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Archaeological evidence across four millennia indicates recent erosion of Chinook salmon age structure in California

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ABSTRACT: Chinook salmon *Oncorhynchus tshawytscha* provide crucial ecosystem services, but their populations are in steep decline throughout their native range. Recent decades have seen widespread erosion of age structures, but the lack of long-term baselines makes it difficult to assess this change. We collaborated with the Estom Yumeka Maidu Tribe of Enterprise Rancheria and used otoliths to reconstruct changes in age structure for California Central Valley Chinook salmon over the last 4 millennia. Specifically, we compared the returner age structure of present-day hatchery and natural populations in the Feather and Yuba rivers (2002–2020) with archaeological data from the same watershed, spanning the Middle-Holocene (1800–1000 BCE), Late-Holocene (500–1770 CE), and post-European-contact (1770–1870 CE) periods. We observed a shift to younger ages, from dominantly age-4 returners in the archaeological samples to age-3 fish in both hatchery and natural populations today. The recent time period also shows reduced variance and diversity in return ages compared to the post-European-contact time period, which has the most robust sample size of the archaeological collection. The shift toward younger ages in returning fish may have caused losses in productivity, while the decrease in variance and diversity may have reduced their resilience to environmental stochasticity. The erosion of age structure since European contact suggests anthropogenic factors — such as loss of freshwater and estuarine habitats, and industrialized ocean fishing and hatcheries — as potential contributors. Incorporating archaeological data into ecological assessments can help guard against hidden shifting baselines and inform restoration targets for more resilient populations.

KEY WORDS: Ancient otoliths · Sclerochronology · Salmon · Age structure · Shifting baselines

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1. INTRODUCTION

Diversity in life history strategies, both within and among populations, plays a critical role in buffering species against environmental variability and anthropogenic impacts (Luck et al. 2003, Schindler et al. 2015, Price et al. 2021). One important phenomenon that confers such stability is the portfolio effect, where the presence of multiple asynchronously functioning phenotypes or subpopulations reduces overall variability in abundance in the aggregate population or stock complex (Figge 2004, Greene et al. 2010). The loss of diverse life histories impacts species worldwide and often precedes abundance declines as species lose their ability to compensate for unfavorable conditions. Consequently, assessing and conserving life history diversity is crucial for promoting ecosystem resilience and stabilizing ecosystem services and functions (Des Roches et al. 2021, Price et al. 2021).

Pacific salmon *Oncorhynchus* spp. exhibit highly diverse life history strategies adapted to local climatic, hydrologic, and landscape conditions (Quinn 2018). A diverse age structure in returning fish can provide long-term resilience and stability at the population and stock complex level by spreading out reproductive risk through time and space (Hilborn et al. 2003, Greene et al. 2010, Schindler et al. 2010, Buoro & Carlson 2014, Moore et al. 2014). Widespread shifts in age structure to younger ages have been documented in Pacific salmon in recent decades, and have likely contributed to declines in fisheries and ecosystem functions throughout their range (Ricker 1981, Oke et al. 2020, Price et al. 2021).

Chinook salmon *O. tshawytscha* are an important cultural and economic resource in the Northeast Pacific, but populations are in steep decline (Moyle et al. 2017, Crozier et al. 2021, Atlas et al. 2023). Recent decades have seen decreases in both the mean age and size of Chinook salmon across their native range (Lewis et al. 2015, Ohlberger et al. 2018, Oke et al. 2020, Buckner et al. 2023). Given the positive, nonlinear relationship between fish size, age, and reproductive output (Barneche et al. 2018, Ohlberger et al. 2020), these trends are negatively affecting the viability of populations, as well as the ecosystems and economies that rely on them (Ohlberger et al. 2018, Oke et al. 2020).

California's Central Valley hosts a complex of Chinook salmon populations (see Fig. 1) which are classified into 3 distinct evolutionarily significant units (ESUs) and display a range of life history strategies (Williams 2006). The decline of Central Valley Chinook salmon is primarily attributed to the combined impacts of habitat loss, overharvest, water diversions, prolonged droughts, nonnative predators, and impacts from hatchery fish (HRSG 2012, Herbold et al. 2018, Crozier et al. 2019). These impacts disproportionately affect the winter-run and spring-run Chinook salmon ESUs, which are both at a high risk of extinction (Yoshiyama et al. 1998, 2001, Johnson et al. 2023), leading to their listing under the federal and state Endangered Species Act (Good et al. 2005). The fall- and late-fall-run ESU that spawns primarily in the lower river reaches on the Valley floor is supported by 5 production hatcheries and is now the most abundant ESU. However, hatchery release practices have created synchrony among populations, weakening the fall-run Central Valley stock complex (Williamson & May 2005, Carlson & Satterthwaite 2011). Today, Central Valley Chinook salmon predominantly return at age-3, with age-2 and age-4 fish also common and other age classes very rare (Satterthwaite et al. 2017, Sturrock et al. 2020, Carvalho et al. 2023, Chen et al. 2023a).

Little is known about the age structure of Central Valley Chinook salmon prior to industrialized anthropogenic disturbances to the ecosystem (Munsch et al. 2022, Carvalho et al. 2023). Early fishery records indicate a potentially more diverse age structure in the first half of the 20th century (Clark 1929, Williams 2006), but long-term data are lacking. This knowledge gap is problematic, as the age structure in returning fish observed today may contain just a fraction of the age diversity that once existed. Fish remains recovered from archaeological sites provide a unique window into the long-term ecological baseline. For example, ancient DNA analyses show an extended historic range of Chinook salmon in the southern San Francisco Estuary (Lanman et al. 2021). Among various fish remains, otoliths (ear stones) are of particular importance, as they are reliable biological chronometers (Campana & Thorrold 2001, Miller et al. 2011).

