

RESEARCH ARTICLE

Ancient DNA analysis of archaeological specimens extends Chinook salmon's known historic range to San Francisco Bay's tributaries and southernmost watershed

Richard B. Lanman^{1,2*}, Linda Hylkema³, Cristie M. Boone⁴, Brian Allée⁵, Roger O. Castillo⁶, Stephanie A. Moreno¹, Mary Faith Flores⁷, Upuli DeSilva⁷, Brittany Bingham⁷, Brian M. Kemp⁷

1 Guadalupe-Coyote Resource Conservation District, San Jose, California, United States of America, **2** Institute for Historical Ecology, Los Altos, California, United States of America, **3** University Operations, Cultural Resource Management Program, Santa Clara University, Santa Clara, California, United States of America, **4** Albion Environmental, Inc., Santa Cruz, California, United States of America, **5** South Bay Clean Creeks Coalition, San Jose, California, United States of America, **6** Salmon and Steelhead Restoration Group, Inc., San Jose, California, United States of America, **7** Department of Anthropology, University of Oklahoma, Norman, Oklahoma, United States of America

* ricklanman@gmail.com



OPEN ACCESS

Citation: Lanman RB, Hylkema L, Boone CM, Allée B, Castillo RO, Moreno SA, et al. (2021) Ancient DNA analysis of archaeological specimens extends Chinook salmon's known historic range to San Francisco Bay's tributaries and southernmost watershed. *PLoS ONE* 16(4): e0244470. <https://doi.org/10.1371/journal.pone.0244470>

Editor: Paolo Ruggeri, Natural History Museum of London, UNITED KINGDOM

Received: December 15, 2020

Accepted: March 18, 2021

Published: April 15, 2021

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Data Availability Statement: All sequence data generated in this study are deposited in GenBank (accession numbers MW086771–MW086828, NC_002980.1, and MW113717–MW113719). All data needed to evaluate the conclusions in the paper are present in the paper and/or the [Supporting information](#).

Funding: The ancient DNA sequencing analysis was funded by a grant from the Guadalupe Coyote Resource Conservation District (GCRCD), a non-

Abstract

Understanding a species' historic range guides contemporary management and habitat restoration. Chinook salmon (*Oncorhynchus tshawytscha*) are an important commercial and recreational gamefish, but nine Chinook subspecies are federally threatened or endangered due to anthropogenic impacts. Several San Francisco Bay Area streams and rivers currently host spawning Chinook populations, but government agencies consider these non-native hatchery strays. Through the morphology-based analysis of 17,288 fish specimens excavated from Native American middens at Mission Santa Clara (CA-SCL-30H), Santa Clara County, circa 1781–1834 CE, 88 salmonid vertebrae were identified. Ancient DNA sequencing identified three separate individuals as Chinook salmon and the remainder as steelhead/rainbow trout (*Oncorhynchus mykiss*). These findings comprise the first physical evidence of the nativity of salmon to the Guadalupe River in San Jose, California, extending their documented historic range to include San Francisco Bay's southernmost tributary watershed.

Introduction

Chinook salmon (*Oncorhynchus tshawytscha*), also known as king salmon, are the largest salmon species in the world, and an important commercial and recreational gamefish. North American Chinook salmon currently range from Point Hope, Alaska (USA) to the Sacramento and San Joaquin Rivers in California's Central Valley [1]. Nine different Chinook salmon evolutionary significant units (ESUs) are either federally threatened or endangered, with overall populations lingering at 1% or less than historic populations [2]. The California Central Valley

profit California State Agency to BMK. Stephanie A. Moreno is Executive Director and Richard B. Lanman is President of the Board of Directors of the GCRCD and were co-authors involved in study design, data analysis, decision to publish and preparation of the manuscript. The funder provided support in the form of salary for author SAM. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: Author CMB was employed by Albion Environmental, Inc., but this organization played no role in funding the current study. This does not alter our adherence to PLOS ONE policies on sharing data and materials. All of the authors declare no competing interests.

fall-run Chinook salmon ESU, at the species' southernmost limit, comprise 90% of recent California spawning fish, and traverse San Francisco Bay on their way to spawning in the Sacramento and San Joaquin Rivers' inland watersheds [3]. For the past several decades, Chinook have successfully spawned and reared in San Francisco Bay tributary streams and rivers, a region where they are not considered historically native by government agencies [4]. Skinner's extensive 1962 review opined that "although the fishery for king salmon is centered in the Bay Area, few kings actually spawn in any of the local streams" . . .and instead "pass through the Golden Gate to ascend the Sacramento and San Joaquin rivers on the way to ancestral spawning grounds in these rivers and their tributaries" [5]. Similarly, current National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Sciences (NMFS) historic range maps do not show spawning and rearing habitat for Chinook salmon in San Francisco Bay's tributary watersheds. The southernmost coastal watershed on the range maps for the California Coastal Chinook salmon ESU is the Russian River, whose mouth is 120 km (75 miles) north of San Francisco (see Fig 1) [6]. Similarly, the historical range map for the Central Valley fall-run Chinook salmon ESU completely excludes San Francisco Bay's coastal watersheds even though they are more proximal to the Pacific Ocean (see Fig 2) [7]. These reports

