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

RH: Hatchery versus natural maturation

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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.

Keywords: maturation, age at maturity, Sacramento River, winter-run, sexual selection, fishing impact

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 & 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 & 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. 2009). 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. 2019, 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 & Mills 1985) and spring-run Chinook salmon populations (Larsen et al. 2013, 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 (Pacific Fishery Management Council 2023). 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 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 & 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 & 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 (National Marine Fisheries Service 2011). 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 (US Fish and Wildlife Service 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 & 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*.

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

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,

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

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.

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

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 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*.

$$i = \frac{I}{N} \tag{4}$$

$I = F + R + D$

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).

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

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).

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

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.

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

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, US Fish and

Wildlife Service 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 (California Department of Fish and Wildlife 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 1; Figure 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 1).

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 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 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 1 vs. Table A1) 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 2 vs. Table A2).

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 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.

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 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 4).

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 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 Figure 1).

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 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 & 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 & 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 (US Fish and Wildlife Service 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 & 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. 2013) as well as Atlantic salmon (Piggins & 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 & Quinn 2012). 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 & Healey 1990, Kendall & Quinn 2012). 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 & Healey 1990, Kendall & Quinn 2012). 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 (Pacific Fishery Management Council 2023). 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 & 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 & 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.

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Tables

Table 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)

Table 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)

Table 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

Figures

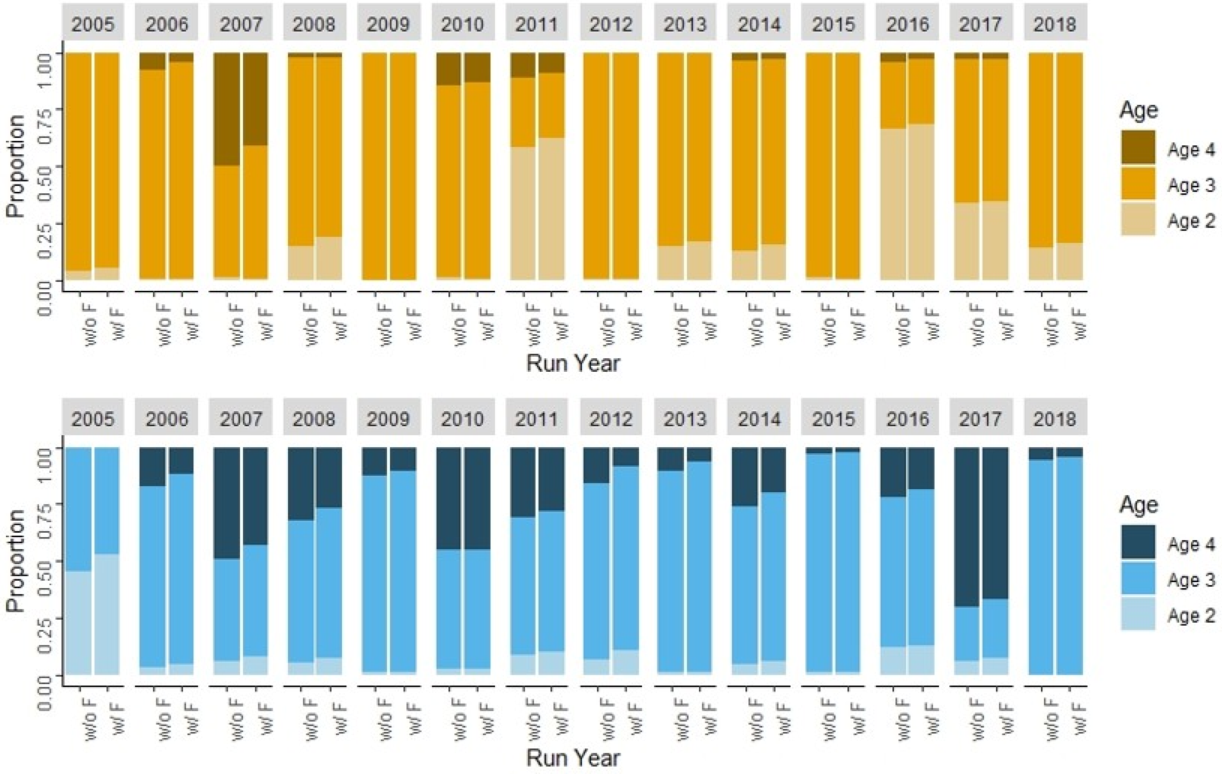

Figure 1. Age composition of hatchery (top) versus natural-origin (bottom) winter-run Chinook salmon escapement, excluding age 1 and age 5 (Materials and Methods 2.2 and 2.3). Left side of paired bars reflects the expected age composition in the absence of fishing while the right side of paired bars 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).