Otoliths are paired calcium carbonate structures located in the inner ear of fishes, serving as organs for balance and hearing. Pacific salmon, like most bony fishes, have 3 pairs of otoliths, including the sagittae, lapilli, and asterisci. Sagittae are commonly used to study these fish, as they are the largest of the 3 pairs. Otoliths are metabolically inert and accrete continuously, forming incremental growth layers of $CaCO_3$ and protein. This growth process forms a time series of translucent and opaque bands, which are deposited on a daily and seasonal basis in response to photoperiod, temperature, diet, and endogenous rhythms throughout the life of the fish (Neilson & Geen 1982, Campana & Neilson 1985). Consequently, otoliths provide a valuable record for reconstructing a wide range of life history characteristics, including annual

ages of fish. Here, we use ancient Chinook salmon otoliths to reconstruct a long-term baseline of returner age structure for the Feather River, an important salmon watershed in California's Central Valley. Specifically, we compare the mean, variance, and diversity in return ages between present-day hatchery and natural-origin fish and their ancient counterparts from the same watershed, encompassing 3 distinct time periods over the last 4 millennia.

2. MATERIALS AND METHODS

2.1. Archaeological samples

Ancient otoliths were collected from Native Maidu village sites, in collaboration with the Estom Yumeka Maidu Tribe of Enterprise Rancheria, along an 11 km stretch of the lower Feather River, in close proximity to the present-day spawning grounds (Fig. 1, Table 1). Careful stratigraphic excavation of more than 300 m^3 from those sites, combined with 110 radiocarbon dates, represents the largest and best-dated assemblage of ancient salmon remains from California's Central Valley, documenting indigenous use of the fishery for more than 6000 yr (Rosenthal 2020). Approximately 51 000 fish bones from Feather River sites were identified to family or species based on morphology by Ken Gobalet (Emeritus Professor, California State University, Bakersfield, CA) (unpubl. data), using comparative collections housed at the California Academy of Sciences, San Francisco, CA. *Oncorhynchus* spp. are the most abundant genus in the assemblage (43%). However, bones representing a range of other genera are also present, including Sacramento sucker *Catostomus occidentalis* (16%) and sturgeon *Acipenser* spp. (11%),

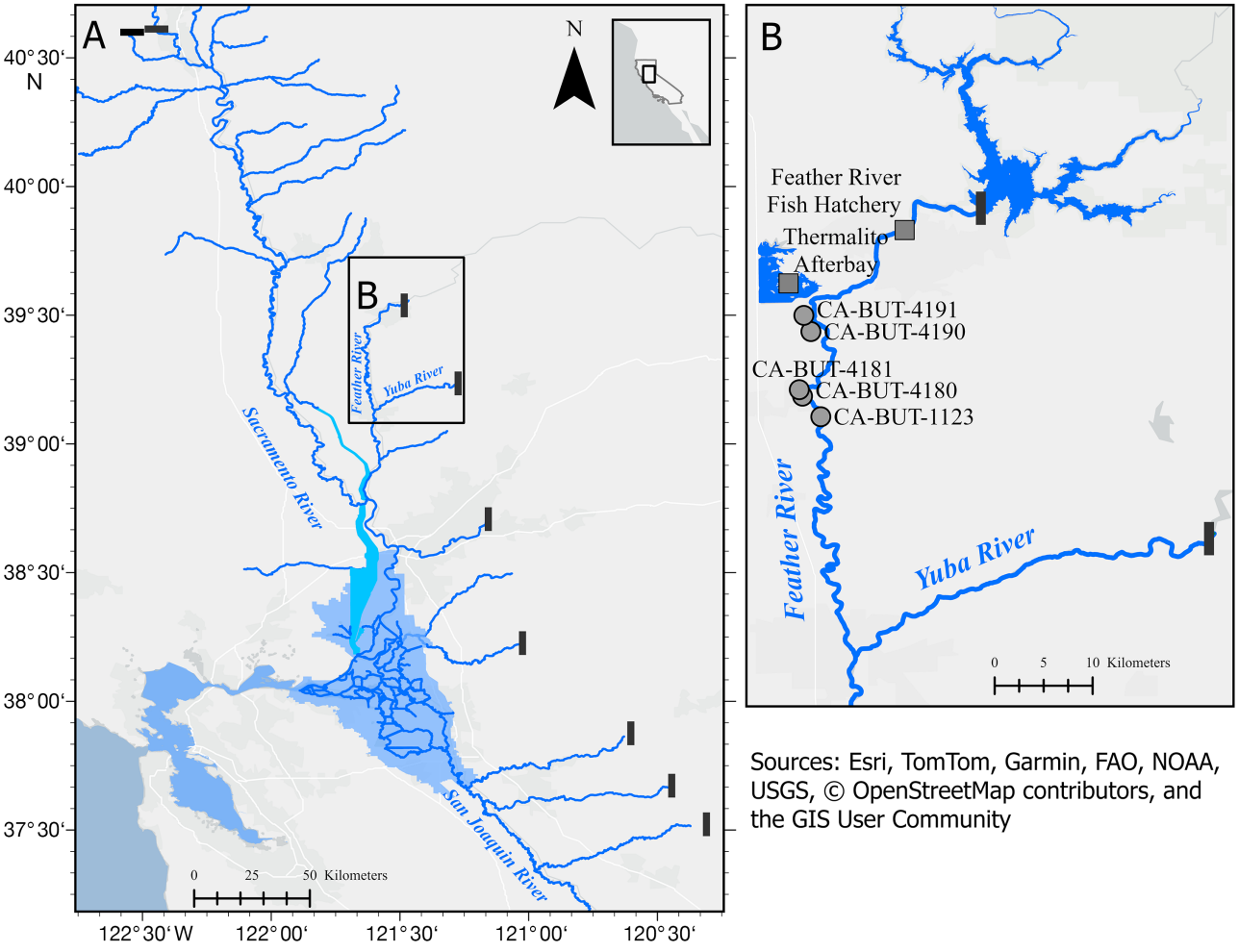

Fig. 1. (A) Major Chinook salmon rivers in California's Central Valley. Black lines: dams and the upper limit of the anadromous reach. (B) Locations of the samples analyzed from the Feather River and Yuba Rivers. The locations of the archaeological sites, the Feather River Hatchery, and the Thermalito Afterbay are indicated

