2.6 Sensitivity Analysis

While sublegal-sized winter-run Chinook salmon are not harvested, mortality can occur after they are captured and released. Estimated population impacts from release mortality depend on the release mortality rate assumed and estimates of the proportion of catches that are released based on the size-at-age model and size limits in effect when fish were contacted (O'Farrell et al. 2012). We evaluated the sensitivity of impact, maturation, and spawner reduction rate estimates to 1) release mortality rates and 2) the proportion of catch that was sublegal. For release mortality rates, we evaluated vital rate estimates with higher, lower, and zero release mortality. We increased and decreased release mortality rates six percent for recreational fisheries and two percent for commercial fisheries based on the set of recommend rates considered by California salmon managers (Salmon Technical Team 2000). The proportion of the population that is sublegal depends on the size at age, which can deviate from long-term mean estimates due to annual variation. To evaluate the potential variability in fishery impact due to annual variation in size at age, we increased and decreased estimates of the mean size at age each month by 46 mm, the standard deviation in annual mean size reported for winter-run Chinook salmon in Satterthwaite et al. (2012) at age 3 in July, when the most data were available. We evaluated the sensitivity of impact, maturation, and SRR estimates generated for hatchery-origin cohorts.

3. RESULTS

3.1 Age structure and maturation schedules

A mean of 373 coded-wire tags (range: 25–1280) were recovered and processed for hatchery-origin adults on the spawning grounds and at the hatchery each year. Most hatchery fish recovered were two-, three-, or four-years-old, except for two age-5 females (0.0005 of all CWTs) and eight age-1 hatchery males (0.002 of all CWTs). Seven of the eight age-1 males were recovered at the hatchery, and six of the eight males were recovered in 2015 from the 2014 brood year. Recoveries of hatchery-origin adults from the in-river fisheries were rare, totaling seven recoveries from 2005–2018. At least 100 samples from natural-origin spawner carcasses were aged each year from 2005–2018 (mean: 410 samples; range: 135–849 samples), except for 2017, when only 16 natural-origin samples were recovered. In both hatchery and natural-origin winter-run Chinook salmon, three-year-olds dominated the returns from 2005–2018, but to a greater extent for the hatchery-origin subset (Table II-1; Figure II-1). Natural-origin fish had more diverse age composition from having a larger proportion of spawners returning at age 4. Reconstructed estimates of the potential age composition in the absence of fishing (Eq 9) did not differ largely from the observed age composition of spawners (Figure II-1).

Table II-1 Mean age composition of winter-run Chinook salmon entering the river to spawn from 2005–2018. Hatchery-origin age composition is based on coded-wire tags recovered from the in-river fishery, the hatchery, and spawning ground. Natural-origin age composition is based on the age distribution of analyzed scale samples with adjustments for aging error.

	Age 2	Age 3	Age 4
Hatchery-origin combined	0.18 (σ = 0.22)	0.76 (σ = 0.25)	0.07 (σ = 0.12)
Natural-origin combined	0.11 (σ = 0.17)	0.74 (σ = 0.21)	0.15 (σ = 0.16)
Hatchery-origin males	0.30 (σ = 0.29)	0.62 (σ = 0.32)	0.08 (σ = 0.15)
Natural-origin males	0.19 (σ = 0.23)	0.44 (σ = 0.30)	0.37 (σ = 0.31)
Hatchery-origin females	0.11, (σ = 0.21)	0.84 (σ = 0.22)	0.05 (σ = 0.08)
Natural-origin females	0.07 (σ = 0.15)	0.85 (σ = 0.18)	0.08 (σ = 0.10)
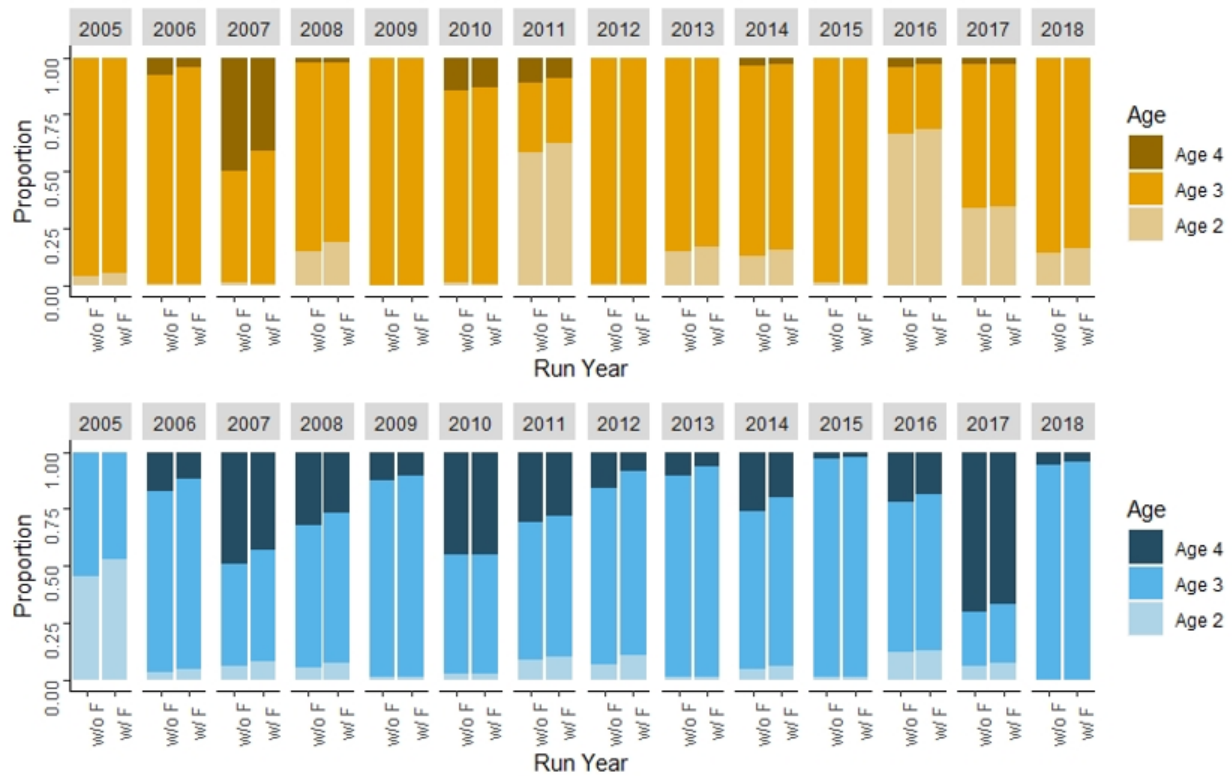
Figure II-1. Age composition of hatchery (top) versus natural-origin (bottom) winter-run Chinook salmon escapement, excluding age 1 and age 5 (Materials and Methods 2.2 and 2.3). Left side of paired bars reflects the expected age composition in the absence of fishing while the right side of paired bars reflects the observed age composition using coded-wire tags and scales (with adjustments for aging error) for hatchery and for natural-origin fish, respectively (Materials and Methods 2.5).

Maturation rate estimates from parallel cohort reconstructions of hatchery and natural-origin fish from 2002–2015 brood years indicate hatchery fish mature at higher rates at age 3 than natural-origin fish (Table II-2). We did not detect consistent differences in their age-2 maturation rates. For both sources, females had very low age-2 maturation rates and high age-3 maturation rates (Figure II-2). In contrast, the age-2 maturation rate for males were similar for both sources, but natural-origin males had a much lower age-3 maturation rate compared to hatchery-origin males. The adjustment for aging error generally raised the proportion of age-4 fish (Table II-1 vs. Appendix B Table B-1) and lowered the age-2 maturation by a mean of 0.01 and age-3 maturation rate of natural-origin fish by a mean of 0.02 (Table II-2 vs. Appendix B Table B-2).

Table II-2 Mean maturation rates for hatchery and natural-origin winter-run7 Chinook salmon for 2002–2015 brood years.

	Age-2 maturation rate	Age-3 maturation rate
Hatchery-origin combined	0.040 (σ = 0.076)	0.96 (σ = 0.070)
Natural-origin combined	0.030 (σ = 0.16)	0.77 (σ = 0.13)
Hatchery-origin males	0.13 (σ = 0.27)	0.96 (σ = 0.19)
Natural-origin males	0.078 (σ = 0.17)	0.46 (σ = 0.31)
Hatchery-origin females	0.0049, (σ = 0.060)	0.97 (σ = 0.026)
Natural-origin females	0.000079 (σ = 0.17)	0.94 (σ = 0.042)

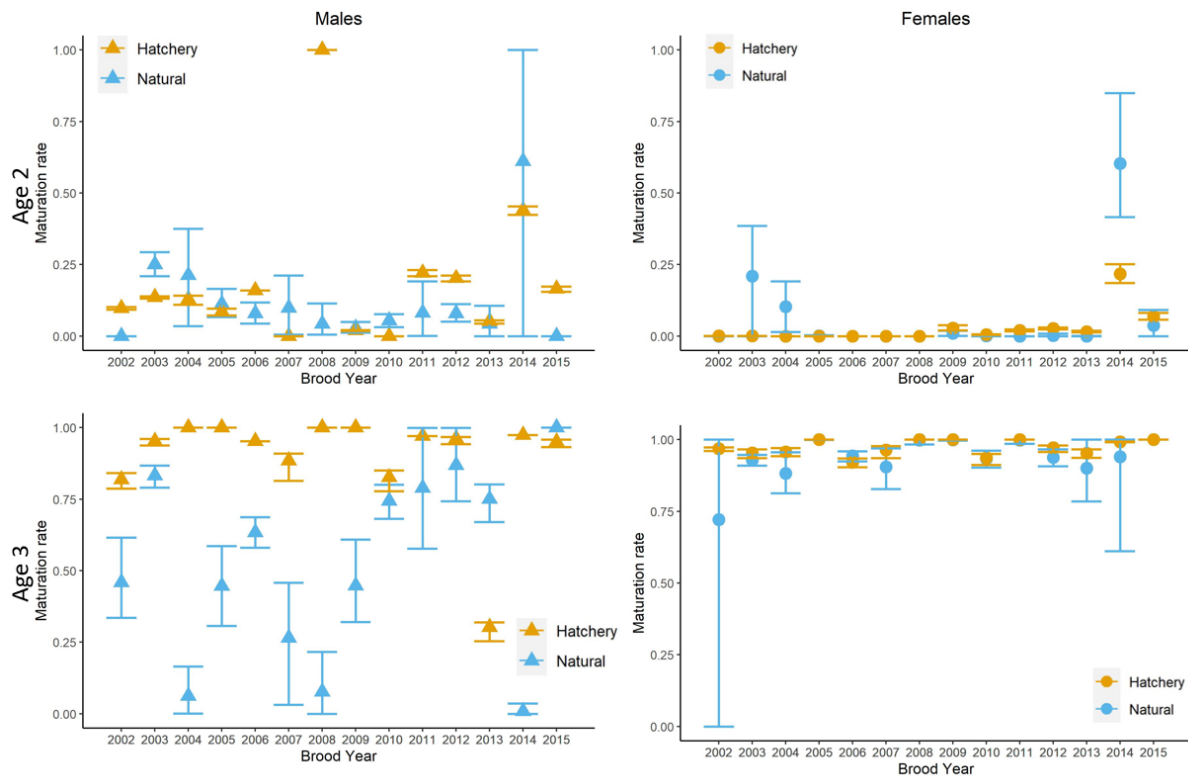**Figure II-2** Age-, sex-, and origin-specific maturation rates for winter-run Chinook salmon brood years from 2002–2015. Points indicate the mean while error bars indicate the 95% confidence intervals from resampling.

3.2 Fishing impact and exposure

From 2004–2018 harvest seasons, coded-wire tags were recovered from age-3 fish every year except for 2008 and 2009, when the fishery was closed. No coded-wire tags were recovered from age-4 fish in those years and in 2007, 2012, 2014, and 2017, despite fishing occurring those years. Age-4 returns following those years had minimal or no tag recoveries on the spawning grounds, suggesting low age-4 abundance for those cohorts. The average fork length of age-3 harvested fish was 598 mm (σ = 57.0 mm) while the average fork length of age-4 harvested fish was 789 mm (σ = 81.0 mm). Age-3 winter-run Chinook salmon impacts were predominately observed in the recreational fisheries whereas the majority of age-4 winter-run fish impacts were observed in the commercial fisheries. An average of 82 percent of age-3 impact each year was from the recreational fisheries compared to 18 percent from the commercial fisheries. At age 4, an average of 29 percent of the impact was recreational and 71 percent was commercial. We estimated non-harvest mortalities (i.e., release mortality and drop-off mortality) comprised 26 percent of age-3 total impact compared to comprising 6 percent at age 4.

The mean age-3 impact rate for 2002–2015 brood years (excluding fishery closures in 2008 and 2009) using cohort-specific contact rates was 0.16 (σ = 0.073), while the mean age-4 impact rate was 0.19 (σ = 0.25). Estimating the fishery impact rates for hatchery-origin fish using cohort-specific impact rates versus aggregating ages did not substantially affect the age-3 impact rate (Figure II-3). However, aggregating data from the same year reduced the variability in age-4 impact across years, raised the estimated impact rate for age-4 fish from zero when no CWTs were recovered from age-4 fish, and lowered the impact rate when low sample size led to spuriously high impact (i.e., brood year 2008). The age-3 impact rate was on average 68 percent (σ = 14 percent) of the age-4 impact rate from the same year.
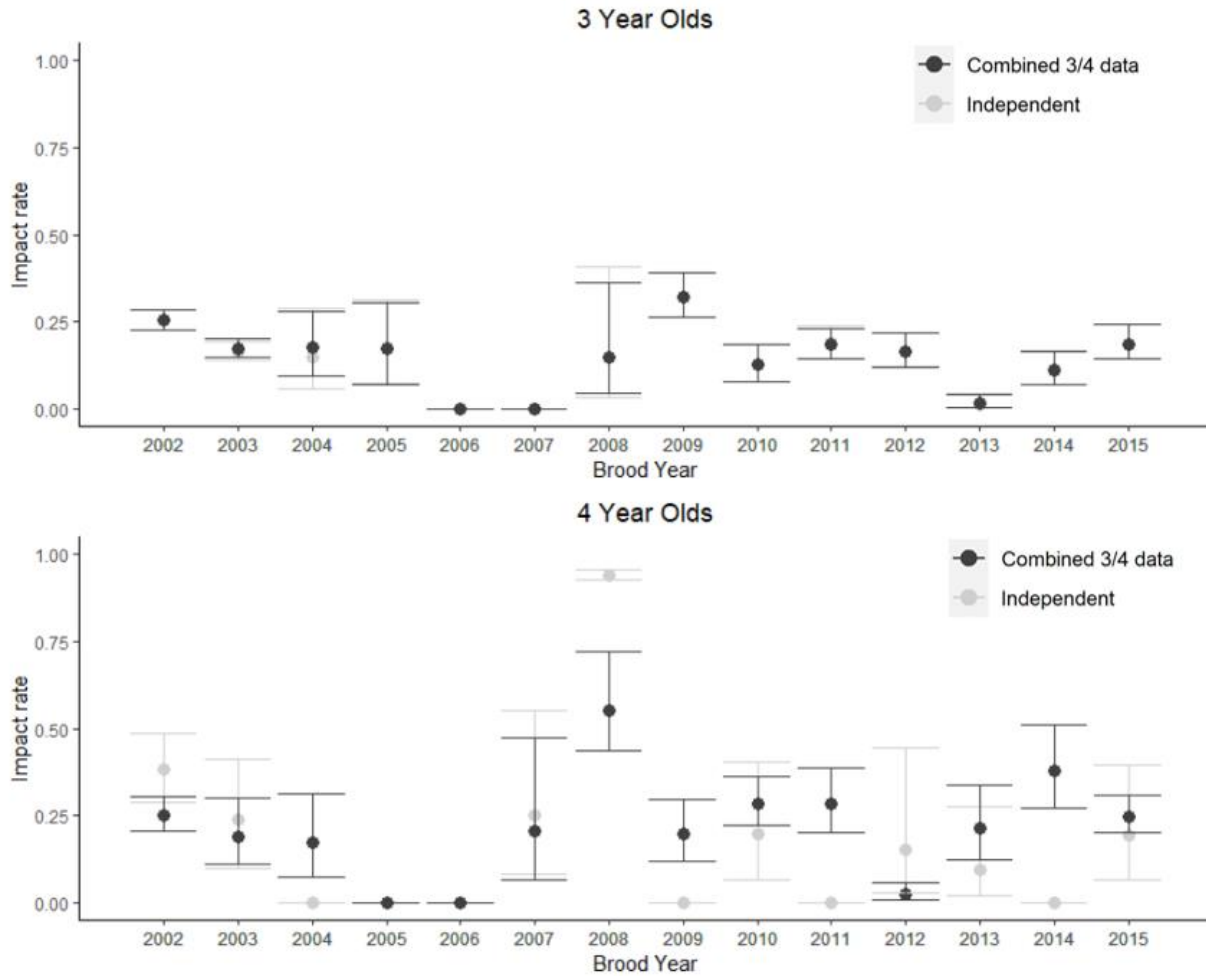
Figure II-3. Mean fishing impact rates (bars indicating 95% confidence intervals) at age 3 and age 4 for winter-run Chinook salmon. Grey indicates i, impact rates estimated using cohort specific coded-wire tag recovered while black indicates i^*, impact rates estimated using age-aggregated recoveries.