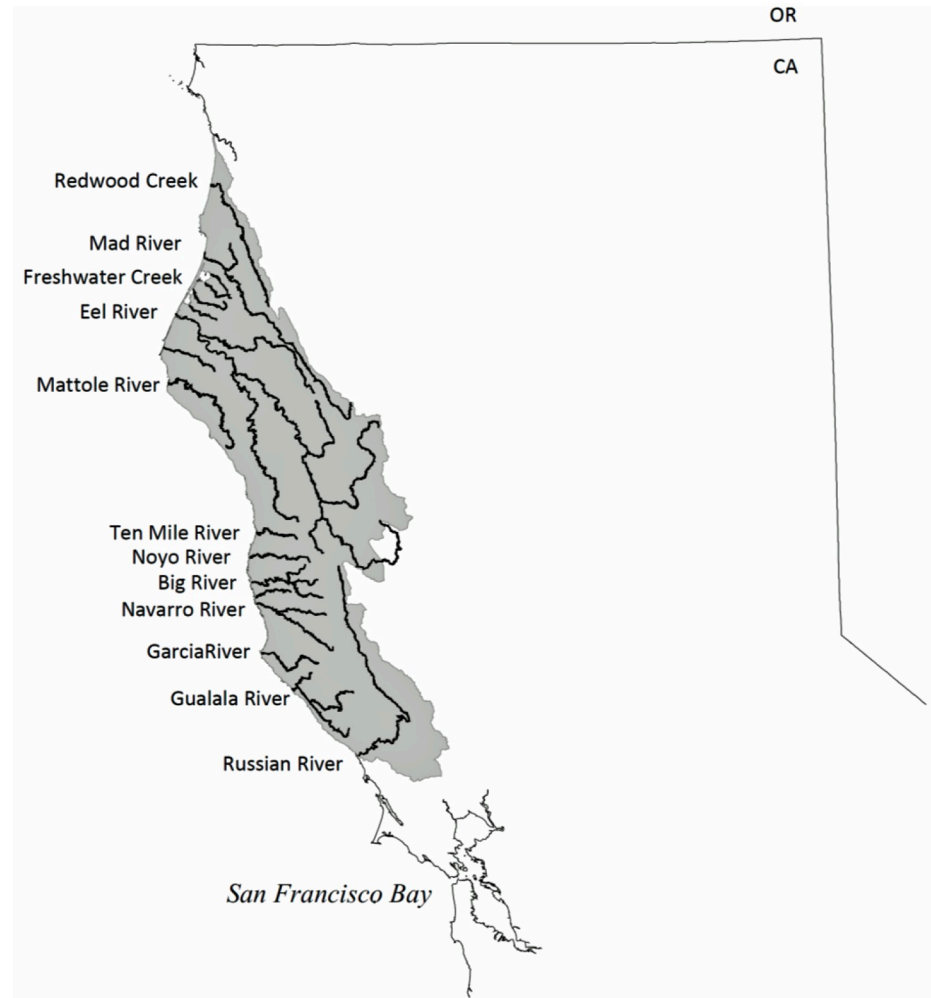


Fig 1. Map of the California Coastal Chinook salmon ESU excludes San Francisco Bay, from NOAA Fisheries, Southwest Fisheries Science Center.