Table 1. Analyzed otolith samples. Time ranges give the lower and upper bounds of sample collection dates for present-day samples and radiocarbon date ranges for the otoliths from the archaeological horizons. cal BP: calibrated years before the present (1950)

Time period	Origin	Site	Time	No. of fish
Present-day hatchery origin	Yuba River	Spawning area	2009–2011, 2018–2020	112
Present-day hatchery origin	Feather River	Spawning area	2002–2011, 2018, 2020	521
Present-day natural origin	Yuba River	Spawning area	2009–2011, 2018–2020	167
Present-day natural origin	Feather River	Spawning area	2002–2011, 2018, 2020	376
Post-European contact (1770–1870 CE)	Feather River	BUT-4181	115–110 cal BP	58
Post-European contact (1770–1870 CE)	Feather River	BUT-4185	180–80 cal BP	110
Late Holocene (500–1770 CE)	Feather River	BUT-4181	430–110 cal BP	29
Late Holocene (500–1770 CE)	Feather River	BUT-4184	530–385 cal BP	1
Late Holocene (500–1770 CE)	Feather River	BUT-4191	555–540 cal BP	2
Late Holocene (500–1770 CE)	Feather River	BUT-4191	750–600 cal BP	6
Late Holocene (500–1770 CE)	Feather River	BUT-4190	1610–1470 cal BP	1
Middle Holocene (1800–1000 BCE)	Feather River	BUT-1123	3285–3045 cal BP	9
Middle Holocene (1800–1000 BCE)	Feather River	BUT-4190	3405–3265 cal BP	3
Middle Holocene (1800–1000 BCE)	Feather River	BUT-1123	3450–3045 cal BP	7
Middle Holocene (1800–1000 BCE)	Feather River	BUT-1123	3850–3415 cal BP	18

as well as various cyprinids (30%), including Sacramento perch *Archoplites interruptus*, pikeminnow *Ptychocheilus grandis*, hardhead *Mylopharodon conocephalus*, splittail *Pogonichthys macrolepidotus*, and the now-extinct thicktail chub *Gila crassicauda*. In addition to fish bones, the sample also includes 349 Chinook salmon *O. tshawytscha* otoliths, identified by Ken Gobalet (unpubl. data) based on their size and shape, following established protocols using primary and secondary characteristics (Casteel 1974). To avoid duplicating data from the same fish and to avoid highly fragmented samples, we selected 247 otoliths from the available samples. The samples represent 6 sites that include 11 discrete chrono-stratigraphic components. Each component represents an ancient living surface that includes residential features, such as hearths and house floors, tools, and food waste, such as shells, charred seeds, and animal bones. Based on stratigraphy and associated radiocarbon dates, the archaeological samples were then binned into 3 distinct time periods: Middle Holocene (1800–1000 BCE), Late Holocene (500–1770 CE), and post-European contact (1770–1870 CE). Based on the location of the archaeological sites in the lower reaches of the watershed and the associated flora and fauna from the excavation, we expect much of our ancient samples to represent either fall- or spring-running Feather River origin Chinook salmon (Yoshiyama et al. 2001, Rosenthal 2020).

2.2. Contemporary samples

The present-day Feather and Yuba River watershed is a major contributor to the Central Valley Chinook salmon stock and has both fall- and spring-run populations (Yoshiyama et al. 2000, Lindley et al. 2004). While these are considered different demographic units, there is a great deal of connectivity between these 2 rivers and genetic homogenization between the fall- and spring-run phenotypes (Williamson & May 2005, Willmes et al. 2024). To provide a comparison to the archaeological data, contemporary otolith samples were chosen from the Feather River (2002–2011) and its main tributary, the Yuba River (2009–2011, 2018–2020). These samples have been described in previous publications (Willmes et al. 2018, 2024). In addition, new otolith ageing was carried out for the Feather River (2018 and 2020) to increase sample sizes. Briefly, these otoliths come from spawner or carcass surveys conducted yearly on the lower Feather and Yuba rivers (Bergman et al. 2012) and cover both natural-origin and hatchery-origin fall- and spring-run individuals (Fig. 1, Table 1). We use the term 'natural origin' to indicate fish that had been assigned as having been born in natural riverine spawning areas based on their otolith chemistry; however, they may still represent the offspring of hatchery-origin fish, which are common in both watersheds.

We focused our quantitative comparisons on present-day samples from the same watershed, which should provide the closest modern-day analog we have to the ancient samples. We used otolith-derived ages because that is the only data source available for the archaeological periods, and we wanted to avoid any confounding factors such as potential effects of ageing methodology or differences among populations in our comparisons. However, we do make further com-

parisons to other populations in the discussion based on other methods, including scale reads (Chen et al. 2024) and tag recoveries (Text S1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m773p149_supp.pdf).