Due to differences in age structure, the mean reduction in run size (SRR) for hatchery fish between 2005 and 2018 was 12.5 percent (σ = 9.5 percent) compared to 14.6 percent (σ = 8.5 percent) for natural-origin fish (Figure II-4). In years that natural-origin fish had higher age-2 maturation rates than hatchery fish, they had reduced exposure to the fisheries and smaller reduction in their run sizes compared to hatchery fish. In years that natural-origin fish had lower age-3 maturation rates, they had greater exposure to the fisheries and greater reduction in run sizes. Although natural- and hatchery-origin females incurred comparable impact from fishing, natural-origin males experienced higher reductions than hatchery males (Figure II-4).
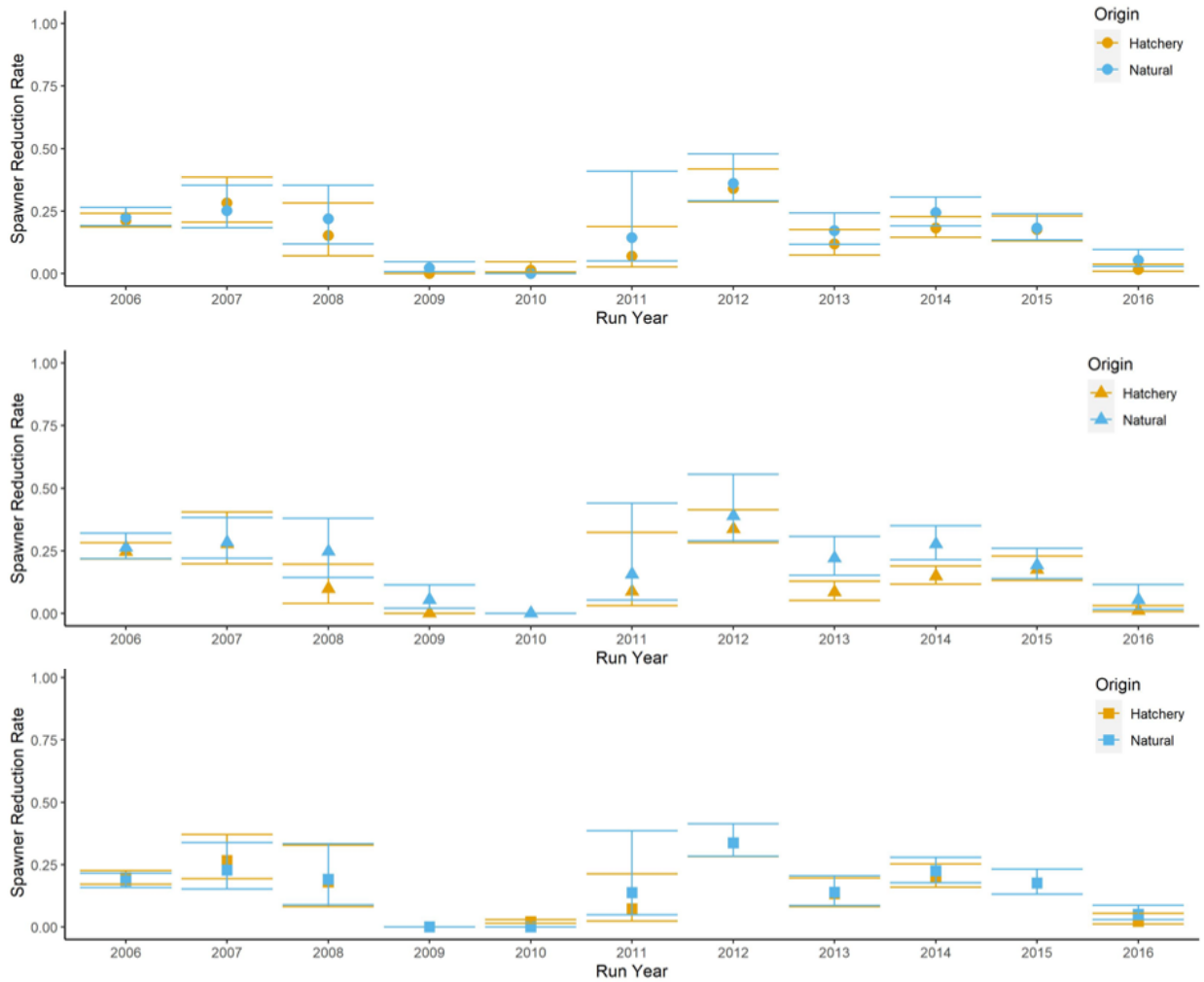
Figure II-4. Mean reduction (bars indicating 95% confidence intervals) of natural- and hatchery-origin winter-run Chinook salmon (top), male (middle), and female (bottom) run size from fishing.

3.3 Sensitivity Analysis

SRR and age-3 impact rate estimates were more sensitive to changes in release mortality than maturation rates and age-4 impact rates. Increasing release mortality (i.e., if release mortality was underestimated) increased estimates of fishery impacts and spawner reduction and marginally decreased maturation rates. Adjusting the release mortality higher versus lower had equal and opposite effects on estimates of fishery impact, maturation, and spawner reduction rates (Table II-3). The effect of adjusting release mortality within the range explored was minor compared to not accounting for release mortality at all. Impact was more sensitive in years when fishing was concentrated early in the summer when a greater proportion of fish are of sublegal size (Appendix B Figure B-1).

Table II-3 Sensitivity of impact, maturation, and spawner reduction rates to changes in release mortality (six percent for recreational and two percent for commercial) and size at age (1.8 inches) inputs. Values are the mean change in impact and maturation rates for 2002–2015 brood years and in spawner reduction rates for 2006–2016 run years.

	Release mortality			Size at Age	
	% increase	% decrease	no release mortality	-1 SD	+1SD
Age-3 impact	0.0034	-0.0033	-0.025	0.091	-0.022
Age-4 impact	0.000036	-0.000036	-0.00047	0.0015	-0.00042
Age-2 maturation rate	-0.00031	0.00031	0.0020	-0.015	0.0054
Age-3 maturation rate	-0.000015	0.000015	0.00017	-0.00048	0.00014
Spawner reduction rate	0.0025	-0.0025	-0.021	0.076	-0.020

For size at age, the sensitivity of vital rates depended on the direction in which size at age deviated from the model. When size at age was lower (e.g., years of below average sizes), estimates of impact rates deviated more from the baseline estimates than when size at age was higher (Table II-3). Raising size did not affect impact estimates when nearly all fish of the age class were already of legal size. Changes in impact estimates from different sizes at age ultimately resulted in marginal inverse shifts in maturation rates estimates.

4. DISCUSSION

In salmonids, an individual's age at maturation is influenced by its genetics and environment (Kuparinen et al. 2009; Larsen et al. 2019). Broodstock selection and rearing practices at hatcheries can result in differences in maturation schedules, and subsequently age structure, between hatchery-origin and natural-origin fish. Within the context of the winter-run Chinook salmon conservation hatchery on the upper Sacramento River, we found evidence that hatchery cohorts had a more truncated age structure compared to their natural-origin counterparts. Specifically, hatchery fish had lower rates of returning at the older age, age 4, across brood years 2002–2015 because of their high age-3 maturation rate. A truncated age structure reduces the variation in maturation ages and lowers the spreading of risk of spawning failure across time (Siskey et al. 2016; Oke et al. 2020). However, it also reduces cumulative exposure to ocean mortality from natural sources and from fisheries (Davison and Satterthwaite 2017; Carvalho et al. 2023). The fishing impact during the study period was at an intensity that did not dramatically alter the age composition of escapement each year, although the increased mortality for the

population due to fishing would be expected to select for early maturation and reduce the mean escapement age over time (Bromaghin et al. 2011).

4.1 Maturation schedule by sex and source

Males and females differ in reproductive investments and therefore can have different reproductive strategies and maturation schedules (Hutchings 2021). Like Chinook salmon populations elsewhere (Healey 1991), male winter-run Chinook salmon had more variation in age at maturity compared to females. Hatchery females had very similar maturation schedules to natural-origin females, potentially because age at maturity in females is less plastic, more genetically homogenous, or selection for females at the hatchery is similar to that experienced in nature (McKinney et al. 2021). We found that an overwhelming majority of females return to spawn at age 3, suggesting there are evolutionary disadvantages or physiological constraints for females to mature at age 2 or age 4. Females require much more energy to mature and may not have sufficient lipid levels to begin egg production at age 2 (Jonsson et al. 1997; Mobley et al. 2021). Winter-run Chinook salmon are and historically were smaller in body size compared to other runs (Stone 1874). They travel furthest upstream in the Sacramento River, and the energetic cost of migration could limit female size and age at maturity (Crossin et al. 2004). Winter-run Chinook salmon now spawn in dramatically different habitat, below Shasta and Keswick dams, where water temperatures can be warmer than the spring-fed tributaries they spawned in historically. Occupying warmer water requires greater metabolic demands, diverting energy away from egg production, and can further constrain body size and age at maturity in females (King et al. 2003; Fenkes et al. 2016). This change potentially altered the drivers of selection for age at maturity during spawning.

While female hatchery fish had very similar maturation schedules relative to their natural-origin counterparts, we observed divergence in the rate at which hatchery males returned at older ages. Fewer hatchery-origin males returned at age 4 compared to natural-origin males. On the spawning grounds, males compete to spawn with females, and females may choose mates by depositing eggs when ideal mates are nearby (Fleming and Gross 1994). Sexual selection on the spawning grounds can result in reproductive success skewed towards larger males. This selection can be relaxed in the hatchery setting if broodstock selection and reproductive success is random (Hankin et al. 2009). Without sexual selection, we would expect a long-term reduction in the age of maturation and size of males. A goal of the winter-run Chinook salmon hatchery program is to maximize genetic diversity and select broodstock that are representative of the entire run (USFWS 2016). Adults of different sizes are incorporated into the broodstock at the rate of their collection. Introducing a mating regime that is skewed towards larger males can better mimic sexual selection but can also reduce effective population size (Quader 2005). For endangered populations that have undergone genetic bottlenecks, the trade-off between the brood's genetic variation and mimicking selection experienced in the wild needs to be carefully evaluated when selecting broodstock and mating regimes (Ryman and Laikre 1991).

Although we observed accelerated maturation at age 3 in hatchery fish, we did not observe regularly elevated rates of precocious maturation (i.e., maturing at age 2), which has been observed in other Chinook salmon populations with hatchery supplementation (e.g., spring-run, Larsen et al. 2019) as well as Atlantic salmon (Piggins and Mills 1985). At hatcheries, diet composition, water temperature, and photoperiod optimal for growth can increase the size of released fish for survival but also rate of early maturation (Shearer et al. 2006, Harstad et al. 2014). Species differ in how genetics and environmental factors interact to determine the probability of maturation, and therefore the sensitivity of maturation to hatchery influence. Winter-run Chinook salmon are released as sub-yearlings and rear for shorter periods in freshwater than spring-run Chinook and Atlantic salmon that are released as yearlings, reducing their exposure to hatchery influence. The precocious maturation rates we estimated may in part be lower compared to rates estimated in other hatchery populations because of methodology (recovered escapement versus retained fish). Age-1 males were only observed in hatchery-origin fish, although the probability of recovering an age-1 natural-origin male on the spawning grounds would be very low due to their much smaller size and propensity for males to drift downstream after spawning (Harstad et al. 2014). Retaining and studying winter-run Chinook salmon at the hatchery would provide a more accurate estimate of precocious maturation in hatchery fish.

4.2 Fisheries Management Implications

Because natural-origin winter-run Chinook salmon are more likely to remain at sea until age 4, they are exposed to fishing for an additional year and are less protected by minimum harvest size restrictions relative to hatchery fish. Based on the size-at-age model we used (Appendix A of O'Farrell et al. 2012), only a very small percentage of age-4 fish are protected by size limits, primarily from the commercial fisheries early in the season. Indeed, from the coded-wire tag recovery data, the age-3 sizes of harvested winter-run Chinook salmon fish were close to the size limit of the fishery while the age-4 sizes were much larger than the size limit. Commercial fisheries, which have larger minimum size limits than recreational fisheries, have reduced impacts on age-3 fish but comprise a large proportion of the age-4 fishing impact. Natural-origin winter-run Chinook salmon may therefore be harvested by the commercial fishery to a greater extent than hatchery fish.

Natural-origin males matured at an older age and therefore experienced higher cumulative natural and fishing mortality due to longer exposure (Kendall and Quinn 2013). Furthermore, males on the spawning grounds were larger than females at each age, suggesting they may be larger in the ocean and more frequently of harvestable size. Sexual dimorphism and differences in behavior result in higher rates of fishing impact and predation for the larger and more actively foraging sex (Holtby and Healey 1990; Kendall and Quinn 2013). In coho salmon, females are larger at each age than males and more frequently captured by the fisheries, whereas male sockeye salmon are larger than females and more frequently captured (Holtby and Healey 1990; Kendall and Quinn 2013). In both instances, the larger and later maturing sex was less frequent on the spawning grounds.

The observed sex ratio from carcass surveys for winter-run Chinook salmon was skewed towards females, but this may also be because females tend to remain near their redds and are less likely to drift downstream (Murdoch et al. 2009). For the sake of population size, mortality in males has fewer consequences for the productivity of the population compared to mortality in females.

Hatchery fish are a vital tool for managing and monitoring the whole population, and data collected from them provide estimates of quantities important for management and conservation that are difficult to estimate from natural-origin fish directly. However, differences in their life history can result in biases in the output and interpretation of management tools that use hatchery fish as proxies. Because of their differences in maturation rates, natural-origin winter-run Chinook salmon had a spawner reduction rate (SRR) that was an average of 2.8 percent higher than hatchery winter-run Chinook salmon. The degree of bias in SRR that results from borrowing hatchery fish age composition is dependent on both the magnitude of difference in age structure and the intensity of fishing. Fishing impact rates during our study period were relatively low (usually < 20 percent at age 3 and < 40 percent at age 4) compared to winter-run Chinook salmon prior to 2002 (e.g., 55%-72% at age 4 for brood years 1999–2001, O'Farrell et al. 2012) and other managed stocks in California, such as Sacramento River fall-run Chinook salmon (PFMC 2023a). For populations that experience higher fishing intensity, we expect larger bias when using hatchery age composition data as a surrogate for the age composition of the natural population.