<https://doi.org/10.1371/journal.pone.0244470.g001>

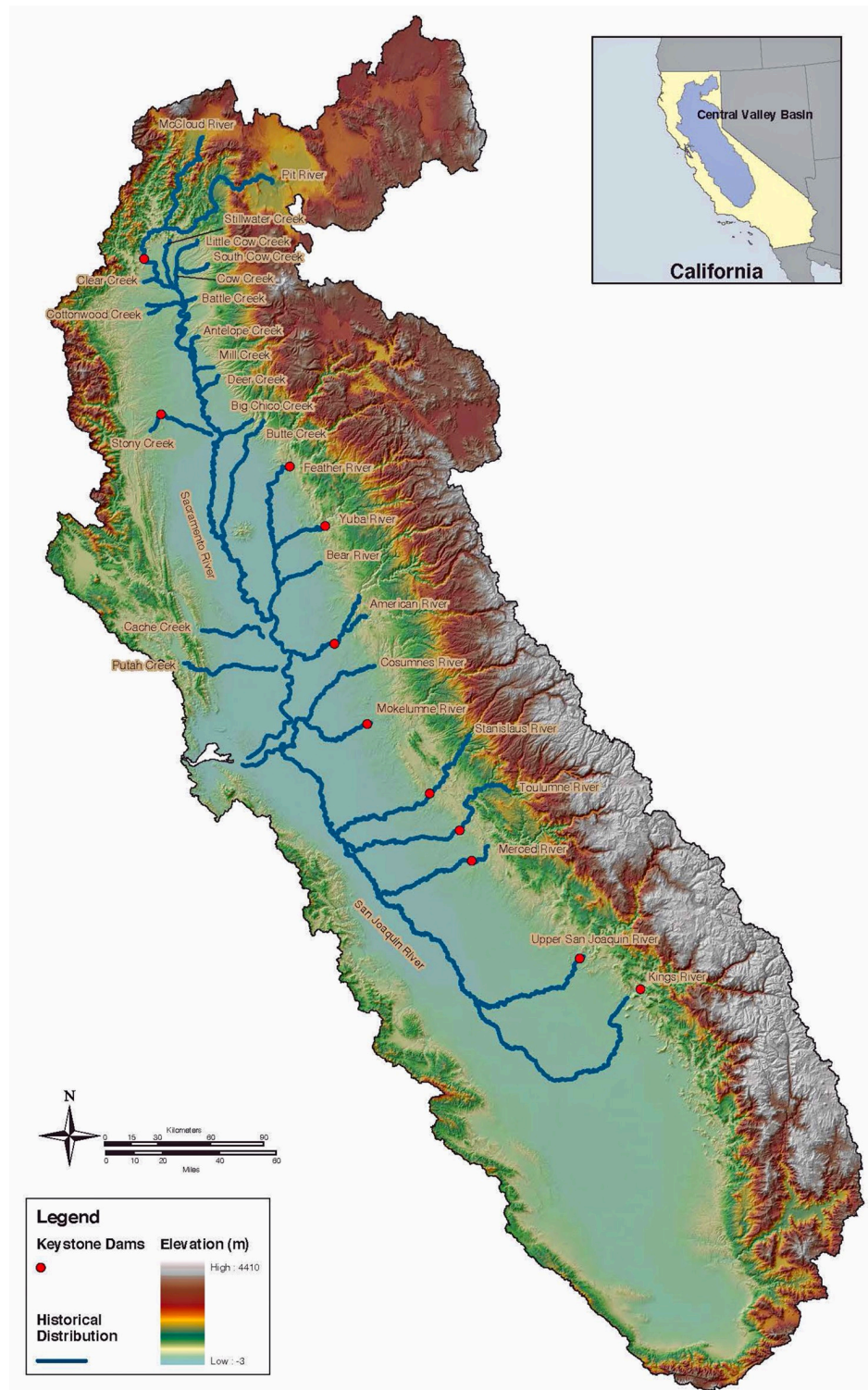


Fig 2. Historical distribution of Central Valley fall-run Chinook salmon ESU excludes San Francisco Bay, from NOAA Fisheries, Southwest Fisheries Science Center.

<https://doi.org/10.1371/journal.pone.0244470.g002>

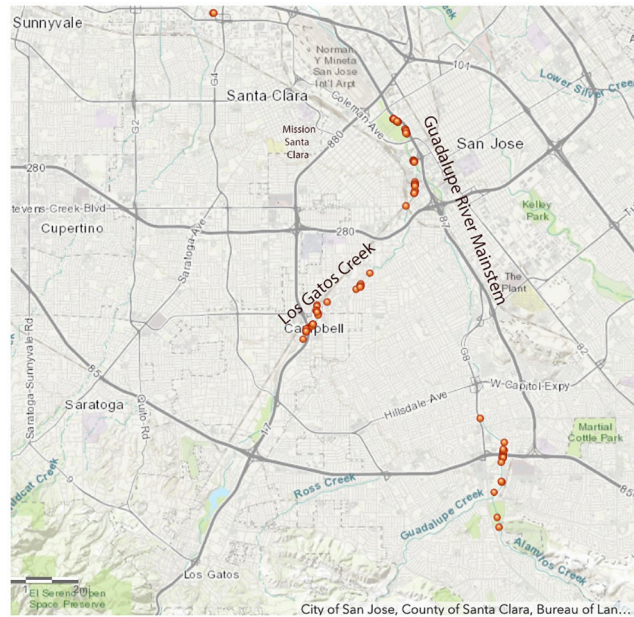


Fig 3. South Bay Clean Creeks Coalition map of Chinook salmon adult carcasses and redds in the Guadalupe River and its tributaries in San Jose, California in January 2019.

<https://doi.org/10.1371/journal.pone.0244470.g003>

on historical ranges are based on a paucity or absence of archaeological evidence, expert observer records, and museum records for Chinook salmon in either Bay Area streams, or in other streams further south on the Pacific Coast.

Chinook salmon in San Francisco Bay watersheds today utilize the lower, perennial reaches of larger streams and rivers, including Walnut Creek and Napa River in the North Bay and the Guadalupe River in the South Bay [4, 8, 9]. The Guadalupe River hosts the southernmost of these nascent San Francisco Bay salmon runs. Salmon spawning has been observed in the river mainstem, which runs through San Jose, California (USA) at the extreme southern limit of San Francisco Bay, and its three main tributaries: Los Gatos Creek, Guadalupe Creek, and Alamosa Creek. For several years, the South Bay Clean Creeks Coalition, a citizens-based watershed advocacy organization, has successfully monitored and conducted Geographic Information System (GIS) mapping of the carcasses of adult salmon and their redds (nests for egg deposition in stream gravels) in the Guadalupe River and its tributaries (see Fig 3). The salmon runs approached 1,000 adult fish in the late 1990s but were nearly extirpated in the early 2000s when the Army Corps of Engineers and Santa Clara Valley Water District completed major anthropogenic alterations to the river mainstem to mitigate flooding. Contemporary San Francisco Bay watershed salmon runs have been attributed to hatchery strays, with very high rates of straying in recent drought years when hatchery-produced juvenile salmon were trucked downstream to the San Francisco Bay estuary to improve smolt survival [10]. Without a natal stream to home to as returning adults, these fish colonize new habitat for spawning.