2.3. Otolith sclerochronology

Ancient and contemporary Chinook salmon sagittal otoliths were cleaned of any adhering particles and rinsed with deionized ultrapure water. It should be noted that any sampling for DNA or other tissues would need to be carried out before this step. Samples were then mounted onto glass rounds using Crystalbond (509) resin. Otoliths were ground on both sides on the sagittal plane using 600 and 1500 grit wet/dry sandpaper to expose the primordia and surrounding microstructure. Surfaces were then polished using 3 µm and 1 µm Al_2O_3 lapping films. Finished samples were mounted to a 1 cm square glass pedestal using Gorilla Glue™. Annual ages were determined along the ventral lobe. Bands were counted as a sequence of winter–spring (opaque) and summer–autumn (translucent) bands (Katayama 2018). Age precision was tested using 2 independent age readers that had been trained on known-age fish, following established methods (Campana 2001). Results were evaluated with the FSA package (Ogle 2016) in R, using the 'agePrecision' function. We tested ageing precision for present-day (Feather River 2018 and 2020) and archaeological samples separately to account for any potential loss in precision due to sample preservation. We found generally good agreement among readers for present-day (percent agreement: 86%, average coefficient of variation: 3.41, average percent error: 2.4, readers: 2, n = 137) and archaeological samples (percent agreement: 84%; average coefficient of variation: 3.36, average percent error: 2.4, readers: 2, n = 195). For fish with age disparities, otoliths were read by 2 additional readers, and age was assigned based on a majority vote; if no consensus could be reached, the sample was removed from the data set (n = 3). The age precision achieved here is comparable to our previous studies (Willmes et al. 2018, 2024), which also included an evaluation of age bias using fish of known age (percent agreement: 95%, n = 23; Willmes et al. (2024).

2.4. Statistical methods

We evaluated potential shifts in age structure by comparing several metrics among the binned time periods. Mean returner age and variance for each time period was estimated using a nonparametric bootstrapping procedure, resampling individual ages with replacement (1000 replicates) to generate bias-corrected means and 95% confidence intervals. To test for changes in overall age-class distributions, we performed a Fisher's exact test and, due to low age class counts in some time periods, used estimated p-values using Monte Carlo simulation (10 000 replicates). Differences in age variance among time periods were assessed using Levene's test for homogeneity of variances, centered on the median to improve robustness to the non-normal distribution of the data. Pairwise comparisons of Fisher's exact test and Levene's test were performed for all combinations of time periods, with p-values corrected for multiple comparisons using the false discovery rate method (Benjamini & Hochberg 1995).

Finally, we used the Shannon diversity index (H'; Eq. 1) (Shannon 1948) as a metric to compare age diversity among time periods:

$$H' = -\sum_{i=1}^{s} p_i \times \ln(p_i) \quad (1)$$

H' was calculated for each time period, where s is the number of age classes with at least one observation and p_i is the proportion of individuals of each age class belonging to the i^{th} age class of the total number of individuals. More diverse age structures are characterized by a high H', while less diverse age structures show lower H'. We assessed uncertainties using bootstrapping (1000 replicates) to obtain 95% confidence intervals.

All statistical analyses were conducted using R (v.4.5.0) (R Core Team 2025). Bootstrapping procedures were implemented using the 'boot' package (Canty & Ripley 2017), Fisher's exact tests and Levene's tests were performed using the 'car' package (Fox & Weisberg 2019), and diversity metrics were calculated with the 'vegan' package (Oksanen et al. 2013).

3. RESULTS

We observe a shift in age structure in Chinook salmon, from predominantly age-4 returners in the past to predominantly age-3 and increased contributions of age-2 fish in both hatchery and natural populations since post-European contact (Fig. 2). We also see age truncation, with the Middle-Holocene and post-European contact time periods including 5–15% age-5 returners, which are nearly absent from our present-day data (<1%). However, we also observe a