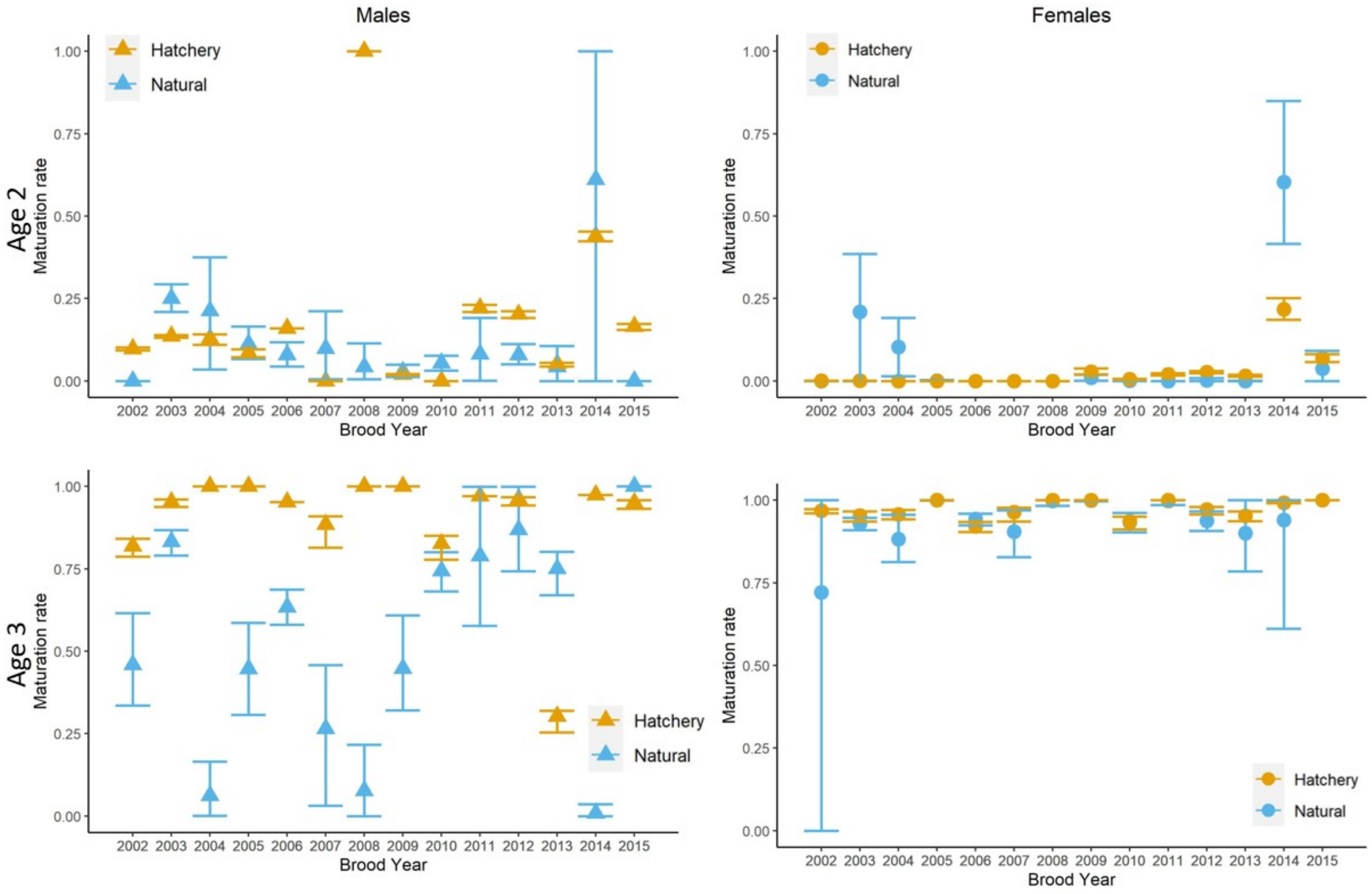

Figure 2 Age-, sex-, and origin-specific maturation rates for winter-run Chinook salmon brood years from 2002–2015. Points indicate the mean while error bars indicate the 95% confidence intervals from resampling.