Until the last four decades, there has been sparse evidence of Chinook salmon utilizing tributaries of San Francisco Bay (defined as the estuary between the Golden Gate strait and the confluence of the Sacramento and San Joaquin Rivers at the Delta). Chinook salmon archaeological specimens have been identified in the Alameda Creek and Walnut Creek watersheds. However, the former were shell middens sites on the bayside shoreline which may reflect salt-water fishing in the South Bay rather than salmon caught in freshwater during in- or out-migration [11, 12]. Two historical observer records noted Chinook salmon in San Francisco

Bay's coastal watersheds. First, an 1879 U.S. Commission on Fish and Fisheries report described obtaining Chinook salmon eggs in San Leandro Creek in the eastern Bay [13]. Second, a February 1904 newspaper account from San Jose, reported that "salmon and steelhead" were being "speared in local streams. . . even within the city limits" [14]. Two other expert accounts suggested that Chinook spawned in coastal watersheds even further south than San Francisco Bay. In 1881, David Starr Jordan, ichthyologist and Stanford University's first president, described Chinook spawning in coastal watersheds "From Ventura River northward to Behring's [*sic*] Straits. . ." [15]; the Ventura River entering the Pacific Ocean 480 km (300 miles) south of San Jose. This reference persists in Behnke's 2010 *Trout and Salmon of North America* [1]; however, this southern limit is not supported by freshwater specimens [16]. John Otterbein Snyder, another Stanford University ichthyologist, indicated in a 1912 report that Chinook salmon spawned in the Pajaro River, about 80 km (50 miles) south of San Jose [17]. However, he also did not collect physical specimens.

Genetic studies of spawned out salmon carcass samples collected in the Guadalupe River watershed found that the majority of these fish are descended from inland Central Valley fall-run Chinook salmon hatchery stock [8, 18, 19]. However, two of these studies also identified several fish with mitochondrial DNA fingerprints indicating that they were strays from wild, non-hatchery stocks. The first, utilizing mitochondrial DNA, found two of nine haplotypes were unique to the Guadalupe River and two to the Russian River (California Coastal Chinook ESU) [18]. A more recent study utilizing microsatellite DNA found three of the 28 fish were more closely related to the Columbia River ESU [8]. Although these genetic studies suggested that today's Guadalupe River salmon may not all be hatchery-derived, they do not resolve the question as to whether Chinook salmon historically utilized south San Francisco Bay streams.

The current study investigates this question by utilizing aDNA sequencing of salmonid vertebrae obtained via archaeological excavation at the historic site of the third Mission Santa Clara de Asís, Santa Clara County, California. This site, designated CA-SCL-30H, dates from 1781–1834 CE, and was located on the now-buried Mission Creek, a tributary joining the Guadalupe River mainstem in San Jose 6–7 km (10–11 km) upstream from San Francisco Bay. Although bone morphology based on vertebrae or other skeletal elements can distinguish salmonid vertebrae from other fishes, it cannot easily separate the five northeastern Pacific salmon species (*Oncorhynchus* spp.) from one another, nor salmon from steelhead/rainbow trout (*Oncorhynchus mykiss*) [11, 20]. However, mitochondrial 12S gene sequences from contemporary fish and archaeological specimens can be used to differentiate these species [21, 22], potentially enabling us to ascertain whether any of the salmonid vertebrae from the excavation were Chinook salmon.

Materials and methods

Museum records search for Chinook salmon in San Francisco Bay tributary streams

Ichthyology databases (FishNet2) and Integrated Digitized Biocollections (iDigBio) were searched for Chinook during the time period 1760–2020. No Chinook museum specimens were found for San Francisco Bay tributary streams, although multiple specimens were collected from the Bay itself. In addition, inquiries to individual museum curators found no Chinook salmon specimens for the above criteria at the California Academy of Sciences, Berkeley Museum of Vertebrate Zoology, Natural History Museum of Los Angeles County, San Diego Museum of Natural History, American Museum of Natural History, Harvard Museum of Comparative Zoology, or the Smithsonian National Museum of Natural History.

Archaeological context

Archaeological excavations of the Native American Rancheria associated with Mission Santa Clara de Asís were conducted by Albion Environmental under the direction of Santa Clara University from 2012–2016. The study site is located 2.5 km (1.5 miles) west of the Guadalupe River mainstem, on its historical Mission Creek tributary [23] in the city of Santa Clara, just west of San Jose. The Mission's Rancheria housed the locally Indigenous Tamien-speaking Ohlone, as well as Bay Miwok and Delta Yokuts recruited from the broader San Francisco Bay Area [24]. The fish remains, which are the focus of this study, were recovered from archaeological features from two projects (Franklin Block 448 and St. Clare) within the Rancheria, specifically from subterranean pits dug into the subsoil between adobe housing blocks [25]. The pits included numerous hearths, food processing tools, and food remains, indicating that these areas were used for the production and consumption of foodstuffs. Very fine-mesh 1.5 mm wet screens were used to isolate bony fish remains [26].