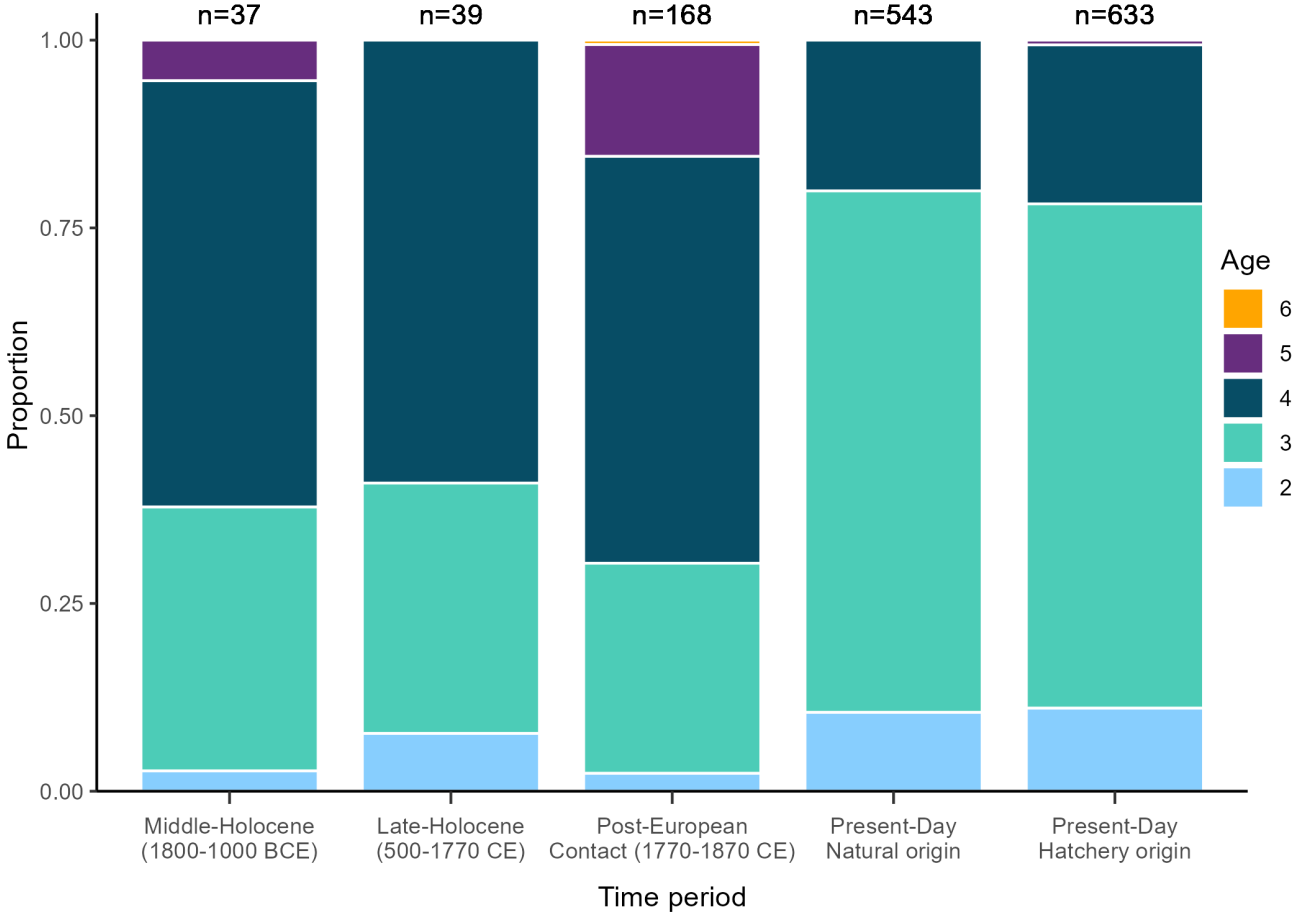

Fig. 2. Temporal changes in the proportion of different age classes reconstructed from sclerochronological analyses of otoliths from returning Chinook salmon. The number of samples for each time period is shown at the top

lack of age-5 returners in our samples from the Late-Holocene time period, for which the sample size was small but similar to the Middle-Holocene time period. Interestingly, we even identify an age-6 fish from the post-European-contact time period, an age class that is completely absent from our present-day otolith samples, despite substantially larger sample sizes in the latter (Fig. 2).

The shift from mainly age-4 returners in the past to age-3 returners in the present samples translates into shifts in the mean return age from 3.65 yr (Middle Holocene), 3.51 yr (Late Holocene), and 3.83 yr (post-European contact) in the ancient otoliths, to 3.10 yr (present-day natural origin) and 3.11 yr (present-day hatchery origin) in the contemporary otoliths (Fig. 3A, Table S2). Fisher's exact tests indicate significant differences in age-class distributions among time periods (simulated $p < 0.001$, $B = 10\,000$). Pairwise comparisons identify differences between the past and contemporary time periods, but no significant differences between present-day hatchery and natural-origin samples, and no significant differences among the 3 archaeological time periods (Table 2).

Variance in return age also decreases from the post-European-contact fish (0.52) compared to present-day natural-origin (0.30) and present-day hatchery-origin (0.33) fish (Fig. 3B, Table S2). Levene's tests reveal a concurrent reduction in age variance ($F = 5.76$, df = 4,1415, $p < 0.001$), with pairwise comparisons showing differences among the post-European-contact time period and contemporary samples (Table 2). We do not observe differences in age variance among the Middle-Holocene and Late-Holocene time periods and the contemporary samples, but this comparison is limited by the large uncertainties in the archaeological time periods due to the small sample size.

Age diversity (H') is lower in the contemporary samples compared to the post-European-contact time period (Fig. 3C, Table S2). This difference is robust to the exclusion of the age-6 individual (change in H': −0.026). The large uncertainties in the H' values for