Because hatchery fish predominantly exit the ocean and return to spawn at age 3, recoveries of coded-wire tags from age-4 hatchery fish are infrequent and sometimes nonexistent. This is of concern for monitoring the natural-origin population if a significant proportion of them are at sea at age 4. Limited or no data from age-4 hatchery fish may misrepresent the impact on natural-origin fish. Aggregating age-3 and age-4 recoveries from the same period to estimate a catch rate raised the age-4 impact rate estimates in years when there were no age-4 recoveries. Additionally, it resulted in impact rate estimates that were more consistent across time because of the combined information.

4.3 Caveats and Uncertainties

Although our goal was to test whether it is appropriate to use hatchery maturation rates for natural-origin fish, it was still necessary for us to use hatchery-origin data for fishery impact parameters where there were insufficient data from natural-origin fish. Data on the recoveries of natural-origin winter-run Chinook salmon by fisheries were limited due to a lack of tagged natural-origin fish and a lack of consistent genetic sampling of harvested fish, so we used impact rates from hatchery fish and assumed natural-origin fish have the same spatial distribution, contact rates, and size at age. Regarding spatial distribution, ocean recoveries of winter-run Chinook salmon via genetic stock identification are spatially comparable to ocean recoveries of winter-run Chinook salmon coded-wire tags (Satterthwaite et al. 2015). Size-at-age to calculate the proportion of fish that are of legal

size was estimated in O'Farrell et al. (2012) and static in our analysis, but likely changes from year to year depending on freshwater and marine conditions (Satterthwaite et al. 2012; Armstrong and Schindler 2013; Woodson et al. 2013). When we evaluated how impact was influenced by not accounting for interannual variation in size at age, the primary drivers were impact estimates at younger ages earlier in the year (i.e., April – July of age-3) when a significant proportion of the population was sublegal. Therefore, greatest uncertainty of impact exists for years in which harvest is concentrated early in the season. Although we assumed size at age to be comparable for hatchery and natural-origin fish, they may potentially differ due to differences in ocean entry and early ocean rearing. Data on the early size at age of hatchery and natural-origin fish would be especially valuable in understanding how they may differ in their ocean survival and exposure to fishing.

Vital rate estimates were insensitive to adjusting release mortality within the range of recommended values relative to not factoring release mortality at all. In particular, maturation estimates were not sensitive to changes in impact rates during the sensitivity analysis. We fixed sub-adult (i.e., age-2+) natural mortality in the ocean because natural mortality and maturation are statistically confounded (Allen et al. 2017). Divergence in the actual sub-adult natural mortality from the fixed values due to misspecification and interannual variability would directly affect the maturation rate through inaccurately estimating ocean abundance. However, estimates of maturation rates via cohort reconstructions are generally insensitive to inputs of natural mortality except when input rates greatly differ from actual natural mortality (Allen et al. 2017).

On the spawning grounds, the probability of recovering carcasses can differ by size (Zhou 2002) and sex (Murdoch et al. 2009). Larger carcasses might have had a higher probability of being seen and recovered, which would result in our estimates of age-2 and age-3 maturation rates being biased low. Because females guard their redds and are less likely to drift downstream, females might have had a higher carcass and tag recovery rate than males, which would primarily bias estimates of their survival but not relative maturation schedules. We do not expect these biases to differ between hatchery and natural-origin fish and so they should not affect the relative differences in maturation rates.

5. CONCLUSION

Due to their accessibility, hatchery fish often serve as surrogates for wild fish to estimate vital rates, movement, fishery contact rates, and other quantities important for management and conservation (Weitkamp 2010; O'Farrell et al. 2012; Sharma and Quinn 2012). Divergence in the behavior and life history of hatchery fish from their natural-origin counterparts can bias tools used to monitor and manage the combined population. Knowing the extent of which hatchery and natural-origin fish differ is critical to accurately interpreting the output of management tools and making informed decisions for populations with hatchery and natural components. Exploring how sensitive outputs are to biases is worthwhile when there is concern that hatchery- and natural-origin fish significantly diverge in life history.

Maturation schedules define the population's age structure and influence its productivity, stability, and duration of exposure to the fisheries. Differences in the age at maturity across sources, sex, and life histories can lead to disproportionate fishing impacts within the population. Harvest rules that aim to limit impact on listed populations guided by data collected from proxies may be less effective at achieving target goals if the proxy fails to represent or capture unique aspects of the population of interest. While hatchery fish data provided SRR estimates we considered similar to the natural-origin population's, the data available did not sufficiently inform fishing impact for older age classes or highlight the differences in maturation schedules by sex we observed in natural-origin fish. Identifying differences in the age at maturity within a population is critical to understanding how fisheries impact a population's long-term population dynamics.

6. ACKNOWLEDGEMENTS

Chapter 3. Incorporating age structure into the assessment and forecasting of Sacramento River Fall Chinook salmon

Abstract

Predicting future fish recruitment accurately is an important component of salmon fishery management objectives. In California, overprediction of Sacramento River Fall Chinook salmon (*Oncorhynchus tshawytscha*) abundance in recent years using an age-aggregated forecast model suggest a need to reevaluate the current abundance index and model and determine whether alternative assessment metrics and information for forecasting are needed. We conducted cohort reconstruction analysis for Sacramento River Fall Chinook hatchery and natural-origin fish and compared cohort-based, age-specific assessments to the current age-aggregated index of abundance. To evaluate the potential improvements from incorporating additional age structure information and using an age-specific forecast model, we conducted closed-loop simulations of two alternative forecast models (age-specific versus age-aggregate). From 1998-2016, hatchery-origin component maturation rate has increased, with higher rates correlating with higher forecast error. No trend in natural-origin maturation rates were detected from 2008-2016, but rates were more uncertain, and the time series of data available was shorter. While age structure information was important for understanding population dynamics over time and improving the accuracy of assessment metrics, having more age structure information did not improve forecasting accuracy for the following year in simulations because of annual variation in the population's maturation schedule and few older-aged individuals (age 4+) contributing to escapement. When considering alternative models, assessing the value of different information types is a necessary step for efficient and cost-effective fisheries management. In changing and more uncertain population dynamics, management should work towards robust and flexible fisheries management that buffer against uncertainty and error.

1. INTRODUCTION

Accurate stock assessments and predictions of future fish recruitment are critical to implementing management that achieves conservation and socio-economic objectives. Stock assessment metrics are the foundation of information guiding fisheries management, and managers rely on appropriately specified targets and accurate metrics to make decisions. Models are used for planning fisheries (Hanson et al. 2006) and evaluating management alternatives (Farmer and Froeschke 2015). Biased assessments and inaccurate forecasts can lead to more harvest than appropriate or unnecessary constraints on fisheries. While it is generally beneficial to collect more or improved data to provide more accurate forecasts, evaluating the potential benefits of additional data is a prudent step for efficient and cost-effective management.

This challenge has come to the fore in California salmon fisheries where, at low abundances in recent years, accurate assessments and forecasts are even more critical to prevent overfishing and overfished status while supporting fisheries. Sacramento River fall-run Chinook salmon (*Oncorhynchus tshawytscha*) compose a large proportion of salmon harvested in the state, and their status significantly shapes annual regulations for commercial and recreational fishing in coastal and inland waters. In recent years, the stock has fallen below escapement goals six times from 2015-2023, was classified as overfished from 2018-2020, and whose low abundances along with concerns about poor recent performance of harvest and planning models contributed to fishery closures in 2023 and 2024. For 2014-2023, preseason forecasts of escapement in the absence of fishing have overestimated postseason estimates of this quantity in 8/10 years and therefore allowed for higher exploitation rates than would be specified by more accurate forecasts (PFMC 2019; PFMC 2023b). For short-lived, cyclical stocks, accurate preseason forecasts are especially important to achieving management goals (Walters 1989).

The management framework for Sacramento River Fall Chinook uses an aggregate age index of abundance known as the Sacramento Index (SI) (O'Farrell et al. 2013). The index is calculated by summing escapement, ocean harvest, and in-river harvest every year. The SI represents both age 3+ ocean abundance and potential escapement absent fishing, even though these values are expected to differ because of natural mortality and not all age 3+ fish mature in the current year. Prior to the season, the SI is forecasted using a sibling regression that models SI as a function of age-2 escapement the previous year, typically estimated using length-based cutoffs (e.g., PFMC 2023b). The maximum allowable exploitation rate for this stock is then determined from the forecasted abundance and a harvest control rule aimed to achieve spawning abundance at maximum sustainable yield. As the Sacramento Index is treated as both ocean abundance and potential escapement, inaccurate representation of these metrics by the SI could contribute to inappropriate recommendations for harvest that lead to escapement falling below the target goal. Using age-specific, cohort-based methods to assess potential escapement and ocean abundance could reduce currently unknown bias in the index's ability to represent potential escapement and ocean abundance.

Frequent over-forecasts of the SI in the past decade may reflect a shift in the population's maturation rates and/or ocean survival. This is particularly alarming because these parameters affect population productivity (Trippel et al. 1997; Oke et al. 2020) and long-term stability (Hsieh et al. 2010). Because adult (age 3+) forecasts for this stock are predicted based on the return of age-2 (precocious) siblings the previous year, one possible explanation for over-forecasting adult escapement is that the population's precocious maturation rate has increased, potentially due to hatchery effects. Understanding whether changes to vital rates have occurred is necessary for adjusting the forecast model for future predictions.

While additional data generally improves the accuracy of assessments and forecasts, collecting additional data and processing it in a timely manner can be costly and may not change assessments and predictions in a meaningful way (Rupp et al. 2012; Ward et al. 2014). A key need for cost-effective management is evaluating when investing in additional monitoring data will be worthwhile. For Sacramento River Fall Chinook, assessing age-specific recruitment rather than an age-aggregate index could reduce currently unknown bias in the index of abundance and help detect changes in underlying dynamics of abundance. For preseason planning, greater use of age-specific recruitment data may improve preseason predictions but would require the California Department of Fish and Wildlife to allocate significant effort to process and estimate age-specific escapement prior to the start of next fishing season. Similar tradeoffs may apply to multiple other salmon stocks where the forecasts do not contain the most recent up-to-date age-specific information (PFMC 2023b). To evaluate whether the expedited effort is justified for improving forecast performance, we need to estimate the degree of improvement and quantify the probability that clarifying uncertainty will likely lead to changes in decision outcomes (Runge et al. 2011).

Our overall goals were to 1) develop and compare age-specific cohort assessments to the current aggregate age index and 2) evaluate whether using age-specific forecasts would improve management outcomes for the Sacramento River Fall Chinook complex. We first conducted an age-specific analysis of past cohorts and estimated vital rates of Sacramento River Fall Chinook over time. We compared cohort-based, age-specific metrics to metrics based on the current age-aggregated index used in management, the Sacramento Index. We tested whether over-forecasts correspond with increases in the population's precocious maturation rate. Next, we compared an age-aggregated versus an age-specific forecast model by conducting closed-loop simulations to measure the accuracy and value of age-specific data in future forecasts and potential impacts on fisheries and conservation goals.

2. MATERIALS & METHODS

2.1 Study system

Sacramento River Fall Chinook (SRFC) salmon currently are the most abundant salmon stock in California and the primary target for commercial and recreational fishing off the coast of California and southern Oregon and recreational fishing in the basin (Huber and Carlson 2015). The stock is composed of multiple populations spawning in natural spawning areas, such as the upper Sacramento River, Feather River, American River, Yuba River, Battle Creek, Clear Creek, and other minor tributaries, and three hatcheries: the Coleman National Fish Hatchery, Feather River Hatchery, and Nimbus Fish Hatchery (Yoshiyama et al. 1998). In addition, the stock serves as an indicator for Sacramento River late-fall Chinook salmon and San Joaquin River fall Chinook salmon. This is a hatchery dominated complex; the proportion of fall-run fish returning to spawning grounds in the Central Valley that are of hatchery-origin averaged 76% from 2010-2019 years (Satterthwaite 2023).

Maximum allowable exploitation rates for this stock are determined from a harvest control rule applied to the Sacramento Index (PFMC 2024). The maximum exploitation rate under the harvest control rule for the stock is F_{abc}, 0.7. The maximum sustainable yield reference point for the population was established as 122,000 hatchery and natural-origin spawners (S_{MSY}) and when potential escapement with an exploitation rate of at least 0.25 exceeds S_{MSY}, allowable exploitation is determined as the rate expected to achieve S_{MSY}. De minimis fisheries may occur when S_{MSY} is not expected to be achievable with an exploitation rate of at least 0.25, with allowable exploitation rates decreasing at the lowest abundances. The stock is considered overfished if the 3-year geometric mean of escapement falls below the Minimum Stock Size Threshold (MSST, equal to 91,500), which most recently occurred from 2017-2019. The stock was considered rebuilt in 2020 when the 3-year geometric mean exceeded S_{MSY}.

2.2 Data

Coded-wire tags (CWTs) are batch tags that have been used extensively for West Coast salmonid management. CWTs have been used for hatchery-produced Sacramento River Fall Chinook and recovered in fisheries along the coast and at some Central Valley hatcheries since the 1970s. Surveys that recovered CWTs on the spawning grounds in the Sacramento Basin began in 2000. Since 2007, all batches of hatchery fish were marked and tagged at a rate of at least 25%, and spawner surveys have become more robust, so it is possible to obtain accurate estimates of escapement and harvest abundance (Bergman et al. 2012). Fish that are implanted with a CWT have their adipose fin removed ("marked") to denote the presence of a tag, although rare instances where fish are tagged but unmarked or marked but untagged occur. The release and recovery information of coded-wire tagged fish are reported to the Regional Mark Information System (RMIS) database provided by the Regional Mark Processing Center (RMPC 2024). We queried the database for recoveries of 1998-2016 brood years (BY) from Coleman National Fish Hatchery, Feather River Hatchery, and Nimbus Fish Hatchery.

In addition to coded-wire tags, scales have been collected from marked and unmarked spawner carcasses during surveys and at hatcheries and aged by the California Department of Fish and Wildlife since 2010. Scales were aged by an individual experienced reader. Sex and length were considered only after the initial aging by the reader. Samples from CWT-tagged, hatchery-origin fish with known age were read to assess for aging bias. The known age from the CWT and the read age from the scale reads were used to develop a confusion matrix to adjust for potential aging bias, so only samples from hatchery-origin fish with CWTs composed the confusion matrix. Samples were grouped by tributary except for natural-origin fish returning to Cow Creek, Cottonwood Creek, Mill Creek, Butte Creek, and Deer Creek, which were aggregated because of limited sample sizes. These tributaries have smaller abundances and generally lower hatchery presence. Scale samples were not collected in Battle Creek so scale samples from unmarked escapement at Coleman National Fish Hatchery were assumed to represent unmarked escapement for the entire subbasin.

Estimates of escapement to major rivers and tributaries were obtained from GrandTab, compiled by the California Department of Fish Wildlife (Azat 2023). Rivers with escapement estimates for the years of our study were the Sacramento River, Feather River, American River, Yuba River, Clear Creek, Battle Creek, Cottonwood Creek, Butte Creek, Mill Creek, Deer Creek, and Cow Creek. Minor tributaries with infrequent sampling (e.g., Paynes Creek, Bear Creek) were not included in the analysis.