All archaeological work undertaken by Santa Clara University, consultants, and contractors is subject to mitigation under California Environmental Quality Act (CEQA) as defined by the approved Final Environmental Impact Report (FEIR) for this project. The FEIR, Cultural Resources Treatment Plan, and all other entitlement documentation is on file at the City of Santa Clara Planning Department, Santa Clara County, California (USA). The archaeological program conforms to the cultural resources requirements of CEQA and City of Santa Clara procedures and regulations. CEQA was the permit granting lead agency where all necessary permits were obtained. Archaeological specimens are stored at Santa Clara. Further details on the FEIR, Cultural Resources Treatment Plan, permitting and the locality of the excavation sites are found in [S1 File](#).

Zooarchaeological procedures

Following standard zooarchaeological procedures, individual archaeological fish specimens were identified to element and taxon using Boone's personal comparative collection [25]. Of particular relevance to this project, salmonid vertebrae have a unique diagnostic structure, and are identifiable from small fragments. Because excavations at this site used very fine mesh wet screens consistently for all materials, the faunal assemblage was especially large, and only a sample of the fish remains were analyzed. Eighty-eight unspecified salmonid vertebrae were identified.

Ancient DNA sequencing of salmonid vertebrae

Ancient DNA extracted from all 88 vertebrae specimens identified as unspecified salmonids were sequenced at the Laboratories of Molecular Anthropology and Microbiome Research (LMAMR) ancient DNA laboratory at the University of Oklahoma to resolve specific *Oncorhynchus* species type using 148 base pair (bp) sequences from the mitochondrial 12S gene. Next, mitochondrial DNA from samples identified as Chinook salmon were sequenced along a different 563 bp stretch (from the end of the D-loop through tRNA-Phe and into the 12S gene) to gain additional phylogeographic information.

Further details on methods of ichthyofaunal analysis and ancient DNA sequencing are available in [S1 File](#).

Results

Ichthyofaunal analysis

Fish remains were analyzed from multiple spatially distinct features at the Rancheria site, reaching a numeric total of 17,288 identifiable fish specimens (NISP). Freshwater fishes

Table 1. Numbers of identified specimens (NISP) by habitat and project for fish remains at the Mission Santa Clara Rancheria archaeological site.

Habitat	Franklin Block Projects		St. Clare Project		Total	
	NISP	%NISP	NISP	%NISP	Total NISP	Total %NISP
Freshwater	14,999	95.6%	1,260	78.8%	16,259	94.0%
Indeterminate freshwater/euryhaline	202	1.3%	32	2.0%	234	1.4%
Euryhaline	437	2.8%	305	19.1%	742	4.3%
Marine	51	0.3%	2	0.1%	53	0.3%
Total	15,689	100.0%	1,599	100.0%	17,288	100.0%

<https://doi.org/10.1371/journal.pone.0244470.t001>

comprised 79–95% of the site assemblages by NISP, with most of the remaining specimens representing indeterminate freshwater/euryhaline species or euryhaline. Less than 1% of specimens were from marine fishes (Table 1). Of the 58 vertebrae identified as salmonid that also produced aDNA results, most of the vertebrae were very small, measuring ≤ 4 mm across the centrum diameter. Three specimens were all fragments but estimated at > 10 mm or as “large” (Table 2).

Results of ancient DNA sequencing

Based on the 148 bp sequence of the mitochondrial 12S gene, all vertebrae with adequate DNA (58 of 88, or 65.9%) were identified as *Oncorhynchus* species, confirming the ichthyofaunal determination (Table 2). Of these 58 salmonid specimens, 55 were identified as steelhead/rainbow trout. Results for 53 of these 55 specimens were replicable. In the case of the other two samples, we were able to only produce results from a single PCR reaction. However, given their small size and the overall abundance of rainbow trout/steelhead found archaeologically, these identifications are likely correct. The remaining three specimens (sample numbers 3.4, 3.6, and 7.4) were identified as Chinook salmon (Table 2) and these results were replicable, and further validated by the additional mitochondrial DNA sequences described below. No fish DNA was observed in any negative controls. The 12S sequences were deposited in Genbank (accession numbers MW086771–MW086828).

Specimens 3.4, 3.6, and 7.4 were additionally sequenced from nucleotide positions (nps) 570–1121 relative to a comparative full mitochondrial genome of Chinook salmon (Genbank accession number NC_002980.1). All of these sequences were replicable and have been deposited in Genbank (MW113717–MW113719). Each of the three samples exhibit unique SNPs in the analyzed D-loop fragment, indicating that they represent three distinct individual fish (see S1 File). These sequences make phylogenetic sense, in that they are closely related to other Chinook salmon sampled from lower Pacific coast (Washington, Oregon, and California) watersheds, further validating our species identification based on our mitochondrial 12S gene sequences.

Discussion

We combined aDNA sequencing and ichthyofaunal analysis of archaeological samples to show that Chinook salmon were utilized by the Indigenous peoples living at Mission Santa Clara de Asís in the 18th and 19th centuries. As discussed below, the salmon are not likely to be trade items. Therefore, these results establish the first physical evidence that Chinook salmon spawned historically in a San Francisco Bay tributary watershed, the Guadalupe River.

Zooarchaeology and ancient DNA analysis, when combined, can improve our understanding of a species historical range. For example, Stevenson et al. [27] utilized ancient DNA sequencing to confirm historical and ethnographic accounts of Chinook salmon and

Table 2. Species, archaeological context, and estimated vertebral centrum diameter for 58 salmonid vertebrae that produced aDNA results.