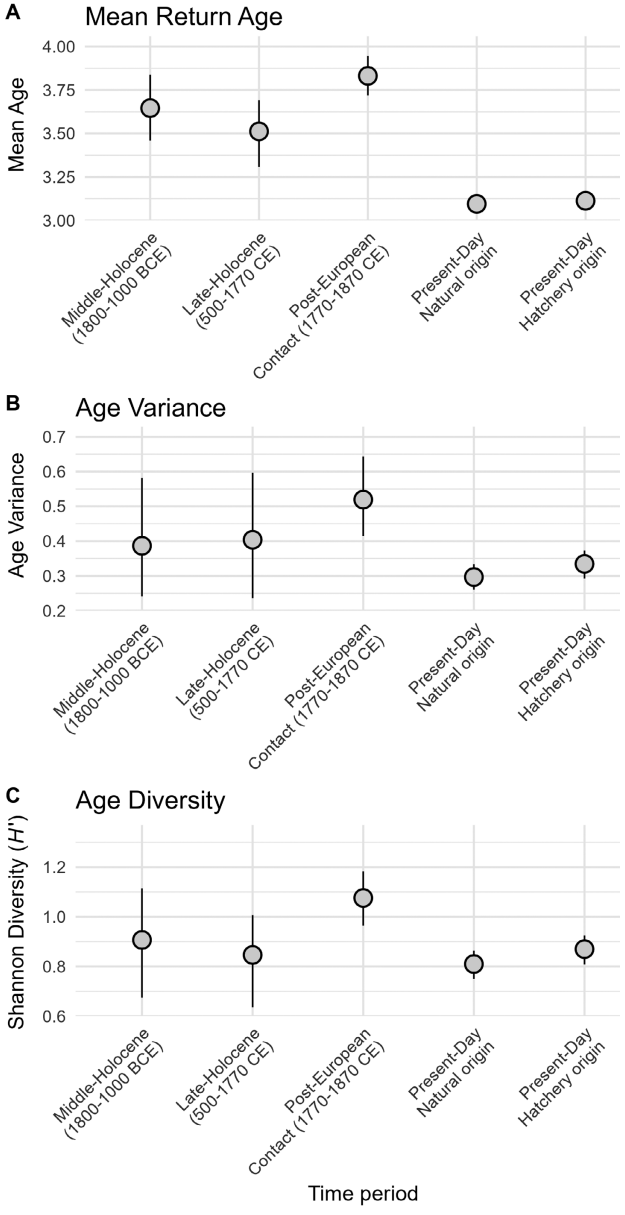

Fig. 3. Temporal changes in (A) mean return age, (B) age variance, (C) and age diversity (*H'*) of returning Chinook salmon. Error bars: bootstrapped 95% confidence intervals. Note that the confidence intervals are sometimes smaller than the dot size for present-day samples

the Middle Holocene and Late Holocene due to small sample sizes limit the comparisons with the contemporary time period.

4. DISCUSSION

Widespread declines in age structure in Chinook salmon throughout their native range have been documented using fishery and escapement surveys over the last decades (Lewis et al. 2015, Ohlberger et al. 2018, Oke et al. 2020). However, little is known about the long-term age structure of these fish before our monitoring started. In this study, we use otoliths to reconstruct the age structure of Chinook salmon in an important Central Valley watershed for 3 distinct time periods covering the last 4 millennia. Our findings indicate that present-day salmon are returning to spawn, on average, around 6 mo younger than they were during the Middle-Holocene, Late-Holocene, and post-European-contact time periods. A pronounced shift toward younger and less diverse age classes occurred sometime between the post-European-contact period (1770–1870 CE) and the present-day period. In the following sections, we first outline potential limitations associated with obtaining ecological data from archaeological samples and how we tried to minimize their effects, and then discuss the observed temporal trends and explore processes that could explain the observed changes and potential consequences.

4.1. Reconstructing ecological data from archaeological samples

Interpreting ages from ancient otoliths presents several challenges related to sample preservation, excavation strategy, and sampling bias. Environmental factors can influence otolith preservation in midden deposits, potentially degrading their physical structure or chemical composition (Disspain et al. 2016), but none of these processes should preferentially preserve or alter samples from specific ages of fish. Recovery methods often miss otoliths in archaeological contexts due to their small size, and identification can be difficult, as they can appear more like stones or unidentifiable bone fragments. The archaeologists and Maidu collaborators involved in laboratory processing were specifically trained in otolith identification, and all processed samples originated from sediments water screened through a 3 mm mesh, resulting in excellent recovery of even small otolith fragments and bones. The recovery of otoliths in the range of 4–10 mm from smaller fish species, such as Sacramento perch *Archoplites interruptus*, as well as even small otolith fragments down to ~2 mm (Rosenthal 2020), suggests that recovery methods did not preferentially exclude smaller otoliths from potentially younger Chinook salmon (generally >5 mm). Selection bias also needs to be considered, since otoliths represent the direct result of past human fishing activity. Historically, fishing was a year-round enter-

Table 2. Pairwise comparisons for return age for each time period using a Fisher's exact test and a Levene's test for homogeneity of variances; p-values were adjusted using the false discovery rate (FDR) method

Group pairs		N1	N2	Fisher's exact test			Levene's test		
Group 1	Group 2			p	p (FDR-corrected)	df	p	p (FDR-corrected)	df
Middle Holocene (1800–1000 BCE)	Late Holocene (500–1770 CE)	37	39	0.54	0.54	12	0.84	0.94	74
Middle Holocene (1800–1000 BCE)	Post-European contact (1770–1870 CE)	37	168	0.50	0.54	16	0.78	0.94	203
Middle Holocene (1800–1000 BCE)	Present-day natural origin	37	543	0.00	0.00	12	0.05	0.13	578
Middle Holocene (1800–1000 BCE)	Present-day hatchery origin	37	633	0.00	0.00	12	0.13	0.22	668
Late Holocene (500–1770 CE)	Post-European contact (1770–1870 CE)	39	168	0.02	0.02	16	0.99	0.99	205
Late Holocene (500–1770 CE)	Present-day natural origin	39	543	0.00	0.00	8	0.02	0.07	580
Late Holocene (500–1770 CE)	Present-day hatchery origin	39	633	0.00	0.00	12	0.06	0.13	670
Post-European contact (1770–1870 CE)	Present-day natural origin	168	543	0.00	0.00	16	0.00	0.00	709
Post-European contact (1770–1870 CE)	Present-day hatchery origin	168	633	0.00	0.00	16	0.00	0.00	799
Present-day natural origin	Present-day hatchery origin	543	633	0.31	0.39	12	0.29	0.42	1174