2.3 Age-Specific Escapement and Fishery Impacts

Escapement to the spawning grounds of each tributary can include 1) marked and CWT tagged hatchery-origin fish, 2) unmarked and presumably untagged hatchery-origin fish, and 3) unmarked natural-origin fish. CWT recoveries were used to estimate the age-specific abundance of hatchery-origin fish spawning in the river. For each tag recovered, the number of tags present but unrecovered k was estimated by drawing from a negative binomial distribution (Michielsens et al. 2006) where Θ equals the sampling fraction of the survey and probability of recovering the tag. This was done 1000 times for each tag to characterize uncertainty from sampling.

$$k \sim NB(1, \Theta)$$

For each recovery, k + 1 equaled the estimated number of marked fish present per tag. The number of marked hatchery fish was then expanded to include unmarked hatchery fish based on the CWT tagging rate of the batch. Maturing CWT fish may also return to a hatchery or be captured by in-river fisheries. Escapement to the hatchery and in-river harvests were estimated using the same expansion methods as natural spawning ground escapement estimates. Hatchery-origin escapement was grouped by source across all hatchery and spawning ground recovery locations.

Natural-origin escapement to each tributary's natural spawning grounds and to each hatchery was estimated by subtracting the age-specific hatchery-origin escapement

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at that site from total escapement. We used the scale ages of unmarked fish recovered from each site to estimate the age composition of unmarked escapement. Scale samples were bootstrapped for each return year by redrawing samples with replacement 1000 times to evaluate sampling uncertainty. The age distribution of returning runs for each iteration was then estimated using an iterative algorithm to account for bias in scale aging (Kimura and Chikuni 1987). The algorithm used a confusion matrix composed of estimated age from scales to known age from CWTs from the same tributary (or group of tributaries). Unmarked hatchery-origin fish at each age were then subtracted from the total unmarked escapement at each age to estimate natural-origin escapement. In some instances, estimated escapement of natural-origin fish at an age would have been negative because unmarked hatchery-origin fish estimates exceeded total unmarked fish, potentially due to sampling error or the aging and aging bias correction process. This occurred in three percent of all iterations across tributaries, ages, and years. In these cases, ages-specific escapement was set to zero when escapement estimates were negative. For tributaries with hatcheries (Battle Creek, Feather River, and American River), abundance estimates of natural-origin spawners to the hatchery were combined with abundance estimates in-river to estimate total natural-origin escapement to the tributary.

Fish captured by commercial and recreational ocean fisheries are not yet considered to have matured. Coded-wire tags recovered from fisheries sampling were used to estimate the impact of ocean fisheries *I* on CWT fish. Total impact includes harvested fish F and non-landed mortalities, including fish that were hooked but not contacted and fish that were caught and released because they were of sublegal size that died due to injury and stress, *R* and *D* respectively.

$$I = F + R + D$$

F was estimated using the same expansion methods as escapement and in-river fisheries estimates.

Release mortality, *R*, was estimated from the number of released fish and the release mortality rate *r*.

$$R_{a.t} = \left(\frac{F_{a.t}}{h_{g.b.a.t}} - F_{a.t} \right) \times r_{g.b.t}$$

Releases equaled the number of fish contacted (harvest divided by the harvestability for the cohort minus the harvested fish). Harvestability, h, or the proportion of the cohort that is above the legal size and can be kept, depends on the size distribution of the cohort at the time and the size limit for the fishery type *g*, area *b*, and time *t*. We estimated the size distribution of cohorts each month using maximum likelihood estimation methods based on truncated normal distributions described in Satterthwaite et al. (2012). The size distribution of individuals in each cohort was assumed to be normally distributed and the total lengths converted from reported fork lengths of recovered fish represent the subset of fish above the size limit. We estimated the size distribution (mean and standard deviation) specific for each cohort for each month when more than 20 samples of fork length were collected. In months when less than 20 samples were collected, we used the estimated

size distribution across all cohorts from 2000-2016 for the month. The release mortality rate, which varies by the fishery, area, and time, was then applied to releases. *r* was 0.26 for commercial fisheries for all areas and times and ranged between 0.14 and 0.39 for recreational fisheries depending on fishing techniques in the region and time (Salmon Technical Team 2000).

Additionally, fish that were hooked but not caught may still become mortalities. We applied a drop-off mortality rate of 0.05 to all contacted fish to estimate this drop-off mortality (Salmon Technical Team 2000).

$$D_{a.t} = \frac{F_{a.t}}{s_{g.b.a.t}} \times d$$

2.4 Analysis of Past Cohorts

We estimated vital rates (e.g., maturation, impact) for hatchery cohorts from 1998-2016 and natural cohorts from 2008-2016. For each of the 1000 iterations, cohort abundances over time were calculated by reconstructing abundances every month, starting with the last month that an individual from the cohort was recovered. Abundance *N* at each age *a* at each time step *t* is equal to abundance at the next time step and individuals during the current time step that were natural mortalities *V*, fishing mortalities *I*, or matured *M*. Ages are assigned using 1-based indexing (i.e., fish are age one in their first year of life).

$$N_{a.t} = N_{a+1.t+1} + V_{a.t} + I_{a.t} + M_{a.t}$$

Natural mortality was modeled to occur after maturation and fishing mortality every month. *V* at each time step was calculated by multiplying the number of surviving fish and the proportion of fish that were mortalities given a mortality rate *v*.

$$V_{a.t} = N_{a+1.t+1} \times \frac{v_{a.t}}{1 - v_{a.t}}$$

We used monthly natural mortality rates that accumulated to annual natural mortality rates of 0.5 at age two and 0.2 at age three, age four, and age five for *v*, rates used for analyses of other Chinook salmon stocks in California (Klamath River Technical Advisory Team 1986; O'Farrell et al. 2012).

Cohort abundance was calculated from when fish first turn age two on September 1 (after entering the ocean earlier that year, one year after their parents matured) to the last month that an individual from the cohort was recovered. For hatchery cohorts, year-one survival (i.e., from release to age two) was calculated by dividing cohort abundance at age two by number of hatchery fish released. For natural-origin cohorts, we estimated productivity by calculating recruits (age-2 fish) per spawner.

We calculated annual ocean impact rates *i* for hatchery-origin cohorts at each age. Annual impact was grouped from when fish turn the next age in September to August the following year and impact rates were calculated using

$$i_a = I_a/N_{a.t=9}$$

Data to directly estimate ocean and in-river harvest of natural-origin SRFC does not exist, and so age- and year-specific impact rates estimated for hatchery-origin component were assumed to be the same for the two sources such that the rates for hatchery-origin fish were applied to natural-origin fish during cohort reconstructions.

We modeled maturing fish to return to the river on August 31 before they turn the next age. Maturation rates m at each age equaled matured fish that escaped to spawning grounds or hatcheries or were harvested by the in-river fishery divided by the cohort's ocean abundance at the end of August. To evaluate changes in maturation rates over time, we conducted weighted Mann-Kendall tests to assess for monotonic trends using the R package *wdm* (Nagler 2023). We considered the degrees of certainty in maturation estimates across years by using the mean estimates of the maturation rate across the 1000 iterations and weighing each estimate inversely proportional to its variance across iterations (da Graça 2010). We tested for a trend over time in the age-2 and age-3 maturation rate of the hatchery and natural-origin components. To evaluate whether changes in the age-2 maturation rate contributed to overestimates of the Sacramento Index in recent years, we calculated the correlation between the age-2 hatchery-origin maturation rate and forecast error, log(SI) – log((SI))̂.

We evaluated the fishing impact on the population by estimating potential escapement in the absence of fishing, *E'*. To estimate *E'*, ocean abundance in the absence of fishing *N'* was first calculated at every time step starting from the earliest age of reconstructed abundance by applying only natural mortality and maturation over time. *E'* was then estimated by applying the estimated maturation rate for the cohort to *N'* at the end of each August. The spawner reduction rate, SRR, is the reduction of spawning abundance due to all fishing impact and was calculated for each run year.

$$SRR = 1 - \frac{E}{E'}$$

We compared the similarity of our estimates of cohort-based, age-specific metrics to the current index of abundance and metrics of exploitation. Because the Sacramento Index is used to represent both potential escapement and age 3+ ocean abundance at the start of the season, we compared the SI to potential escapement if no fishing had occurred in the current year and to age 3+ ocean abundance in September the previous fall. For metrics of exploitation, we compared the ocean harvest component of the Sacramento Index (south of Cape Falcon) to ocean harvest south of Cape Falcon and impact we estimated for fish age 3+. Additionally, we compared the exploitation rate of the Sacramento Index reported, which includes in-river and ocean harvest (PFMC 2023b), to SRR.

Source-specific vital rates were estimated for each of the hatcheries that produced Sacramento River Fall Chinook (Coleman National Fish Hatchery, Feather River Hatchery, and Nimbus Fish Hatchery) by conducting separate cohort analyses for each hatchery. Cohorts of natural-origin fish in six tributaries with consistent monitoring and scale

collection and aging (Sacramento River, Feather River, American River, Yuba River, Clear Creek, Battle Creek) were also analyzed independently. Natural-origin fish returning to other tributaries (Butte Creek, Cottonwood Creek, Mill Creek, Cow Creek, and Deer Creek) were aggregated into a single cohort and evaluated.

2.5 Operating model

Vital rates estimated during the Sacramento River Fall Chinook cohort analysis were used to simulate biological dynamics. For the hatchery-origin component, each hatchery cohort was initiated with the release of hatchery fish that equaled the mean number of fish released from 1998 to 2016 (Table III-1). Their survival in their first year from outmigration to age two in the ocean was sampled from a beta-binomial distribution with the beta distribution having the mean and SD of year one survival of hatchery cohorts from 1998 to 2016. For the natural-origin component, cohort size at age two was the product of the number of spawners on the natural spawning grounds and freshwater productivity, drawn from a gamma distribution fit to natural-origin productivity estimates of brood years from 2008 – 2016.

Table III-1 Input values and distributions in the operating model

Symbol	Description	Value	Source
$N_{1.o=h}$	hatchery initial cohort size	22,361,802	N1 of BY 1998 - 2016
$S_{1.o=h}$	hatchery first year survival	beta(2.45, 89.98)	S1 of BY 1998 - 2016
$\rho_{1.o=w}$	natural productivity	gamma(0.85, 0.13)	recruits per spawner RY 2008 - 2016
S_2	age-2 survival	.5	(KRTAT 1986; O'Farrell et al. 2012)
S_3, S_4, S_5	age-a survival	.8	(KRTAT 1986; O'Farrell et al. 2012)
$m_{2.o=h}$	age-2 hatchery maturation	beta(1.97, 22.07)	$m_{2.o=h}$ of BY 1998 - 2016
$m_{2.o=w}$	age-2 natural maturation	beta(3.71, 39.90)	$m_{2.o=w}$ of BY 2008 - 2016
$m_{3.o=h}$	age-3 hatchery maturation	beta(4.29, 1.86)	$m_{3.o=h}$ of BY 1998 - 2016
$m_{3.o=w}$	age-3 natural maturation	beta(9.28, 6.17)	$m_{3.o=w}$ of BY 2008 - 2016
$m_{4.o=h}$	age-4 hatchery maturation	beta(32.47, 0.74)	$m_{4.o=h}$ of BY 1998 - 2016
$m_{4.o=w}$	age-4 natural maturation	1.00	$m_{4.o=w}$ of BY 2008 - 2016
m_5	age-5 maturation	1.00	m_5 of BY 2008 - 2016
$i^\star_3$	past age-3 impact rate	0.28	i3 from BY 1999 – 2016
$i^\star_4$	past age-4 impact rate	0.36	i4 from BY 1998 – 2016
$i^\star_2/i^\star$	fractional impact on age-2 fish	0.07	i2 from BY 1998 – 2016 and i from RY 2002-2018

From the start of age two in September, we applied monthly natural mortality rates v that were the same for both hatchery and natural-origin components and the same as those assumed in the cohort analysis. The true potential escapement was used to determine, and apply without error, allowable exploitation $\ddot{i}$ based on the current harvest control rule. In reality, implementing and achieving allowable exploitation for Sacramento River Fall Chinook does not always occur due to implementation error, precautionary policy choices in some years, and episodic constraints due to low abundance of other stocks in the fishery. Because these causes are not the result of easily reproducible processes, we did not simulate implementation error and applied allowable exploitation without error to potential escapement. Fishing impact was applied at an equal rate from May to August so impact across the whole season equaled the allowable exploitation rate. Age-specific impact rates did not differ between hatchery- and natural-origin components. As fish of different age classes are impacted differently due to their harvestability, we scaled fishing impact for the different age classes. Fishing impact was scaled based on past age-specific fishing impact rates (_i*_) from 2002-2020.

$$I_a = \frac{\sum_{a=3}^{5} I_a}{\dfrac{N_{a \neq a} \times i^*_{a \neq a}}{N_{a = a} \times i^*_{a = a}} + 1}$$

Age two was excluded from calculating the scaling because they are not included in Sacramento Index for potential escapement and calculating exploitation rate. Age-2 impact rates were instead applied by a fixed fraction of allowable exploitation based on historical age-2 impact rates relative to age-3 – 5 impact rates (Table III-1). Because age-5 fish were rare and fish age 4+ are generally considered to all be legal size, we assumed age-5 fish have the same impact rate as age-4 fish.

$$\begin{cases} N_{a+1.t+1} = N_{a.t} * (1 - v_{a.t}) & t = October - April \\ N_{a+1.t+1} = N_{a.t} * (1 - v_{a.t}) * (1 - i_{a.t}) & t = May - August \\ N_{a+1.t+1} = N_{a.t} * (1 - v_{a.t}) - M_{a.t} & t = September \end{cases}$$

In the month of September, maturing fish left the ocean to return to the river to spawn. The number of maturing fish M every September for hatchery- and natural-origin components was drawn from a beta-binomial distribution, with beta parameters estimated from maturation rates of hatchery-origin cohorts from 1998-2016 and natural-origin cohorts from 2008-2016. In-river fisheries were not explicitly considered, although in-river fisheries can affect cohorts differently. Potential escapement, i.e., escapement had fishing not occurred during the management year, was calculated by applying only natural mortality and maturation to ocean abundances at the start of September.

2.6 Management Strategy

Two alternative forecast models were evaluated for their performance in predicting potential escapement. The current model used in management forecasts the Sacramento Index using a log-log regression model with autocorrelated error predicting SI as a function

of age-2 spawner abundance (e.g., PFMC 2023b). Model 1 used age-2 spawner abundance to predict the aggregate potential escapement from ages 3 to 5.

$$\log(E_{a=3-5}) = \beta_0 + \beta_1 \log(N_{2.t-1})$$

Model 2 estimated age-specific potential escapement and summed potential escapement from ages 3 to 5 to predict aggregate potential escapement.

$$\sum_{a=3}^{5} \log(E_a) = \beta_{a.0} + \beta_{a.1} \log(N_{a-1.t-1})$$

These models were used to compare the expected performance of age-aggregated versus age-specific forecasts but differ from the current management model as they predict potential escapement in the absence of fishing rather than the Sacramento Index for potential escapement (O'Farrell et al. 2013).

We simulated population dynamics in 1000 simulations using a Monte Carlo approach. During the first five years when there was yet to be a full return of spawners due to the population's incomplete age structure, exploitation rate was fixed to the historical exploitation rate i^*. To best imitate current data availability, forecast models were used to estimate potential abundance once there were ten fishing and run years of data and then for the next thirty years. Each year, models forecasted potential escapement using simulated data from all years (except for initialization years) leading up to the current year, and forecasted escapement from the two models were compared against the true potential escapement.

To evaluate accuracy, we calculated the root mean squared log error of potential escapement across years and simulations for each model.

$$RMSLE = \sqrt{\frac{\sum_{t=15}^{45} \sum_{i=1}^{1000} (\log(E_{i.t}) - \log(\hat{E}_{i.t}))^2}{n}}$$

To compare the degree of bias in each model, we calculated the mean log error (MLE) in forecasted potential escapement.

To evaluate the expected improvements of the forecast and subsequent allowable exploitation, we calculated the Expected Value of Sample Information (EVSI) using Model 2, which contains more information, over Model 1. The EVSI is the mean difference in absolute error.

$$EVSI = |(E' - E^{M1})| - |(E' - E^{M2})|$$
$$EVSI = |(i' - i^{M1})| - |(i' - i^{M2})|$$

This difference, if positive, is the added accuracy in potential escapement forecast and allowable exploitation in Model 2 from Model 1.