Sample no. for aDNA ¹	Archaeological Feature ²	Species ID by aDNA	Vertebra Size Estimate ³
2.4	155	<i>O. mykiss</i>	3 mm
2.5	155	<i>O. mykiss</i>	3 mm
2.6	155	<i>O. mykiss</i>	2–3 mm
2.7	503	<i>O. mykiss</i>	1–2 mm
3.1	79	<i>O. mykiss</i>	1–2 mm
3.2	155	<i>O. mykiss</i>	2–3 mm
3.4	503	<i>O. tshawytscha</i>	> 10 mm
3.5	91	<i>O. mykiss</i>	4 mm
3.6	155	<i>O. tshawytscha</i>	> 10 mm
4.1	79	<i>O. mykiss</i>	2 mm
4.3	119	<i>O. mykiss</i>	2 mm
4.5	119	<i>O. mykiss</i>	3 mm
4.6	119	<i>O. mykiss</i>	1–2 mm
5.1	119	<i>O. mykiss</i>	2–3 mm
5.3	119	<i>O. mykiss</i>	2 mm
5.4	119	<i>O. mykiss</i>	2 mm
5.5	119	<i>O. mykiss</i>	2–3 mm
5.6	119	<i>O. mykiss</i>	1–2 mm
5.7	119	<i>O. mykiss</i>	2–3 mm
6.2	155	<i>O. mykiss</i>	2–3 mm
6.3	155	<i>O. mykiss</i>	2–3 mm
6.4	155	<i>O. mykiss</i>	2–3 mm
6.5	155	<i>O. mykiss</i>	2–3 mm
6.6	155	<i>O. mykiss</i>	2–3 mm
6.7	503	<i>O. mykiss</i>	2 mm
7.1	155	<i>O. mykiss</i>	2 mm
7.2	155	<i>O. mykiss</i>	3 mm
7.3	230	<i>O. mykiss</i>	1–2 mm
7.4	503	<i>O. tshawytscha</i>	Large
8.1	66	<i>O. mykiss</i>	2–3 mm
8.2	66	<i>O. mykiss</i>	2–3 mm
8.3	66	<i>O. mykiss</i>	2–3 mm
8.4	66	<i>O. mykiss</i>	2–3 mm
8.5	79	<i>O. mykiss</i>	1–2 mm
8.6	119	<i>O. mykiss</i>	2–3 mm
9.1	119	<i>O. mykiss</i>	2–3 mm
9.6	119	<i>O. mykiss</i>	2–3 mm
10.1	119	<i>O. mykiss</i>	2–3 mm
10.2	119	<i>O. mykiss</i>	2 mm
10.3	119	<i>O. mykiss</i>	2 mm
10.4	119	<i>O. mykiss</i>	2 mm
10.5	119	<i>O. mykiss</i>	2 mm
10.6	119	<i>O. mykiss</i>	2 mm
10.7	119	<i>O. mykiss</i>	1–2 mm
11.3	503	<i>O. mykiss</i>	2 mm
11.5	155	<i>O. mykiss</i>	3 mm
11.6	155	<i>O. mykiss</i>	3 mm

(Continued)

Table 2. (Continued)

Sample no. for aDNA ¹	Archaeological Feature ²	Species ID by aDNA	Vertebra Size Estimate ³
11.7	155	<i>O. mykiss</i>	2–3 mm
12.3	155	<i>O. mykiss</i>	2–3 mm
12.4	155	<i>O. mykiss</i>	2–3 mm
12.5	155	<i>O. mykiss</i>	3 mm
12.6	155	<i>O. mykiss</i>	2–3 mm
12.7	155	<i>O. mykiss</i>	2–3 mm
13.1	155	<i>O. mykiss</i>	2–3 mm
13.2	155	<i>O. mykiss</i>	2–3 mm
13.3	155	<i>O. mykiss</i>	2–3 mm
13.4	155	<i>O. mykiss</i>	3 mm
13.5	155	<i>O. mykiss</i>	2–3 mm

¹ 30 specimens did not produce aDNA results and are not included in this table.

² Feature 503 is from the St. Clare project; all other features are from the Franklin Block projects.

³ Vertebral centrum diameter is an estimate based on pictures with scales. The two *O. tshawytscha* specimens with sizes > 10 mm are based on approximately 1/4 of the centrum. The *O. tshawytscha* noted as "large" was heavily fragmented, but clearly from a large vertebra.

<https://doi.org/10.1371/journal.pone.0244470.t002>

steelhead/rainbow trout spawning as far upstream the Klamath River as the Upper Klamath Lake, but this finding did not extend the known historical range limits of these anadromous fishes. However, the discovery that the Atlantic sturgeon (*Acipenser oxyrinchus*) was native not only to North America, but to Europe [28, 29], and that the vyrezub or Black Sea roach (*Rutilus frisii*) was native to the Danube River [30], as well as the current study, demonstrate the power of this combined approach to refine modern conservation efforts. The current study also enabled us to determine that the mitochondrial DNA from the three Chinook salmon vertebrae represented three different individuals. This finding was consistent with one of the three fish coming from a different archaeological feature than the other two (Table 2).