prise for the Maidu, but seasonal salmon runs were specifically targeted (Kroeber 1925). Archaeological evidence suggests that salmon fishing techniques changed very little through the studied time periods, with the exception of the construction of weirs that started around 600 yr ago (Rosenthal 2020). In archaeological components dating to the Late Holocene and post-European-contact periods, similar fishing technologies were identified by ethnographers, consisting of net and line weights, gorge hooks, J-shaped hooks, leisters (multi-pronged fishing spears), and harpoons. Construction of weirs to capture a range of resident freshwater fish in addition to the migrating salmon started around 600 yr ago (Rosenthal 2020). Maidu weirs recorded historically on the Feather River are thought to have had gates with enclosures above for fish collection with nets (Kroeber & Barrett 1960). This capture technique was likely non-selective with respect to the size and age structure of the netted fish. The same is likely true for individual fish caught with gorges, hooks, and nets. Spearing may have selected for larger fish, but it seems unlikely that smaller fish would have been avoided, since the main goal of salmon fishing was year-round provisioning. The range of other and much smaller species, such as Sacramento perch and Sacramento splittail *Pogonichthys macrolepidotus*, suggests that the techniques used by native fishers captured smaller fish, and therefore would also include all ages and sizes of returning salmon. Furthermore, the tendency for fish to grow faster at younger ages means that differences in salmon size decrease with age (Satterthwaite et al. 2017). Indeed, while the mean sizes of age-3 and age-4 Chinook salmon in the modern population are different, the tails of the distribution overlap substantially (Chen et al. 2024). In addition, the proportion of age-5 fish is so much higher in the post-European-contact period that it is difficult to imagine a level of size-selectivity that could yield such an amplification. For these reasons, we argue that fishing likely targeted migrating salmon of all sizes as they moved toward their spawning grounds and would not preferentially harvest fish of particular ages. Another point to consider is that the length of time within each binned time period differed substantially due to sample availability and differences in temporal resolution for individual archaeological components. As a result of this difference, age diversity and age variance reflect diversity and variance within the entire time period and do not represent the diversity and variance in individual years.

Despite the complexities associated with reconstructing ecological information from ancient otoliths, the samples provide a unique and important window into past ecosystems, offering insights from a time before industrialization and before modern survey methods were established. We offer a conservative and broad interpretation of the data, assuming

that the ancient otoliths represent the Chinook salmon spawning in the Feather River in these time periods.

4.2. Temporal trends in Chinook salmon age structure in California

The ancient otoliths spanning the last 4 millennia provide evidence for a shift to younger ages, from dominantly age-4 returners to age-3 fish in both hatchery and natural populations today. Compared to the post-European-contact time period, which has the most robust sample size of the archaeological collection, the recent time period also shows reduced variance and diversity in return ages. The loss of age-5 fish is especially striking, as these were detected in the Middle-Holocene and post-European-contact time periods but are nearly absent in the present-day populations, despite the much larger sample sizes. The observed lack of age-5 returners in the Late-Holocene time period may indicate they were less prevalent at that time or reflect the low sample sizes of the available otolith samples. The Late-Holocene time period samples also mainly come from the later part of the period, and more samples covering the entire time range would be needed for a more nuanced interpretation.

Early records from California's inland fishery in 1919 and 1921 (Clark 1929) show that this mixed-population fishery was dominated by age-4 fish (1919: ~49%; 1929: ~44%), followed by age-5 and age-3 age classes, estimated using scale circuli counts. While these fishery records may underestimate age-2 and age-3 returners (Williams 2006), they do suggest that the age structure observed in the post-European-contact time period continued, at least initially, through the early 20th century, a time that was defined by extensive loss of freshwater habitats, hydraulic mining, and an intensive inland fishery. Furthermore, a sample of the ocean gill net fishery from 1947 to 1951 suggested that age-4 fish still contributed about half of the fish, but age-3 fish had become the second-most common age class, given a decline in age-5 fish (Williams 2006). By 1955, ocean harvest data show that age-3 fish were most common, followed by age-4 fish, and age-5 fish were relatively rare (Williams 2006).

Today, Central Valley Chinook salmon predominantly return at age-3 but with some variability among runs, watersheds, sexes, and years (Satterthwaite et al. 2017, Sturrock et al. 2020, Chen et al. 2023a, 2024). It has been suggested that fall- and late-fall-run Chinook salmon have a greater tendency to mature later than spring- and winter-run Chinook salmon (Fisher 1994). However, contemporary populations of fall-, winter-, and spring-run Central Valley Chinook salmon are all dominated by age-3 returns, and fall-run have been observed returning as young as age-1 (Satterthwaite et al. 2017, Chen et al. 2023a, Satterthwaite et al. 2023). Tagged hatchery returns to the Sacramento Basin of known age (Table S1) show a highly similar age structure to the contemporary otolith samples in this study. Importantly, this independent data set also shows that age-5 or older fish are now exceedingly rare. Of the 226 799 tag recoveries for fall- and spring-run, there were no fish older than age-5, and only 171 (0.08%) age-5 fish (Table S1). Furthermore, the tag recovery data set has age-3 fish contributing at ~66%, with age-4 at only ~12%. An additional independent data set using scale reads indicated that 0.017% (2 out of 11 672) of fish sampled in the Feather River Hatchery, and none of the 7780 and 2907 fish sampled in the Feather and Yuba River natural spawning areas, respectively, were age-5 (Chen et al. 2024).

4.3. Potential drivers of age structure erosion

Many factors influence the age structure of salmon returners, including tradeoffs and interactions between food availability, competition, predation, temperature, and harvest pressure (Ricker 1981, Lewis et al. 2015, Oke et al. 2020). The data in this study cannot unequivocally identify the factors driving these changes in return age, but the timing of the observed age shifts can provide clues as to the most likely drivers. While indigenous peoples inhabited and shaped California for thousands of years, making extensive and sustainable use of salmon resources (Yoshiyama 1999), the situation changed dramatically after European contact. Starting with European contact, and especially since the Gold Rush period (1848), population growth, habitat degradation, and salmon harvest increased rapidly (Yoshiyama 1999, Munsch et al. 2022). The fragmentation and degradation of freshwater habitats and the construction of large dams likely had a profound impact on Chinook salmon populations, potentially leading to the loss of entire cohorts and life history variants (Yoshiyama et al. 1998, Munsch et al. 2022). Taken together, these changes to the available salmon habitat in the Central Valley and San Francisco Estuary may have decreased age structure through the reduction of distinct populations with different genotypes and phenotypes and through the removal of habitats that support longer freshwater rearing, especially in the

upper watershed (Cordoleani et al. 2021, Munsch et al. 2022).