We quantified the effect of model choice on fisheries and conservation outcomes if we had applied each model. For fisheries outcomes, we quantified the mean harvest in the thirty years of the simulation and the number of years of de minimis fisheries (allowable exploitation rate below 0.25) to evaluate whether model choice impacted mean harvest and the number of de minimis fisheries years. We summarized the mean number of years each model erroneously recommended de minimis fisheries and thereby constrained the fisheries when it was unnecessary and the mean number of years each model did not recommend de minimis fisheries when it was appropriate. For conservation outcomes, we quantified the mean escapement in the thirty years and the number of years the spawning abundance fell below the minimum stock size threshold (91,500 spawners) to evaluate whether model choice can impact escapement and the risk of the stock becoming overfished.

2.7 Sensitivity Analysis

We evaluated the error, value of information, and outcomes between the alternative models with potential changes in maturation schedules and survival rates. The age structure of the stock is shaped by the maturation schedule of the population, and variation in maturation across cohorts affects the ability to model age-specific escapement accurately. To measure how variation in the maturation schedules affected error, value of information, and fishery and conservation outcomes, we compared the results to simulations with no variation in maturation schedules across cohorts in the operating model ("NoMat"), aside from differences between hatchery and natural-origin fish. Additionally, we evaluated a scenario with higher variation in maturation schedules across years by doubling the standard deviation of hatchery and natural-origin maturation rates ("VarMat"). As higher ratios of fish age two to fish age three+ in recent years (PFMC 2023a) could indicate higher maturation rates, we evaluated the performance of alternative models under increasing maturation schedules ("HighMat"). We compared the alternatives under an operating model with maturation rates for all ages increasing half a percent every year (15 percent over 30 years).

Juvenile survival and production can be highly variable across years and influence the escapement size of cohorts. Higher variation in juvenile survival from year to year would therefore increase the variation in escapement size of cohorts. We evaluated the sensitivity of outcomes to annual variation in juvenile survival by doubling the standard deviation of hatchery-origin year-one survival and natural-origin productivity ("VarS1").

3. RESULTS

3.1 Analysis of Past Cohort

From 1998 to 2016, the average number of hatchery fish released every year in the Sacramento Basin and reported on the RMIS database was 22,361,802 fish (SD = 4,437,241

fish). Release information of fish from Nimbus Fish Hatchery was not available in 1998, 1999, 2002, 2004, and 2005 even though releases occurred these years, and significant proportions (>10 percent) of releases from Feather River Hatchery for 1998-2001 brood years and Nimbus Fish Hatchery for 2001 and 2003 brood years were not reported in the RMIS database that were reported in Huber and Carlson (2015). These cohorts, and all cohorts prior to 2008 when natural-origin data were unavailable, were not included in comparing the cohort-based, age-specific methods to the Sacramento Index. Coleman National Fish Hatchery released the most fish (mean = 12,516,003), followed by Feather River Hatchery (mean = 9,368,277, excluding 1998-2001) and Nimbus Fish Hatchery (mean = 4,066,443, excluding 1998-2005).

First year survival of 1998 – 2016 hatchery cohorts (i.e., survival from release to age 2) was a mean of 0.024 (median 0.017; SD = 0.02). For the natural-origin component from 2008-2016 brood years, productivity was a mean of 6.4 recruits (age-2 fish) per spawner (SD = 7.3). These metrics of year-1 production have a correlation of 0.84 between the hatchery and natural-origin component (Figure III-1). Impact rates increased with age. The mean impact rate was 0.021 (SD = 0.025) at age two, 0.28 (SD = 0.14) at age three, 0.36 (SD = 0.20) at age four, and 0.64 (SD = 0.31) at age five (Figure III-2).
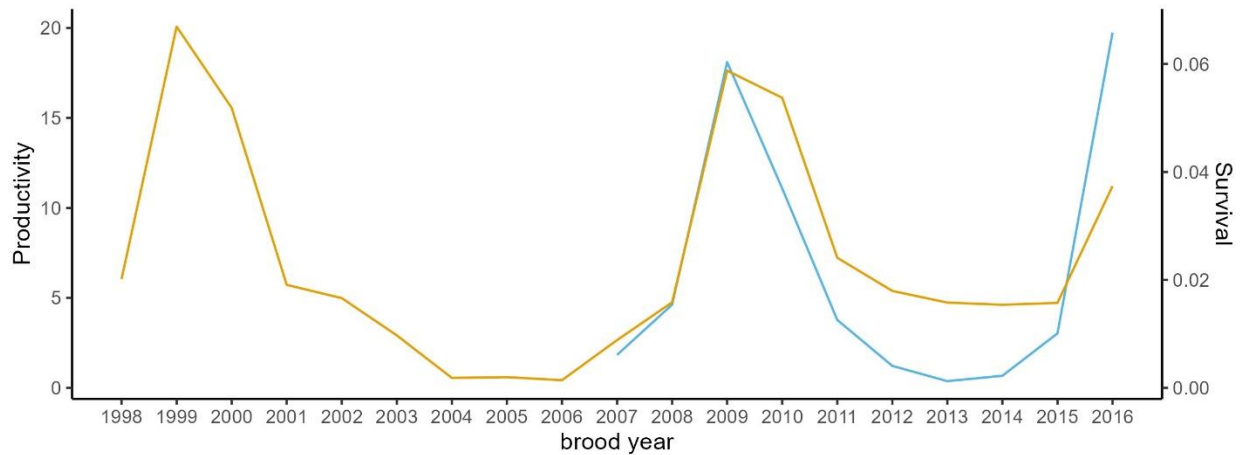

Figure III-1 Year-1 survival (i.e., from release to age-2) of hatchery cohorts (gold) and productivity (age-2 recruits per spawner) of natural-origin broods (blue).
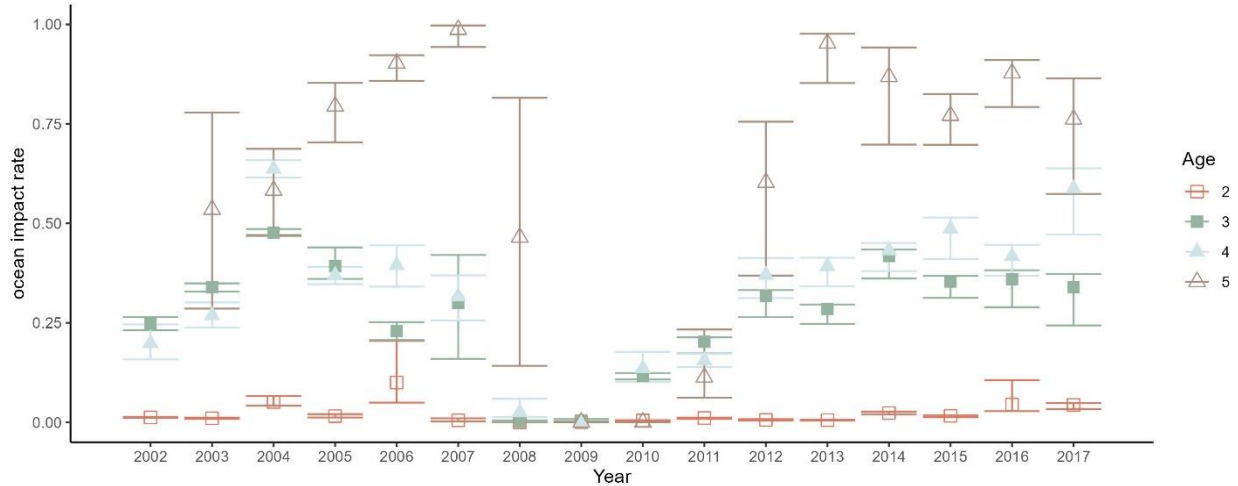
Figure III-2 Age-specific ocean impact rates every harvest year. Points indicate the mean while error bars indicate the 95% credible intervals from resampling.

The mean age-2 maturation rate of the entire natural-origin component for 2008 – 2016 brood years was 0.085 (SD = 0.048), while the mean for the entire hatchery-origin component during the same period was 0.118 (SD = 0.057) (0.080 for BY 1998 – 2016) (Figure III-3). The mean age-3 maturation rate was 0.585 (SD = 0.121) for the natural-origin component in 2008-2016 BY and 0.765 (SD = 0.146) for the hatchery-origin component during the same period (0.708 for BY 1998 – 2016). From 1998 to 2016, the age-2 and age-3 maturation rates have increased for hatchery-origin fish (age-2: Kendell's τ – correlation coefficient = 0.509, p = 0.002; age-3: Kendell's τ = 0.333, p = 0.049). There was no significant trend for the natural-origin age-2 maturation rate (p = 0.920) and age-3 maturation rate (p = 0.477) from 2008 to 2016. Increases in the age-2 hatchery maturation rate are negatively associated with log error (corr = -0.737), so high age-2 maturation rates correlate with overestimating escapement. Age-specific maturation rates for each tributary and hatchery population are shown in Appendix C Figure C-1 and Appendix C Figure C-2.
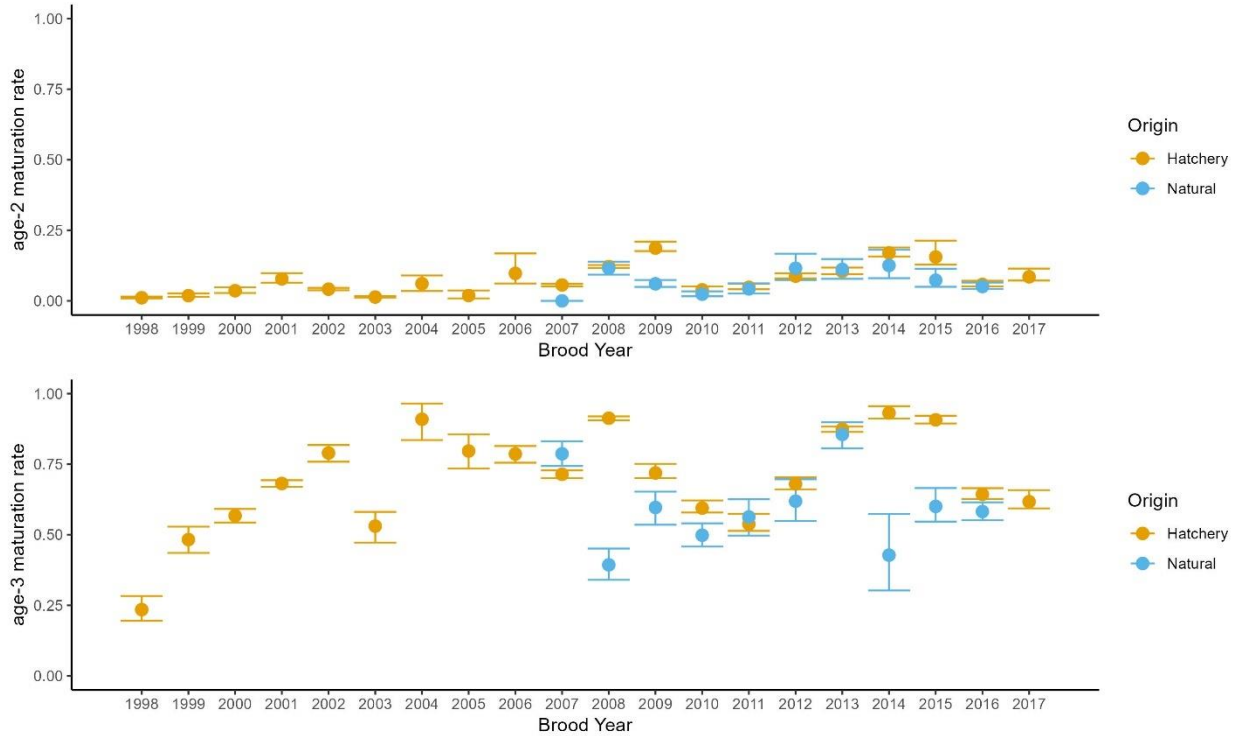
Figure III-3. Maturation rate at age two (top) and age three (bottom) for Sacramento River Fall Chinook salmon from hatcheries and natural production. Points indicate the mean while error bars indicate the 95% credible intervals from resampling.

The Sacramento Index was highly correlated (99 percent) with potential escapement of age 3+ fish absent fishing but exceeded potential escapement in all years and was an average of 20 percent greater than potential escapement in the absence of fishing in the current management year (Table III-2). Compared to abundance of age 3+ fish on September 1, the Sacramento Index was lower than September 1 abundance by an average of 32 percent and had a correlation of 98 percent. The ocean harvest component (south of Cape Falcon) of the Sacramento Index had a correlation of 97 percent and on average was very similar to ocean harvest (south of Cape Falcon) using cohort-based methods (Table III-2). The average ratio of ocean harvest calculated for the SI versus ocean harvest calculated using cohort reconstructions was 1.01 (median 0.98). Impact, which considers non-landed mortality like release mortality and drop-off mortality, was greater than harvest and had a correlation with the SI's ocean harvest of 95 percent and was on average 13 percent greater (median 7 percent) than SI's ocean harvest. The exploitation rate for the Sacramento Index, which includes in-river and ocean harvest, was almost always higher than the spawner reduction rate (Figure III-4).

Table III-2. Indices of abundances estimated in the cohort analyses versus the Sacramento (thousands of fish).

Year	Potential escapement[1]	Sept 1 abundance[2]	PFMC Sacramento Index	Harvest[3]	Impact	PFMC Ocean Harvest[3]
2011	192	325	207	59	63	70
2012	528	958	628	276	297	277
2013	697	1504	869	399	438	405
2014	487	900	551	343	376	303
2015	228	410	255	141	161	125
2016	177	264	205	85	97	92
2017	114	197	137	61	70	71
2018	183	306	220	81	88	99
2019	499	1040	507	452	531	323

[1]Potential escapement of fish age 3+ in the absence of fishing in the given year
[2]Ocean abundance of age 3+ fish on September 1 the previous fall
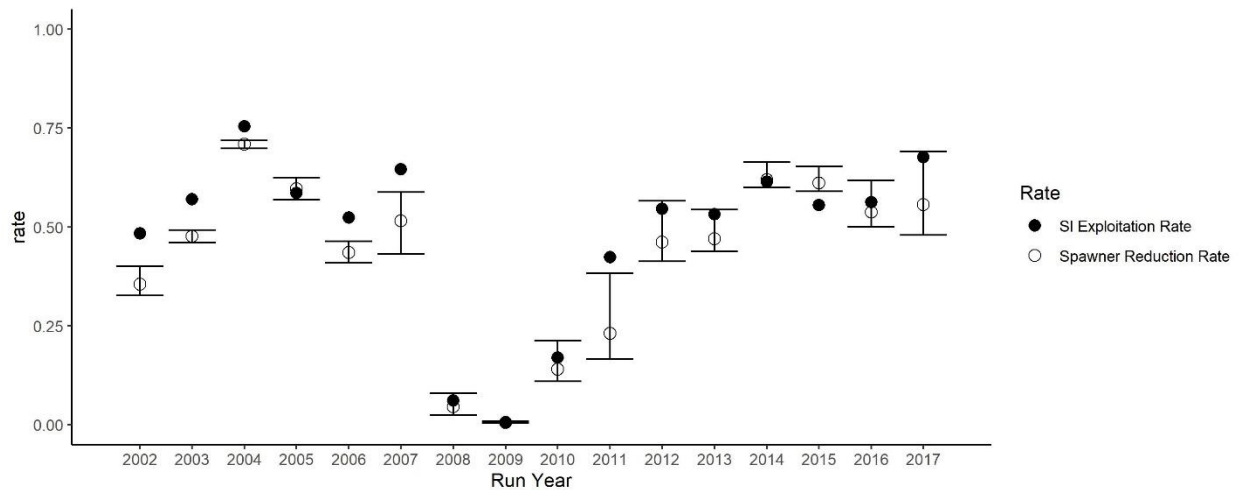[3]South of Cape Falcon

Figure III-4. Spawner reduction rate (SRR) and exploitation rate of the Sacramento Index every run year. For SRR, points indicate the mean while error bars indicate the 95% credible intervals from resampling. Only point estimates were reported for the exploitation rate.