Furthermore, the three vertebrae identified as Chinook in our study were all from large individuals, indicating that these were adult fish that ascended the Guadalupe River watershed to spawn. Adult salmon are semelparous, dying after spawning, unlike steelhead which are iteroparous. The fish remains found in the Mission Rancheria could not be hatchery strays, as these samples significantly antedate the first salmon hatcheries established in California—in 1870 for trout and 1874 for salmon [31]. Although we cannot definitively exclude that the three Chinook salmon identified by aDNA were not trade items from other regions, multiple lines of evidence support the argument that these salmon specimens were locally caught. First, less than one percent of the of 17,000+ analyzed specimens were marine fishes, and many of the latter were species caught intertidally, indicating that local Indigenous peoples were not exploiting pelagic marine fish species. Second, there are no historical accounts of pelagic salmon fishing by California tribes north of San Luis Obispo [298 km (185 mi) south of San Jose], although there is archaeological evidence of salmon being taken in northern San Francisco Bay, and the Central Valley's watersheds [32]. Third, adult salmon are large, averaging 13–14 kg (29–31 lbs) and may reach 59 kg (130 lbs) [33], unwieldy for transport whole even over short distances. Although we could not estimate the weight of the Mission Rancheria salmon, their vertebral diameters were conservatively estimated from small fragments, so may have been larger than 10 mm. The large diameter of the vertebrae genetically identified as Chinook salmon also supports the genetic identifications, as the results of previous studies have demonstrated that only Chinook and chum salmon (*Oncorhynchus keta*) regularly have

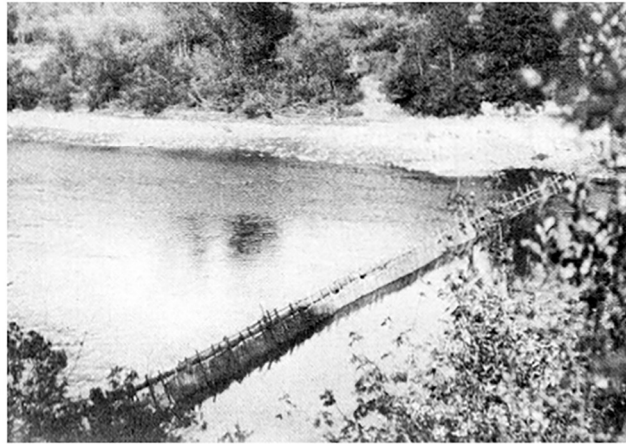


Fig 4. Hupa salmon weir on lower Trinity River, After P. E. Goddard, *Life and Culture of the Hupa*, University of California Publications American Archaeology and Ethnology 1, 1–88 (1903).

<https://doi.org/10.1371/journal.pone.0244470.g004>

diameters exceeding 10 mm, and the latter do not spawn south of central Oregon [22, 34]. Based on ethnographic descriptions of other Indigenous Californian peoples, larger fish species, such as adult Chinook salmon, are generally filleted to remove bones, then either dried into strips or pounded into fish flour for trade, and thus traded salmon were generally devoid of large vertebrae [35, 36].

The Guadalupe River watershed habitat is suitable for salmon spawning as several San Francisco Bay tributary streams and rivers currently host successful Chinook salmon runs. Successful spawning and rearing have been documented in the Guadalupe River in the South Bay not only over the last four decades, but was also reported in a newspaper record from 1904 by a writer that appeared capable of differentiating steelhead/rainbow trout from salmon [14].

Ethnographic researchers describe the Ohlone and most other Northern California Indigenous people as catching steelhead/rainbow trout and salmon effectively by use of weirs or long nets stretched across streams (see Fig 4), and also via loop nets and harpoons or spears at rapids [35, 37]. John Peabody Harrington, an ethnologist and linguist who studied California's Indigenous peoples, specifically described the Ohlone people in the Santa Clara Valley as using spears and nets to fish [38]. Of interest, no fishhooks or spearheads were found in the Mission Santa Clara excavations, although fishing net weights were identified. Although the majority of Mission Rancheria residents were Ohlone, Bay Miwok, and Delta Yokuts peoples for whom there are no records of major salmon ceremonies [38], an analysis of West Coast tribes who utilized salmon extensively for food found no correlation with tribes who had salmon ceremonies versus those that did not [39].

Why would there be apparent discordance between an absence of museum records and our finding of late 18th/early 19th century Chinook salmon in San Jose? First, only two California museums established ichthyology collections before the 20th century, the Stanford Museum and the California Academy of Sciences, and these were damaged or destroyed in the 1906 San Francisco earthquake and fire [40]. Second, our search of Chinook salmon museum records in the Bay Area revealed only fish caught in the Bay itself. These specimens were likely most easily obtained from fish markets or from commercial fisherman targeting the large salmon runs traversing the Bay en route to the Central Valley, rather than sourced from the smaller numbers of fish in the Bay's tributary streams. Third, difficulty discriminating between different

salmonid species below the *Oncorhynchus* genus level utilizing vertebral remains may have prevented identification of Chinook salmon in both archaeological and museum specimens [12].