Concurrent with the rapid habitat loss in the Central Valley and San Francisco Estuary, the commercial salmon fishery in California expanded starting in the mid-1850s. The Chinook salmon fishery initially focused on the lower watershed, with several canneries in operation (Yoshiyama et al. 1998). Although these fisheries targeted all runs and, due to their location in the lower watershed, intercepted fish bound for multiple tributaries, they preferred the winter- and spring-run Chinook salmon, as these runs enter the river less mature, resulting in higher-quality meat (Yoshiyama et al. 1998). With the advent of motorized boats, ocean trolling for salmon became increasingly significant in the early 1900s, allowing fisheries to target salmon before they had matured and started their return journey to freshwater. Archaeological evidence suggests that open-ocean fishing for salmon was negligible in the past, likely because native peoples of the region lacked boating technologies capable of surviving open-ocean conditions for extended periods of time, and salmon were easily caught when they ran upstream and became concentrated. Since the advent of ocean fisheries for salmon, the fishing impact on Central Valley Chinook salmon has remained high (PMFC 2024).

Globally, harvested fish populations often exhibit truncated age structures and declines in size-at-age as a result of fishing pressure and size-selective fishing methods (Berkeley et al. 2004, Hixon et al. 2014, Heino et al. 2015, Barnett et al. 2017). In the ocean, Feather River Fall and Spring Chinook salmon appear to be distributed similarly to the rest of the Central Valley Fall Chinook stock complex, which is the main target of marine fisheries (Satterthwaite et al. 2013, 2018). Harvesting salmon in the ocean can reduce the spawner-age structure by increasing mortality through exposure of older fish to consecutive years of fishing and through selective harvest of older and larger fish (Barnett et al. 2017). Landings of Chinook salmon have been highest in the San Francisco and surrounding areas, and Central Valley Chinook salmon comprise a large proportion of harvested fish (PMFC 2024). California Coastal Chinook and Upper Klamath–Trinity River Chinook are 2 other ESUs in the state and have larger proportions of older spawners (age-4+) compared to Central Valley Chinook salmon (KRTT 2023, Chen et al. 2023b). These populations are north of Central Valley Chinook salmon and occupy regions of the ocean where ocean fisheries are less prevalent, potentially resulting in less fisheries influence on their age structure.

Another factor that may have impacted returner age structure since the 1940s is the influence of hatcheries, which were implemented to compensate for the loss of spawning habitats and declining salmon abundance (Huber & Carlson 2015, Sturrock et al. 2019). Hatchery practices tend to select for faster growth, which may lead to earlier maturation (Larsen et al. 2019). Other practices, such as trucking and among-hatchery transfers, have also reduced genetic and phenotypic diversity in Central Valley Chinook salmon populations, potentially further homogenizing return ages (Williamson & May 2005, Carlson & Satterthwaite 2011). For the endangered winter-run Chinook salmon, which has become increasingly dependent on support from a conservation hatchery, the hatchery-origin spawner age structure is dominated by age-3 fish (Chen et al. 2023a). In our contemporary samples, we did not observe a difference in age structure between hatchery- and natural-origin fall-run returners, similar to the results observed for spring-run (Satterthwaite et al. 2023). However, fall- and spring-run Chinook salmon on the Feather River have a long history of hatchery introgression, which means that a large fraction of our present-day natural-origin samples could be the offspring of hatchery-origin fish. By contrast, the archaeological samples pre-date any influences of hatcheries.

4.4. Consequences of age structure erosion

Shifts to younger return ages generally reduce the productivity, transport of marine-derived nutrients, prey biomass for predators, sediment transport, and fishery value (Hocking & Reynolds 2011, Lewis et al. 2015, Ohlberger et al. 2018, Oke et al. 2020). Conversely, the reduction in age diversity can reduce resilience to variability in environmental conditions along migratory routes and spawning streams (Hilborn et al. 2003, Schindler et al. 2010, Oke et al. 2020, Des Roches et al. 2021). In the case of Central Valley fall-run Chinook salmon, life cycle modeling suggests that the erosion of spawner age structure diversity negatively impacts population stability and increases susceptibility to droughts (Carvalho et al. 2023). Population size depends on the underlying process, with reduced mortality of older fishes resulting in increased abundance, while delayed maturation results in decreased abundance (Carvalho et al. 2023). The recent collapse of the fall-run fishery may be driven by proximate factors such as unfavorable ocean conditions (Lindley et al. 2009) or drought, but more broadly it reflects a diminished buffering cap-

acity in Central Valley Chinook salmon populations to withstand environmental perturbations (Carlson & Satterthwaite 2011, Munsch et al. 2022, Carvalho et al. 2023). Climate change is predicted to further increase environmental variability in California, which will transform the Central Valley watershed, the San Francisco Estuary, and coastal oceans (Dettinger 2011, Swain et al. 2025). While Chinook salmon have used their diverse life history phenology to thrive in California's variable climate over millennia, including periods of prolonged and intense drought (Malamud-Roam et al. 2006), they are now facing an uncertain future (Moyle et al. 2017, Herbold et al. 2018). Actions that help to restore and reconnect the freshwater and estuarine habitat mosaic to allow returners to buffer these climate extremes are going to be increasingly important. Increasing age diversity may be possible via coordinated hatchery and fisheries management and could be an important step towards increasing population stability and resilience (Munsch et al. 2022, Carvalho et al. 2023). Incorporating archaeological data into ecological assessments of age structure can help guard against hidden shifting baselines and provide quantitative data to inform restoration targets.

Data availability. Data and scripts are provided on Dryad: https://doi.org/10.5061/dryad.rxwdbrvng.

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