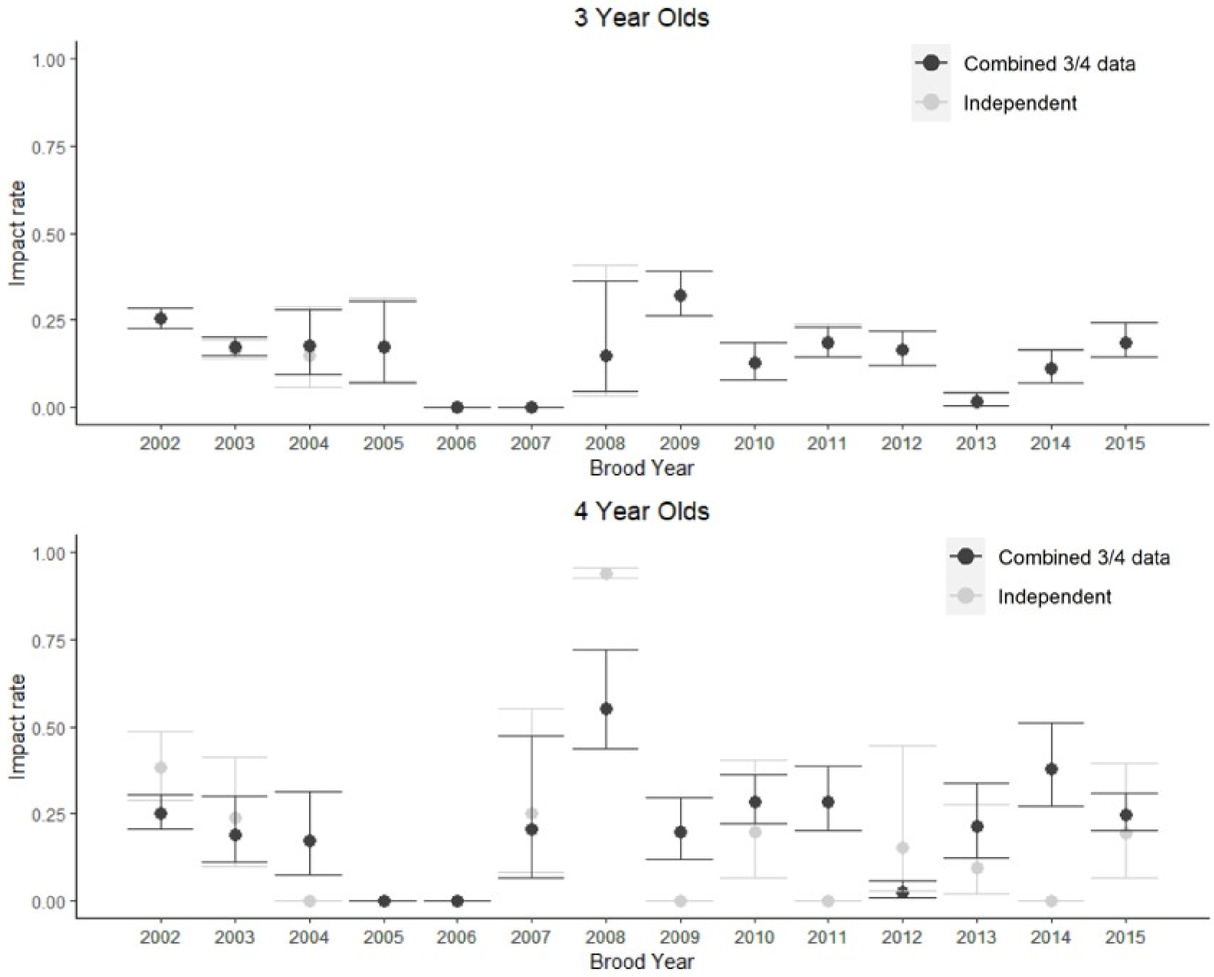

Figure 3. Mean fishing impact rates (bars indicating 95% confidence intervals) at age 3 and age 4 for winter-run Chinook salmon. Grey indicates i, impact rates estimated using cohort specific coded-wire tag recovered while black indicates i^*, impact rates estimated using age-aggregated recoveries.