3.2 Simulations

RMSLE for two alternative models were relatively comparable across all scenarios (Figure III-5). RMSLE was greater in Model 1 when there was no variation in maturation schedules ("NoMat"), increasing maturation schedules ("HighMat") and more variable juvenile survival and productivity ("VarS1") but smaller in Model 1 in the baseline scenario and when maturation schedules were more variable ("VarMat"). Errors in all scenarios that included annual variation in maturation schedules were many folds greater than errors when maturation schedules did not vary across cohorts ("NoMat"). Mean error in Model 2 tended to be positive, which indicates under-estimating abundance, while error in Model 1 was unbiased in most scenarios. When maturation rates were increasing ("HighMat"), both models tended to overestimate abundance.
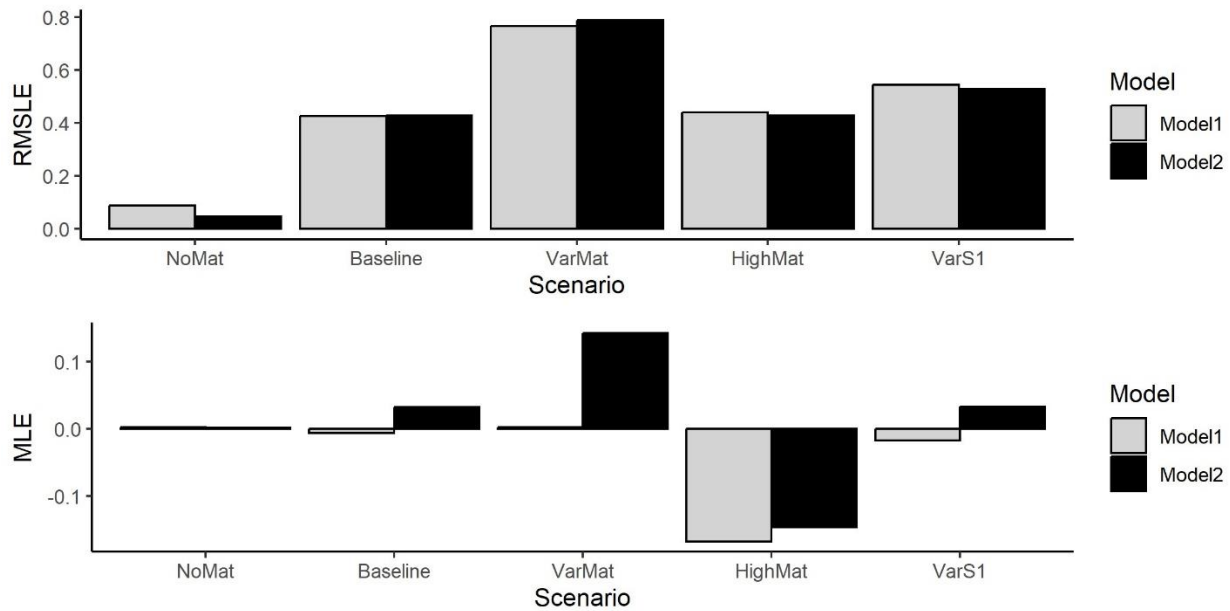

Figure III-5. Root mean square log error (top) and mean log error (bottom) in forecasts of abundance of potential escapement reported over all years in simulations using the age-aggregated model (Model 1) and the age-specific model (Model 2) under five scenarios defined in text.

For conservation and fisheries outcomes, variation within models was usually larger than the average difference between models. Model 2 tended to result in higher escapements (Figure III-6a) and lower harvest (Figure III-6b) than Model 1 because of having greater bias towards underestimating escapement. Under baseline parameters, both models had a tendency to under-recommend de minimis fisheries versus over-recommend de minimis fisheries (Figure III-7), resulting in fewer de minimis fishery years than would result from perfect forecasts when using either model (Figure III-6d). Even though both models tended to un-necessarily constrain the fisheries in some high abundance years, both models still had higher rates of escapement falling below MSST than when having perfect forecast due to directional forecast error (Figure III-6c).

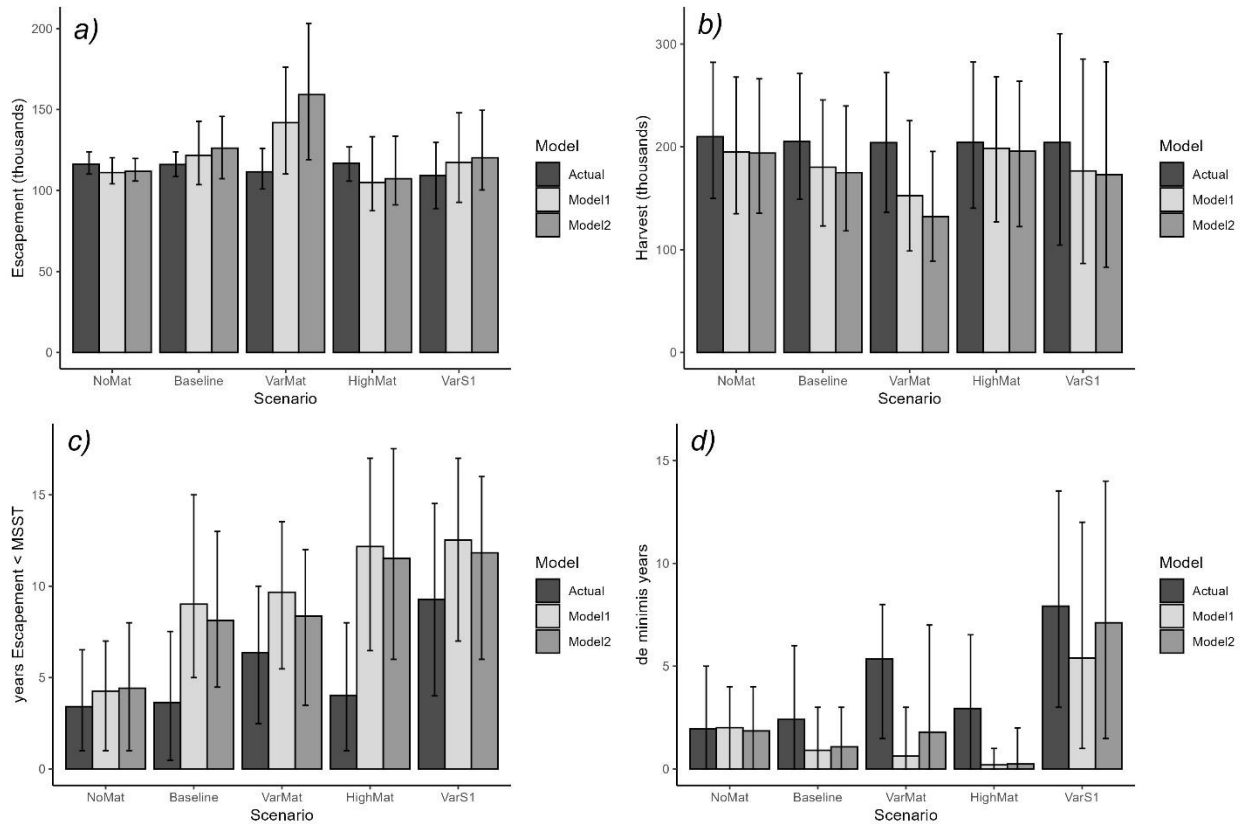**Figure III-6.** Conservation and fisheries outcomes over all years in simulations using the age-aggregated model (Model 1) and the age-specific model (Model 2) under the five scenarios described in text. Conservation outcomes include a) mean escapement, and c) number of years escapement fell below the minimum stock size threshold, and fisheries outcomes include b) mean harvest, and d) number of years with de minimis fisheries.
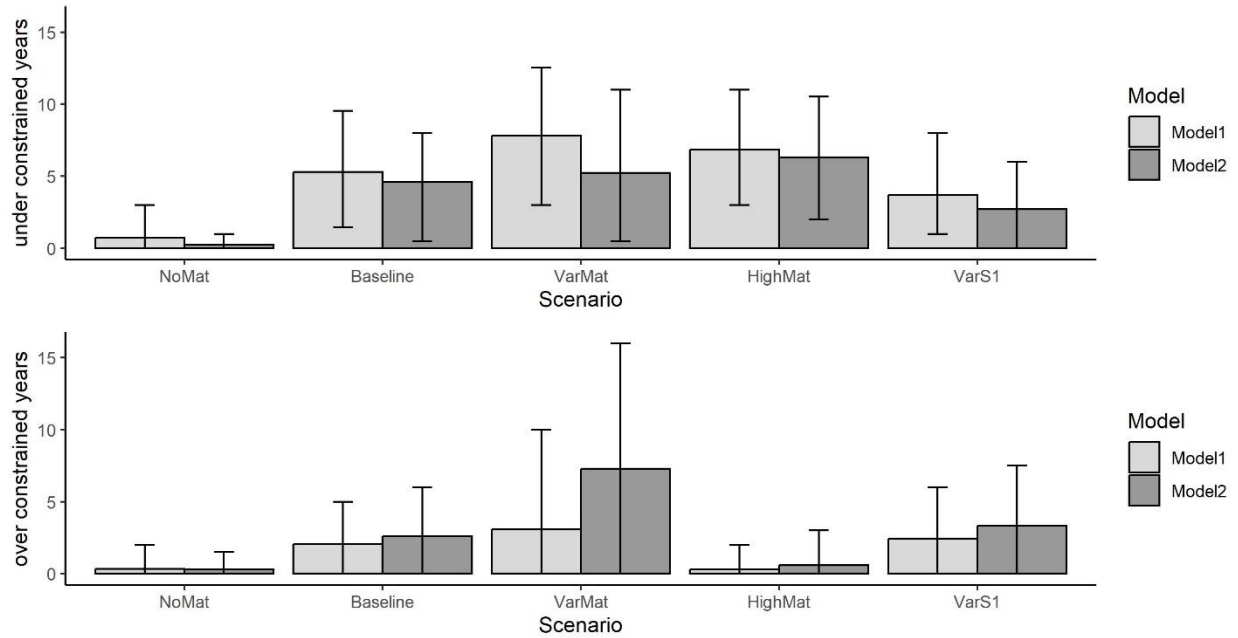
Figure III-7. Average number of times over thirty years in which each model did not recommend de minimis fisheries when appropriate (top) and number of times in which each model recommended de minimis fisheries when not appropriate (bottom).

The EVSI for escapement and allowable harvest with Model 2 versus Model 1 was close to zero under most scenarios (Figure III-8). The mean improvement in accuracy of potential escapement under baseline estimates of vital rates was slightly negative and equaled -500 individuals (CrI: -6,300 – 5,400 individuals). For perspective, the mean potential escapement was 241,000. The 95% credible interval for EVSI overlapped with zero in all scenarios except for when there was no variation in maturation schedules (mean: 5,000; CrI: 800 – 12,000). Increased interannual variation in maturation schedules reduced the EVSI (mean: -6,500; 95% CrI: -35,100 – 8,400), while increasing maturation rates raised he EVSI (mean: 1,600; CrI: -5,700 – 9,300).
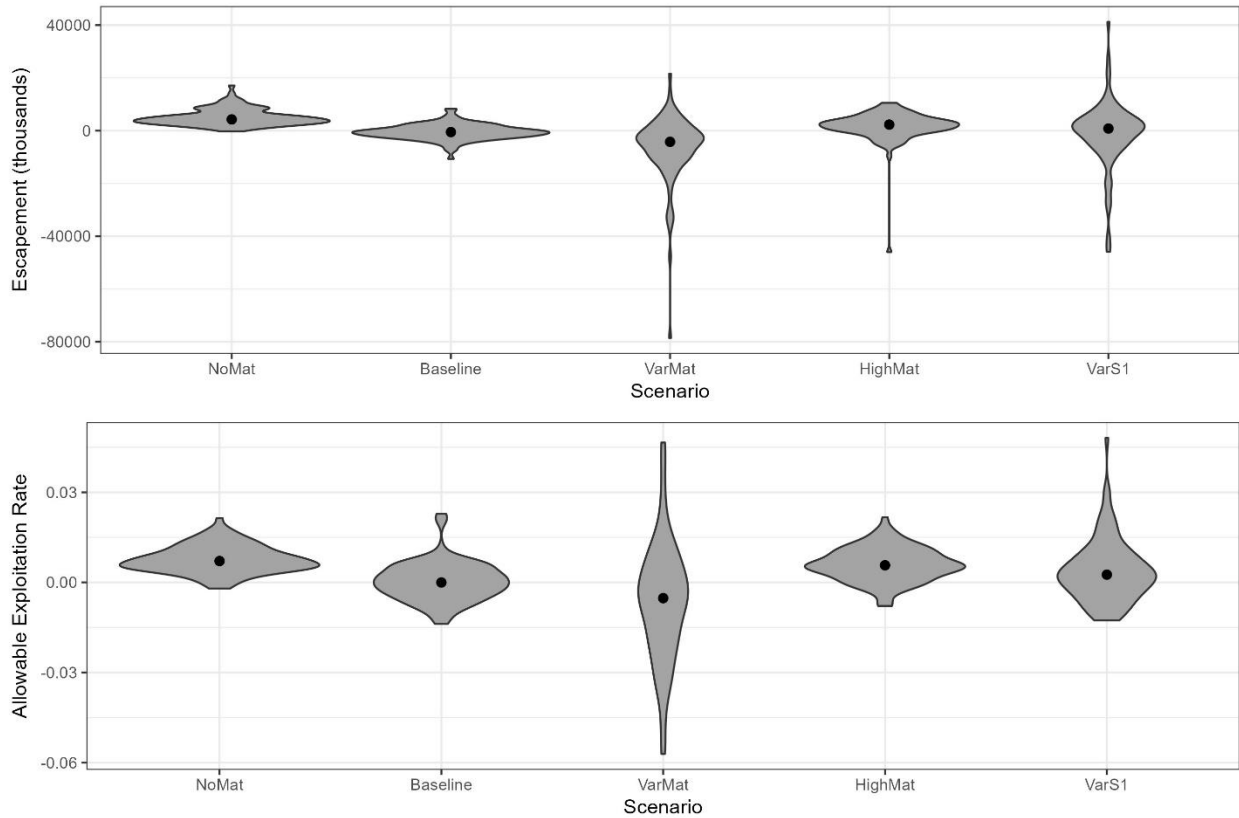
Figure III-8. Expected Value of Sample Information (EVSI) in forecasting accuracy measured as improved accuracy in escapement (top) and improved accuracy in allowable exploitation rate (bottom). Black points indicate the median EVSI across the 1000 simulations.

4. DISCUSSION

Age-structured models have been extensively used for stock assessments, and indicators of year-class strength are common predictors for future abundance (Sammons and Bettoli 1998; Sydeman et al. 2018; Privitera-Johnson and Punt 2020). The current management framework for Sacramento River Fall Chinook salmon uses an aggregate age index of abundance, the SI, and including additional age structure information may improve retrospective assessments by addressing inherent limitations in the SI and remedy abundance forecast model performance (O'Farrell et al. 2013). For retrospective assessments, we found the Sacramento Index tended to overestimate potential escapement and underestimate ocean abundance compared to potential escapement and ocean abundance estimated using cohort reconstructions. For forecasting, we did not find significant improvements using a cohort-based, age-specific forecast model instead of an age-aggregated model for two potential reasons. First, especially at the generally high level of fishing mortality rates observed during our study period, SRFC returned predominantly at age three, so including information on age-4 and age-5 cohorts could have led to only

minor improvements in accuracy. Furthermore, SRFC exhibited high variation in maturation schedules across cohorts which led to inaccurate predictions based on the previous year's returns. In particular, the rate at which age-3 fish mature was highly variable, with estimates ranging from 0.25-1.00, and this variability led to large error in predicting age-4 abundance from age-3 abundance.