Daniel Pauly's "shifting baselines syndrome" suggests that each generation of fisheries scientists accepts as a baseline the stock size and species composition that occurred at the beginning of their careers, and uses this to evaluate changes [41]. This phenomenon may be reflected in overly conservative governmental range maps for the southern coastal limit of Chinook salmon. In fact, the accepted historic ranges of numerous California fishes have been expanded based on observer and museum records through utilization of archaeological specimens [42–45]. For salmon specifically, underestimation of the historic range for salmonids has occurred in at least three North American examples. First, Chinook salmon were considered as nearly absent from the Russian River, now part of the California Coastal Chinook ESU, until a 2007 publication of an underwater camera monitoring study documented an "abundant, widely distributed, and naturally self-sustaining Chinook population in the watershed" [46]. Second, a dearth of Atlantic salmon (*Salmo salar*) remains in the archaeological record were used to refute the nativity of Atlantic salmon to the coastal northeastern United States [47]. These assertions were overturned when Atlantic salmon fish scales were discovered in sediment cores taken from a nearshore pond in coastal New Jersey [48]. Third, based on the lack of archaeological findings in coastal streams south of San Francisco, lumber company affiliated biologists rejected Snyder's determination of the southern limit of coho salmon (*Oncorhynchus kisutch*) at the San Lorenzo River in Santa Cruz County, California [17], and asserted that the coho salmon observed by Snyder in 1912 were hatchery strays [49]. However, one year later, archaeologists identified coho salmon vertebrae in Native American middens in nearby Año Nuevo State Park, reaffirming Snyder's southern limit for coho [50]. These examples, coupled with the current study's findings, should encourage California's natural resource managers and scientists to question received wisdom as to the historic range of California's fauna, and to apply new technologies, such as aDNA sequencing, to re-examine the evidence.

There are several limitations to the current study. Chinook salmon may have been present in the Guadalupe River watershed only intermittently, that is, only when conditions were favorable. All three of the Chinook salmon specimens date broadly to the Mission Period (1760–1834 CE) and while the specimen from the Franklin Block Feature 155 was from the Late Mission Period and could be differentiated spatially from the other two specimens from the St. Clare site, it could not be differentiated temporally from the others. Also, we cannot determine the size of the historic salmon population, which may have been low, or at minimum, highly variable over time in accordance with fluctuating climactic conditions. Lastly, our study does not verify whether today's Chinook population is self-sustaining with local smolts returning as successfully spawning adults. This should be further investigated via isotopic analysis of contemporary adult salmon carcass otoliths, as they possess the same elemental composition as when the otoliths formed in early life, and are thus natal stream specific [10].

Conclusion

The absence of evidence should not be equated with evidence of absence [51]. This study provides the first physical evidence that adult Chinook salmon spawned in any San Francisco Bay tributary watershed historically and extends their nativity to a coastal watershed further south than previously recognized. These results contrast with a paucity of archaeological, historical observer, and museum records. Ancient DNA sequencing of other archaeology specimens may refine our understanding of the historical range of other species. Whether today's Guadalupe River salmon are hatchery strays or not is moot. As stated above, there is evidence that

the recent Guadalupe River population has had at least some genetic introgression from Russian River and Columbia River stocks. If this watershed is managed to enable a self-sustaining coastal Chinook population at the very southern border of its range, these fish may represent an important genetic reservoir of fish buffered against changing climatic conditions, such as global warming [52], and may potentially counter the collapsing diversity extant in this salmon species [53].

Supporting information

S1 Fig.
(PDF)

S1 File. Results of aDNA amplification and sequencing of the three Chinook salmon samples, and additional references [1–11].
(DOCX)

Acknowledgments

The authors wish to acknowledge the encouragement of Kenneth Gobalet to study the possible Chinook salmon archaeology remains discovered at Mission Santa Clara. We also wish to thank the South Bay Clean Creeks Coalition for its contemporary GIS mapping of salmon carcasses and redds in the Guadalupe River watershed, and to Cara Monroe for assistance in the LMAMR laboratory.

Author Contributions

Conceptualization: Richard B. Lanman, Linda Hylkema, Cristie M. Boone, Brian M. Kemp.

Data curation: Linda Hylkema, Cristie M. Boone, Brian M. Kemp.

Formal analysis: Richard B. Lanman, Linda Hylkema, Cristie M. Boone, Brian M. Kemp.

Funding acquisition: Richard B. Lanman, Stephanie A. Moreno.

Investigation: Richard B. Lanman, Linda Hylkema, Cristie M. Boone, Brian Allée, Mary Faith Flores, Brian M. Kemp.

Methodology: Richard B. Lanman, Linda Hylkema, Cristie M. Boone, Brian M. Kemp.

Project administration: Richard B. Lanman, Linda Hylkema, Stephanie A. Moreno.

Resources: Richard B. Lanman.

Supervision: Brian M. Kemp.

Validation: Cristie M. Boone, Brian M. Kemp.

Visualization: Richard B. Lanman, Linda Hylkema, Cristie M. Boone, Brian M. Kemp.

Writing – original draft: Richard B. Lanman.

Writing – review & editing: Richard B. Lanman, Linda Hylkema, Cristie M. Boone, Brian Allée, Roger O. Castillo, Stephanie A. Moreno, Mary Faith Flores, Upuli DeSilva, Brittany Bingham, Brian M. Kemp.

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