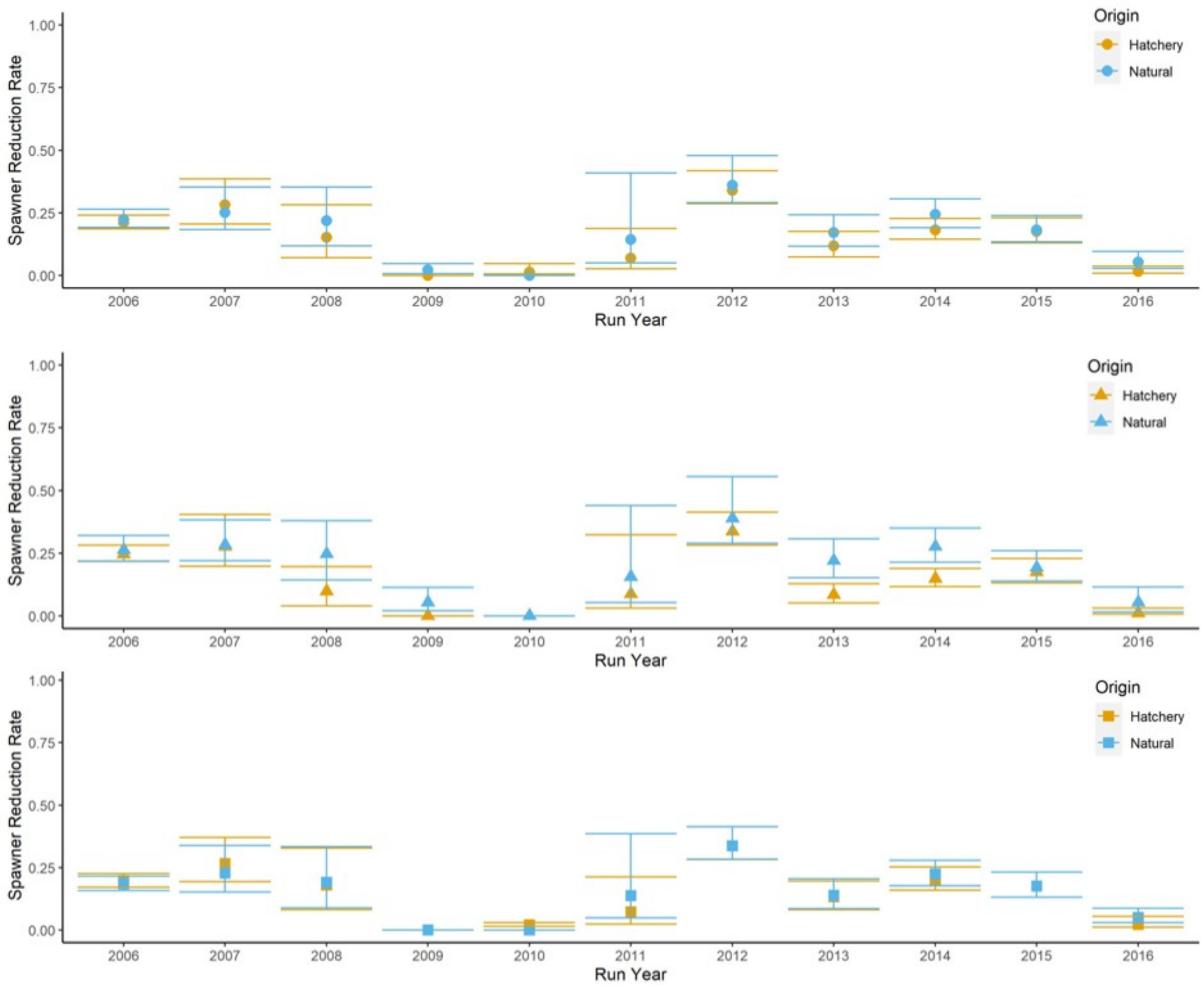

Figure 4. Mean reduction (bars indicating 95% confidence intervals) of natural- and hatchery-origin winter-run Chinook salmon (top), male (middle), and female (bottom) run size from fishing.