To understand the extent that uncertainty in maturation schedules reduced the accuracy of the complete age-structured forecast model, we compared three scenarios: baseline vs. fixed maturation schedules vs. heightened variation in maturation across cohorts. When maturation schedules were rigid, information on all contributing cohorts almost always led to improved accuracy. When the standard deviations of maturation rates were doubled, the value of information was often negative because large differences between the expected and actual maturation rate led to large error in age-specific return predictions. In comparison, additional cohort information was more important when juvenile survival and production across years was more variable and cohorts had larger differences in cohort strength.

The Sacramento Index currently used by management is an index of ocean age 3+ abundance on September 1 and potential escapement the following fall absent fishing in the current management year (O'Farrell et al. 2013). While this index highly correlated with potential escapement and age 3+ abundance in September, it underestimated ocean abundance and overestimated potential escapement. The SI underestimated the age 3+ ocean abundance because the SI does not account for natural mortality and fish that neither mature nor are harvested and remain in the ocean. The ocean harvest component for the SI does not include non-landed mortalities as our analysis did, which would in isolation result in underestimating ocean impact and ocean abundance in September. In general, the SI overestimated potential escapement because the SI includes ocean-harvested age-3 fish that would not have matured and contributed to escapement in the current year and natural-origin fish from stocks other than SRFC (O'Farrell et al. 2013). The natural-origin ocean harvest component of the SI is estimated by subtracting harvest of other key stocks (e.g., Klamath River Fall Chinook, hatchery-origin fish from other stocks) from total harvest south of Point Arena. However, not all contributing stocks are subtracted, and so the harvest of other populations in the fishery (e.g., California Coastal Chinook, Southern Oregon Northern California Chinook, natural-origin fish from other Central Valley stocks) leads to increases in the estimate of the SI.

The age-2 maturation rate of hatchery fish has increased over time, becoming more variable as it increases. Since the late 1990s, all three hatcheries in the Sacramento Basin effectively ceased releasing fish as fry and predominately released fish as subyearlings during our study period (Huber and Carlson 2015). Because of longer periods of rearing in hatchery conditions, subyearling releases may have earlier maturation rates compared to fry releases (Hager and Noble 1976; Harstad et al. 2018). The time hatchery fish enter the ocean has also become earlier over time, potentially changing the food availability and growth rates for smolts upon arriving to the ocean (Sturrock et al. 2019; Satterthwaite and Carlson 2015). Hatcheries in the Central Valley have upcoming plans to reintroduce

releasing fish as fry, which may again shift the maturation schedules of the stock. Natural-origin maturation rates correlated year-to-year with hatchery-origin maturation rates, suggesting climate also influenced age of maturity for both origin groups (Wells et al. 2007). We did not see an increase in the maturation rates of natural-origin fish, but the time series for the natural-origin population was shorter.

Monitoring and understanding changes in maturation schedules are critical to improving age-structured forecast models. There are many possible alternatives for considering changing population dynamics over time. In the current SI model, changes in the jacks-to-adults sibling regression relationship are implicitly considered by evaluating and adding an autocorrelation coefficient but this only considers error in the previous year. In the Klamath River basin, only the most recent ten brood years of data are used to fit the forecast model because of better performance with more recent data only (PFMC 2023b). Alternatively, applying dynamic regression models that have parameters that can vary over time can allow for more explicit consideration of changing parameters over the full time series (Ovando et al. 2022) and has evidence of improved performance for Sacramento River Fall Chinook in more recent years (Winship et al. 2015). Exploring and including predictors for maturation rates such as environmental covariates could also reduce uncertainty in maturation schedules for the coming year, although predictive power of environmental covariates often changes over time (Winship et al. 2015; Wainwright 2021). Nonparametric empirical dynamic models can improve forecast estimates especially in highly complex systems where simple causal relationships do not describe the system well and have been shown to improve forecasting in salmon populations (Ye et al. 2015).

Although improving forecast models can help better meet management objectives, there is a limit to what maximizing predictive ability in forecast models with the data available can do for management (Ovando et al. 2022), and so it is important to develop management strategies that are robust to forecast error (Wainwright 2021; Satterthwaite and Shelton 2023). In changing and more uncertain population dynamics, robust and flexible management can buffer against uncertainty in stock abundance (Walters 1989). Exploitation of SRFC can exceed the appropriate level due to both forecast error and implementation error. Exploitation has exceeded the targeted exploitation rates in recent years due to underestimating harvest that would occur given the designated harvest regulations (Satterthwaite 2023). Harvest of Chinook salmon in California is lower now than in past decades and the fishery may be operating under conditions that the harvest model may not be well parameterized for. In 2023, the California ocean salmon fisheries implemented regulations to allow for more in-season management in future years, including trip limits, fishing areas, and closure dates that can be modified if target harvest is reached or abundance was overestimated (NMFS 2023b). Greater provisions for in-season action and reporting and the development of in-season models would support reducing implementation error and overharvest in the face of greater uncertainty in annual forecast models. In-season quotas based on ocean abundance estimates heightens the issue of the relatively large errors associated with using the SI as a metric of ocean abundance and the importance of being able to forecast ocean abundance well to inform the size of in-season quotas.

Investigating reasons for changes in model performance is an important step to remedy and improve forecast models. For Sacramento River Fall Chinook, the age-2 maturation rate has been increasing, and years of higher maturations correspond to years the SI was overestimated. Because of the age structure of this population, we would not expect more specific age information alone to substantially improve forecast performance. Although age-specific information did not substantially improve forecast performance in most simulations, age-specific information was important for retrospectively understanding the population's vital rates over time and identifying changes to the underlying dynamics. Simulations used in this study to evaluate forecast models would not have been possible without past age-specific information. Thus, performing periodic cohort reconstructions can provide value even if they cannot be completed in time for the most recent year's escapement to inform preseason planning for the next fishing season. This would require continued data collection in all years, but resources could be devoted to processing the data at optimal timing and intervals independent of the annual management cycle. Our simulations were parameterized using data from Sacramento River Fall Chinook, and outputs are specific to this population and may not carryover to others. More generally, examining the value of information prior to committing to the ongoing collection and inclusion of more data in models is a worthwhile task for prudent fisheries management.

5. ACKNOWLEDGEMENTS

CONCLUSION

In the future when increased natural resource demands and climate change are expected to put greater pressure on the Chinook salmon in the Central Valley, effective strategies will be needed for sustaining their populations. Maintaining life history diversity will be a key component for sustaining their abundance and stability. This dissertation demonstrated that improving our understanding of their life history can contribute to more informed and effective decision making and highlighted key themes for hatchery, fisheries, and watershed management to consider for maintaining life history diversity. At the hatcheries, minimizing divergence between hatchery and natural-origin fish can reduce the risk of hatchery propagation altering the life history expression of the natural population. For the mixed-stock fisheries in the ocean, understanding the disproportionate impacts of the fisheries on the different life histories and actively monitoring and managing more stocks can assist decision makers in minimizing impact on at-risk populations. Throughout the basin, targets set by watershed managers should be based on broader objectives and have larger buffers to conserve more life histories and against environmental disturbance.

The Central Valley is a hatchery-dominated system with decades of hatchery influence on the natural populations. Knowing how fish raised in a hatchery and those born in nature differ is necessary for minimizing adverse impacts (e.g., disease, competition) and maintaining the integrity of natural populations. Because many monitoring and management tools in the Central Valley use data collected from hatchery fish, identifying differences between hatchery and natural-origin fish is also important for reducing bias in managing populations with hatchery and natural-origin components. Results from Chapter 1 emphasized that hatchery data can underestimate the importance of habitats to natural populations. In general, hatchery fish had less life history diversity compared to the diversity seen in the natural population. To better understand how to mimic natural-origin fish, future studies should evaluate the relationship between hatchery breeding, rearing, and release practices and life history expression. Experimental releases and tracking of behavior and performance of release groups would advance efforts to minimize divergence between hatchery and natural-origin fish. Future studies that use methods such as parent-based tags to track the survival and reproduction of hatchery fish and their progeny over generations are valuable to understanding potential long-term consequences of hatchery practices on natural populations. The potential for immediate competition and disease on natural-origin fish should not be forgotten when developing strategies to minimize adverse effects on wild populations.

Maintaining the life history diversity present in Chinook salmon of the Central Valley requires understanding how natural resource use (e.g., fisheries, water) impacts the various life histories. In my research comparing the life history of hatchery and natural-origin fish, I identified age structure differences that may result in differential impacts from fisheries. Specifically, populations with older age structures with fish that mature later may

experience greater fishing impacts due to their longer exposure to fishing. We identified the possibility of differential impacts from fisheries for hatchery and natural-origin fish, but many potential differences across other dimensions of Central Valley Chinook salmon remained unexplored. For example, Sacramento River late-fall and San Joaquin fall-run Chinook salmon are represented in fisheries management by the more abundant Sacramento River fall-run Chinook salmon, but these populations may experience different impacts due to differences in age structures and population dynamics. Considering how fisheries disproportionately impact populations is valuable in mixed-stock fisheries such as the California ocean salmon fisheries where multiple populations with diverse life histories and spatial distributions contribute to the fisheries. In changing and more uncertain population dynamics, management should work towards robust and flexible fisheries management that buffer against uncertainty and error.

Each Chapter highlighted that the range of possible life histories expressed is often underestimated and not considered by Western science and management. For example, in Chapter 1, I identified listed Chinook salmon use habitats beyond the critical habitat designated by the Endangered Species Act's. Management centered around a single and static life history can fail to address the requirements of the other life histories and variation that occurs due to a dynamic environment. Limited information on species tends to result in underestimating their conservation needs. Expanding conservation objectives would provide a buffer against this bias. Approaches aimed at maintaining ecosystem processes are more likely to support the population through climate fluctuations and environmental disturbances.

In addition to the importance of life history diversity to the population's productivity and persistence, the diversity of life histories present in Chinook salmon in the Central Valley has inherent significance worth preserving. The complex and diverse landscape of the Central Valley has produced a time-varying mosaic of habitats that Chinook salmon have evolved to exploit. Chinook salmon in this system have adapted their life cycle in multiple forms to fit the many ecological niches. Some life histories found in the Central Valley occur nowhere else, and few basins compare to the diversity of ecotypes present here. Preserving this special example of adaptive radiation is important for the cultural and social significance of this iconic species.

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APPENDICES

Table A-1. GAMM candidate models for increment widths and their Akaike's information criterion scores and difference from the selected model. All models include a random intercept effect grouped by individual samples and an autocorrelation structure of order 1.

Model	AIC	dAIC
~ s(Otolith Radius) + Origin + Habitat + Escapement Year	62401.05	0
~ s(Otolith Radius) + Origin + Life History + Habitat + Escapement Year	62404.87	4
~ s(Otolith Radius) + Origin + Escapement Year	62417.60	17
~ s(Otolith Radius) + Origin	62440.19	39
~ s(Otolith Radius)	62448.67	48

Table A-2. Coefficient estimates for selected GAMM modeling increment widths. Estimates reflect difference from baseline habitat: Sacramento River, origin: natural, and year: 2018.

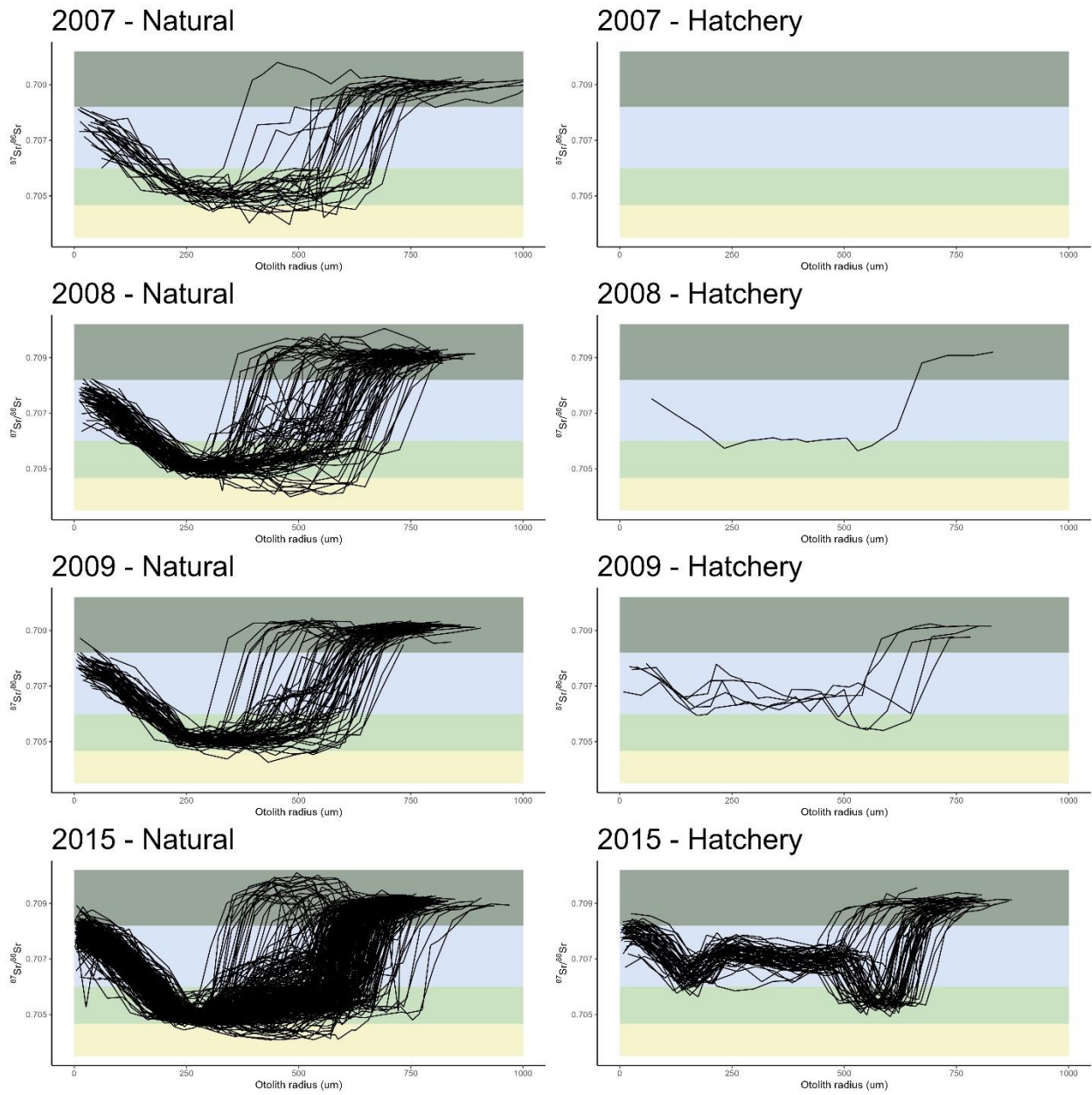| Covariate	Coefficient (SE)	p-value
Intercept	2.72 (0.0314)	< .001
Habitat (Hatchery)	-0.0176 (0.0536)	0.610
Habitat (Lassen tributaries)	-0.105 (0.0392)	< .01
Habitat (American River)	-0.0498 (0.0635)	0.433
Habitat (Delta/Feather)	0.0464 (0.0271)	0.087
Habitat (Ocean)	0.155 (0.0399)	< .001
Origin (Hatchery)	-0.140 (0.0536)	< .01
Escapement (2019)	-0.198 (0.0392)	< .001