Appendix

Table A1 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 A2 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

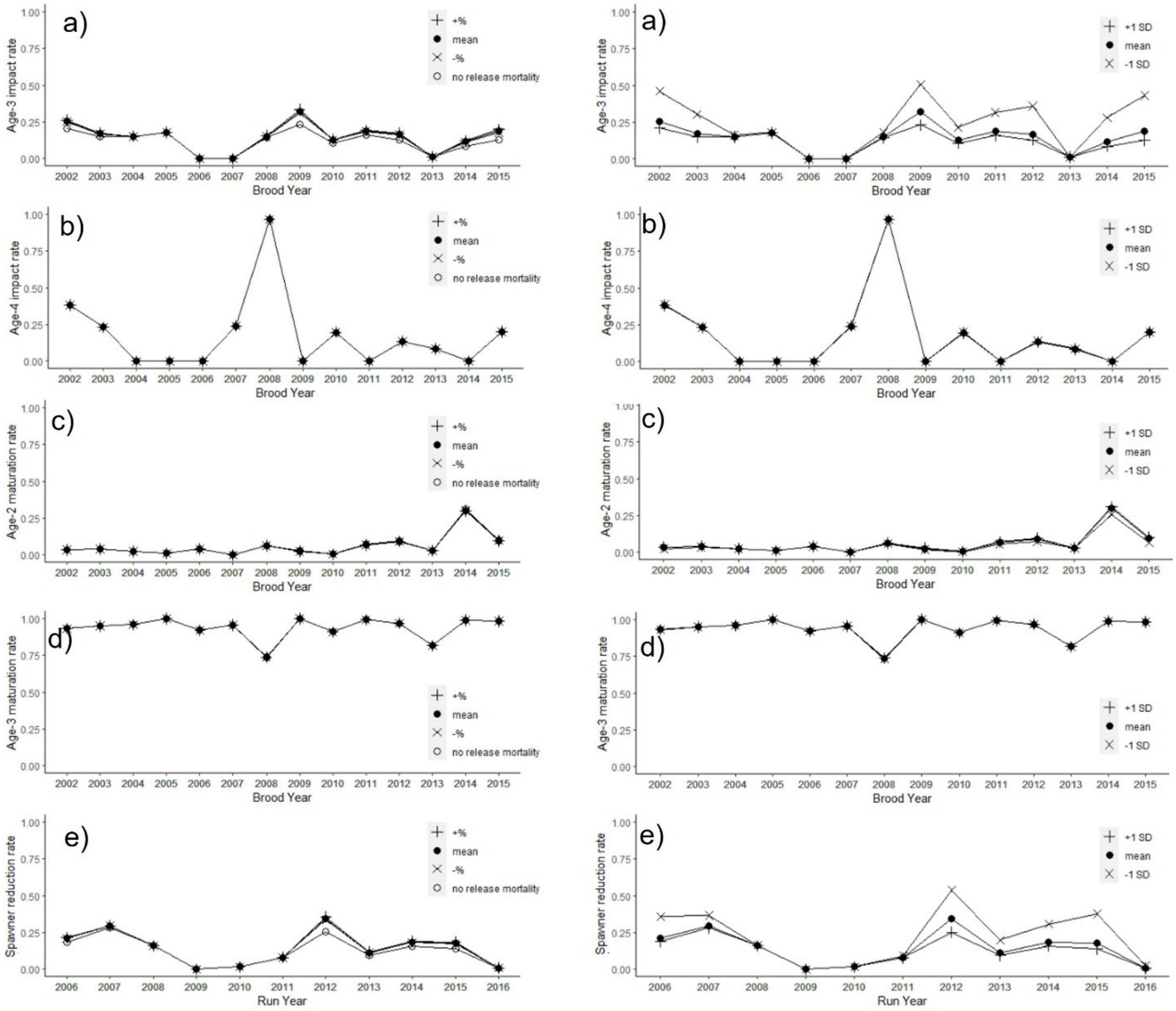

Figure A1. Sensitivity of impact (a & b), maturation (c & d), and spawner reduction rates (e) to changes in release mortality (left) and size at age (right) for hatchery-origin cohorts.