Figure A-1. Strontium isotope profiles for winter-run Chinook salmon from 2007-2009 and 2015-2019 of natural- and hatchery-origin. (Page 1 of 2)
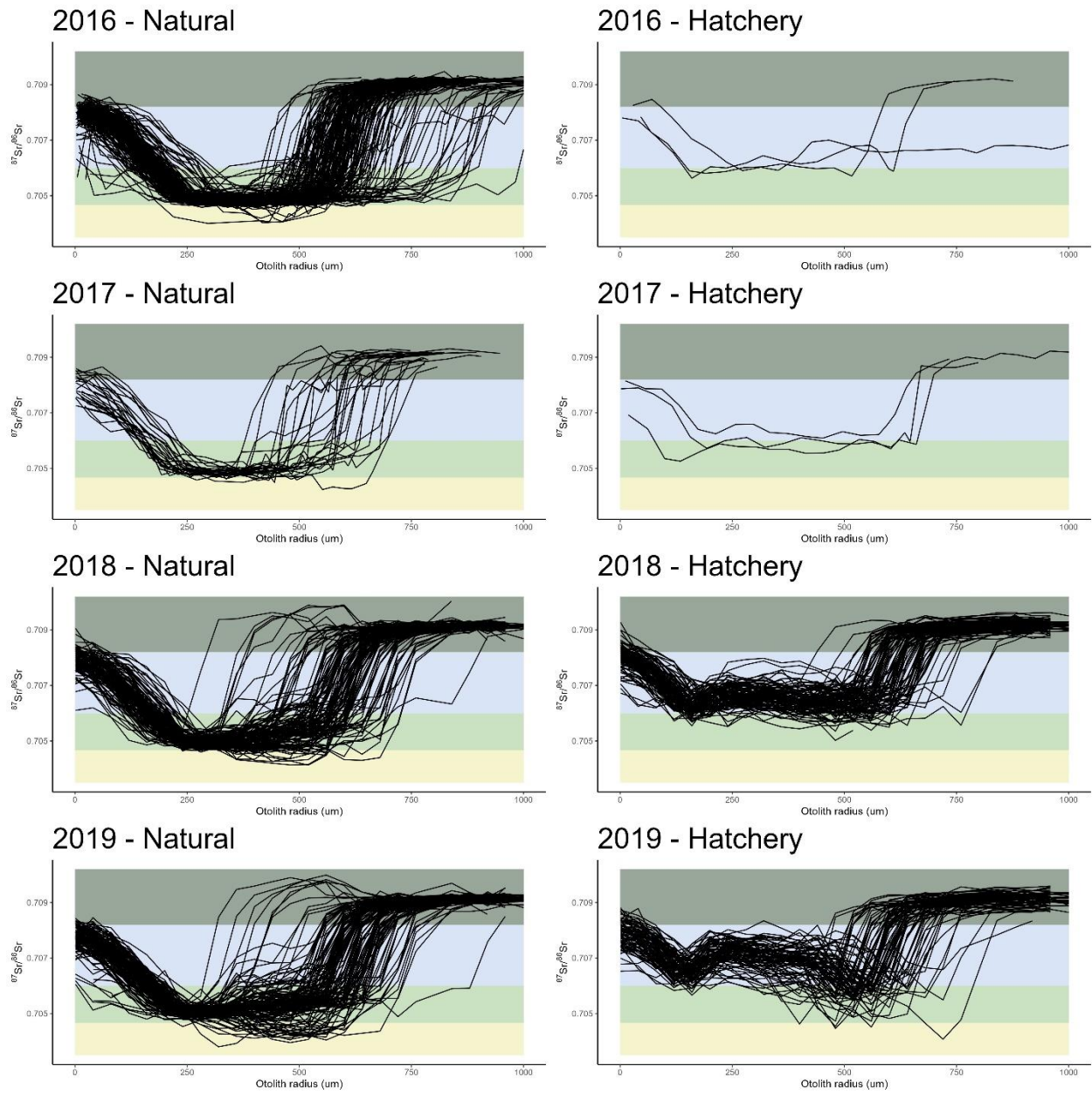
Figure A-1. Strontium isotope profiles for winter-run Chinook salmon from 2007-2009 and 2015-2019 of natural- and hatchery-origin. (Page 2 of 2)

Table B-1 Mean age composition of natural-origin winter-run Chinook salmon entering the river to spawn from 2005–2018 based on the age distribution of analyzed scale samples without adjustments for aging error.

	Age 2	Age 3	Age 4
Natural-origin combined	0.12 (σ = 0.16)	0.75 (σ = 0.16)	0.13 (σ = 0.11)
Natural-origin males	0.18 (σ = 0.20)	0.52 (σ = 0.25)	0.30 (σ = 0.27)
Natural-origin females	0.08 (σ = 0.13)	0.84 (σ = 0.15)	0.08 (σ = 0.07)

Table B-2 Mean maturation rates of natural-origin Sacramento River winter-run Chinook salmon brood years 2002–2015 with adjustment for aging error (Kimura and Chikuni 1987) and without adjustment.

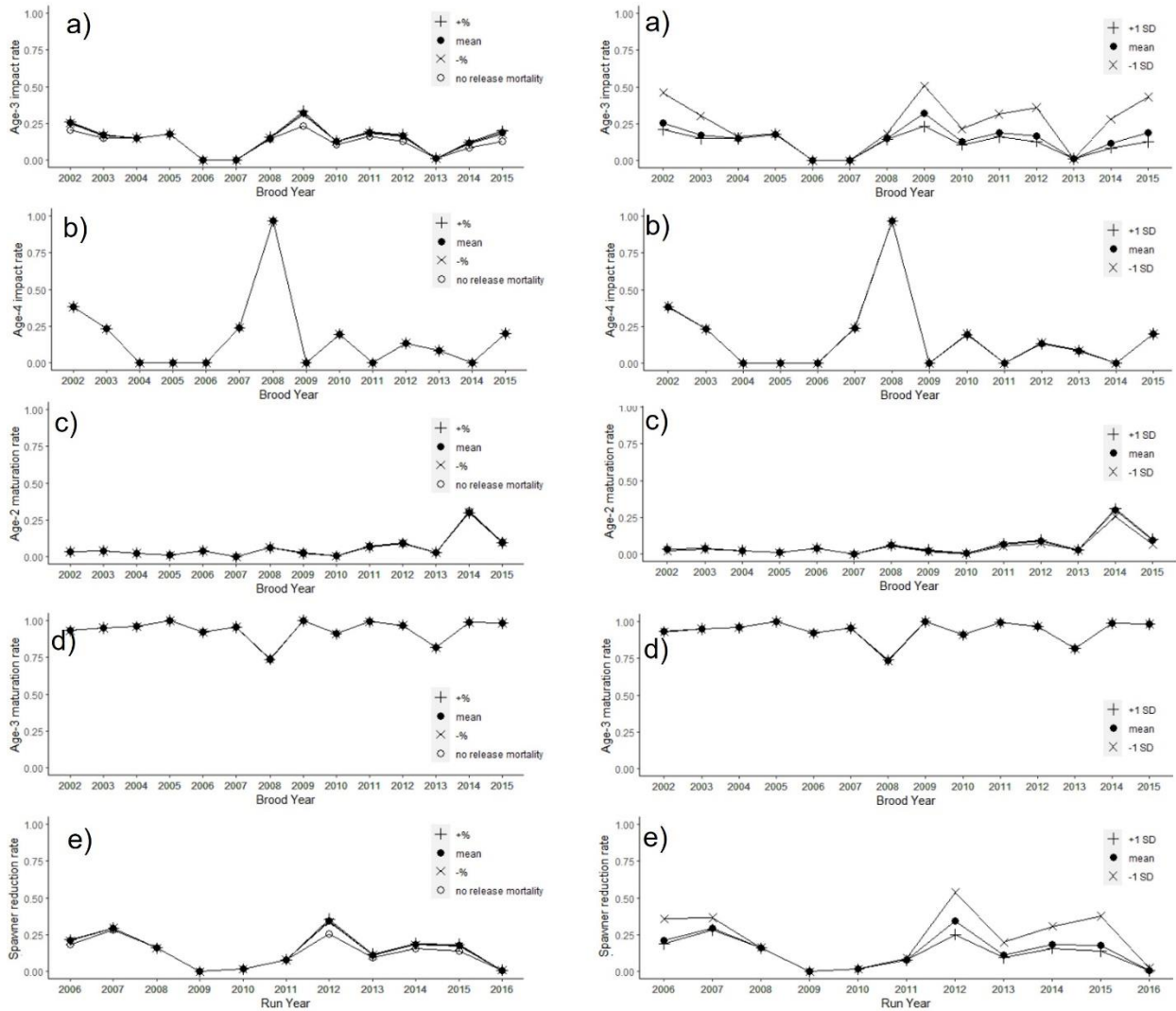| Brood year	With adjustment	Without adjustment	With adjustment	Without adjustment
Age 2			Age 3	
2003	0.25	0.24	0.67	0.69
2004	0.16	0.21	0.89	0.92
2005	0.05	0.05	0.52	0.63
2006	0.03	0.03	0.77	0.80
2007	0.04	0.06	0.82	0.86
2008	0.02	0.02	0.69	0.78
2009	0.02	0.02	0.54	0.58
2010	0.02	0.02	0.72	0.71
2011	0.02	0.04	0.86	0.88
2012	0.03	0.04	0.95	0.90
2013	0.02	0.06	0.91	0.92
2014	0.60	0.58	0.82	0.83
2015	0.03	0.03	0.68	0.64

Figure B-1. Sensitivity of impact (a & b), maturation (c & d), and spawner reduction rates (e) to changes in release mortality (left) and size at age (right) for hatchery-origin cohorts.
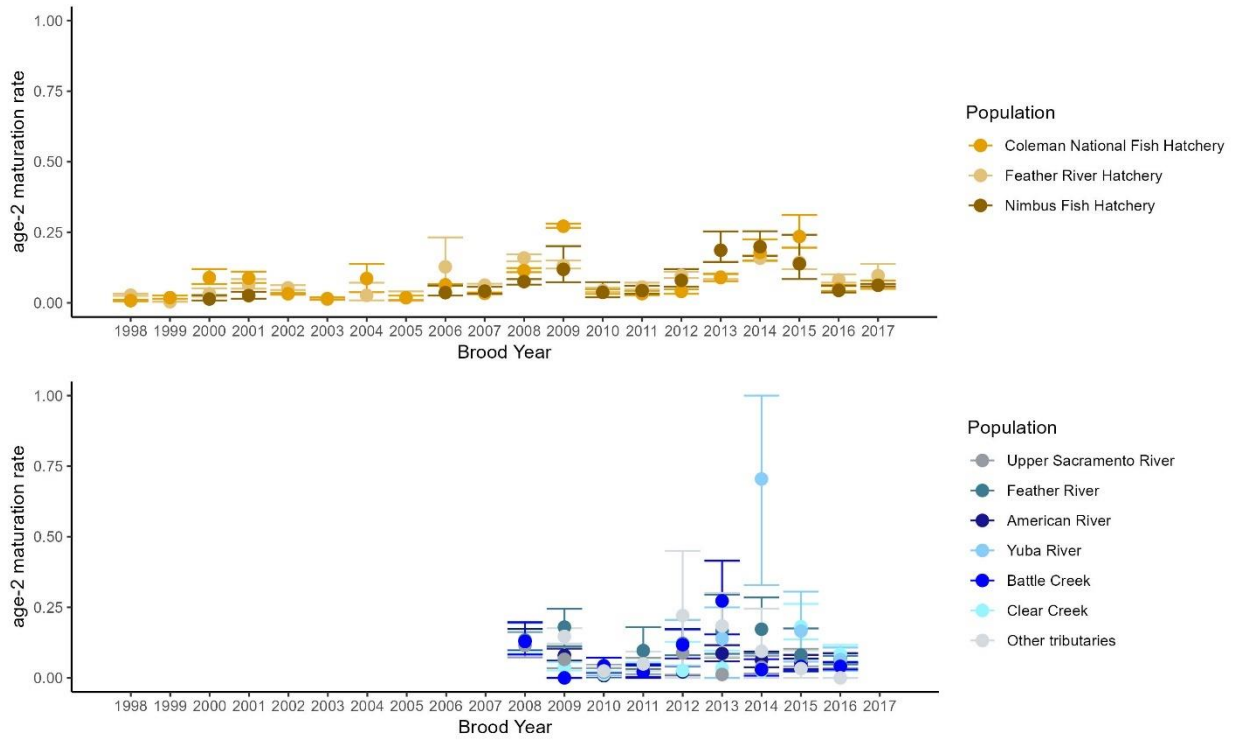
Figure C-1. Age-2 maturation rates for Sacramento River Fall Chinook salmon from hatcheries (top) and natural production (bottom). Points indicate the mean while error bars indicate the 95% credible intervals from resampling.
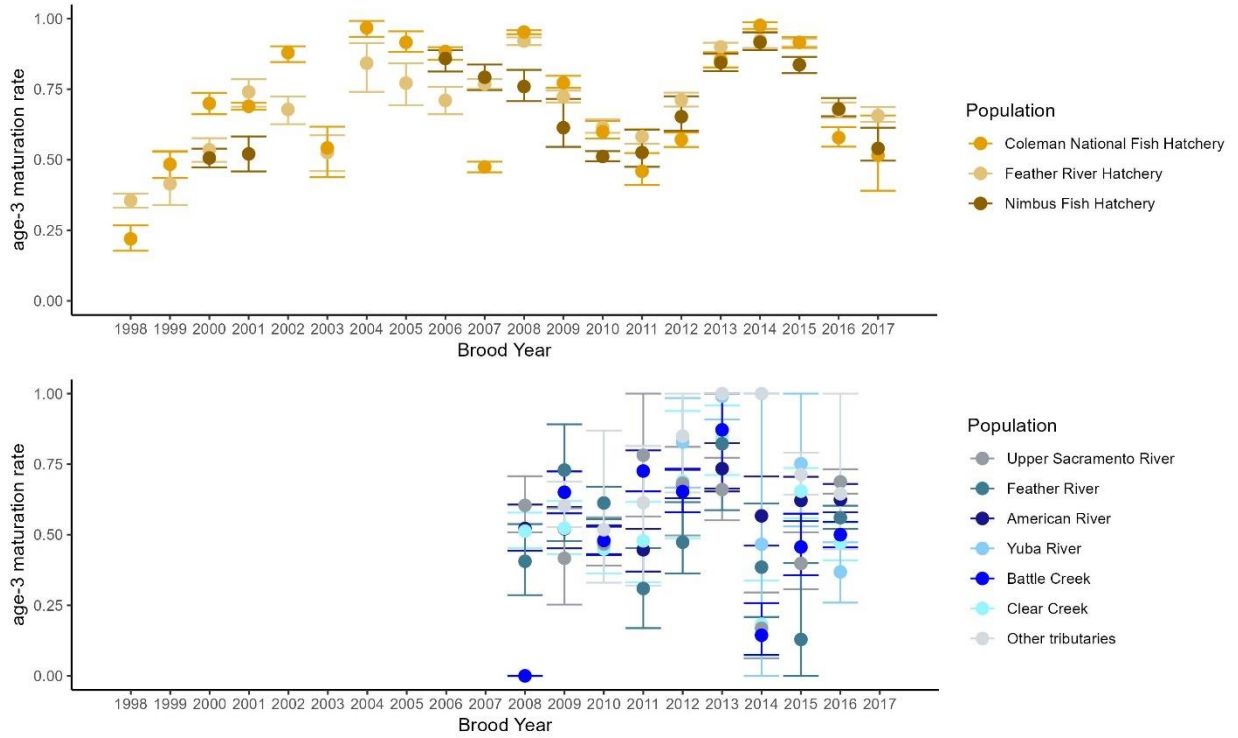
Figure C-2. Age-3 maturation rates for Sacramento River Fall Chinook salmon from hatcheries (top) and natural production (bottom). Points indicate the mean while error bars indicate the 95% credible intervals from resampling.