

FISHERIES

Historical ecology and the conservation of large, hermaphroditic fishes in Pacific Coast kelp forest ecosystems

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The intensive commercial exploitation of California sheephead (*Semicossyphus pulcher*) has become a complex, multimillion-dollar industry. The fishery is of concern because of high harvest levels and potential indirect impacts of sheephead removals on the structure and function of kelp forest ecosystems. California sheephead are protogynous hermaphrodites that, as predators of sea urchins and other invertebrates, are critical components of kelp forest ecosystems in the northeast Pacific. Overfishing can trigger trophic cascades and widespread ecological dysfunction when other urchin predators are also lost from the system. Little is known about the ecology and abundance of sheephead before commercial exploitation. Lack of a historical perspective creates a gap for evaluating fisheries management measures and marine reserves that seek to rebuild sheephead populations to historical baseline conditions. We use population abundance and size structure data from the zooarchaeological record, in concert with isotopic data, to evaluate the long-term health and viability of sheephead fisheries in southern California. Our results indicate that the importance of sheephead to the diet of native Chumash people varied spatially across the Channel Islands, reflecting modern biogeographic patterns. Comparing ancient (~10,000 calibrated years before the present to 1825 CE) and modern samples, we observed variability and significant declines in the relative abundance of sheephead, reductions in size frequency distributions, and shifts in the dietary niche between ancient and modern collections. These results highlight how size-selective fishing can alter the ecological role of key predators and how zooarchaeological data can inform fisheries management by establishing historical baselines that aid future conservation.

INTRODUCTION

Over the past two decades, numerous studies have documented intense overharvesting of many of the world's most important commercial and recreational fisheries [for example, Pauly *et al.* (1), Jackson *et al.* (2), Myers and Worm (3), Coleman *et al.* (4), and Pinnegar and Engelhard (5)]. Even with careful management, global catches have stagnated or declined as fishing efforts have increased (6, 7). At times, the scale of harvest has gone underreported (8), and few case studies document the successful recovery of commercial fisheries (9). Although mapping a route to fisheries recovery is complex (9), new research suggests that two possible pathways may be important for informing ecosystem-based approaches to fisheries management: (i) establishing baselines built from consulting deep historical data sets [for example, Jackson *et al.* (2)] and (ii) enacting management measures that preserve larger (older) fish [for example, Le Bris *et al.* (10)].

Pauly (11) argued that a major pitfall plaguing modern fisheries management is the reliance on restoration baselines that rarely extend beyond the ~100-year history of fisheries science, which corresponds with the widespread commercial exploitation of many global fisheries. He dubbed this the “shifting baselines syndrome,” and other researchers [for example, Pauly *et al.* (1), Jackson *et al.* (2), Pinnegar and Engelhard (5),

Dayton *et al.* (12), and McClenachan *et al.* (13)] have called for the integration of deeper temporal perspectives, gleaned from historical, archaeological, and paleoecological sources, to rethink fisheries management and establish more realistic ecological baselines that consider the long and dynamic history of human interactions with marine ecosystems around the world (14).

Fisheries biologists and ecologists have increasingly recognized the high reproductive value of large (old) fish for maintaining viable and healthy populations (15). Traditionally, resource managers have simply imposed minimum size limits as a staple of commercial and recreational fisheries management plans, and have underappreciated the importance of large fish (16, 17). Recent studies suggest that management measures should be established that help preserve larger individuals (18, 19), who have higher fecundity (20), different spawning cycles and locations (21), size/age-dependent “maternal effects” (10, 22), and different ecological impacts on prey species (23). These traits are important for helping a fish population buffer against environmental fluctuations (24, 25) and human fishing pressures (26). One of the potential challenges in determining the appropriate sizes (and ages) of fish to preserve and protect is deciding what constitutes a “large” fish. Because most restoration baselines rely on data that postdate the advent of intensive commercial and recreational fisheries, the largest fish may have already disappeared, culled from the population as a product of minimum size limits and decades of fishing exploitation pressure on the largest individuals (9, 27).

Here, we explore the deep (pre)history of California sheephead (*Semicossyphus pulcher*) fishing along the northern Channel Islands off of southern California, documenting the increasing harvest intensity on the species over the past 10,000 years. Our study can be used as a model for other hermaphroditic species and combines modern population

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data with zooarchaeological and isotopic data to decode the spatial and temporal variability of the fishery. Our results suggest that, despite significant paleoenvironmental changes and intensified human predation pressure, prehistoric sheephead stocks persisted through millenia. We also reconstruct the average size of California sheephead during prehistoric times using an allometric approach to estimate total length from skeletal elements (28). These data provide a more realistic baseline of the size of California sheephead and may help resource managers evaluate current conservation guidelines and develop strategies that can mediate the shifting baselines syndrome in kelp forest ecosystems. Last, we document prehistoric to modern shifts in the isotopic (dietary) niche of sheephead caught off two northern Channel Islands. These shifts could be driven by a combination of factors, including (i) a shift in the size distribution of sheephead and/or (ii) changes in the importance of kelp production in nearshore ecosystems over time.

California sheephead ecology

California sheephead are a species of temperate wrasse, widely distributed along the eastern Pacific Ocean from Monterey Bay, CA, USA, to Cabo San Lucas, Baja California, Mexico (29). Members of the family Labridae, sheephead inhabit nearshore rocky reefs and kelp beds from the intertidal zone to depths of ~90 m (29). Sheephead can live between 20 and 30 years under ideal conditions, and reach lengths of 94 cm and weights of 16 kg (29). Sheephead are carnivores, with powerful jaws, sharp teeth, and a throat plate (that is, pharyngeal jaw) for grinding shells, and act as important predators of sea urchins, crabs, lobsters, mollusks, and other benthic invertebrates, with feeding preferences and growth rates changing based on prey availability (30–32).

Like many other labrids, California sheephead are protogynous hermaphrodites that are all born female but are capable of changing into males when environmental conditions or other pressures compel them to do so (33). Sex changes are triggered by social cues, such as population sex ratios and the availability of males, and result in marked morphological changes because they entail both internal (gonadal changes) and external (morphological color) modifications (33). Hence, males tend to be larger than females and have black tails and heads, a reddish orange or pinkish midriff, and forehead bumps (Supplement 1). Females are smaller and born with largely monochromatic pinkish coloration (27). Females reach sexual maturity between 3 and 6 years and can remain females for up to 15 years (31, 34). Males establish and defend territories and court females with whom they pair spawn during a reproductive season from May to September (31, 33, 35).

California sheephead are a significant component of kelp forest ecosystems in southern California. Further north in the Pacific (for example, Alaska), the local extinction of sea otters (*Enhydra lutris*) during the Maritime Fur Trade era (ca. 1780 to 1840 CE) resulted in extensive kelp deforestation driven by increased sea urchin herbivory (36). Similar deforestations were not observed in southern California until approximately 150 years after sea otters had been extirpated. The presence of other urchin predators, such as the California sheephead, spiny lobsters (*Panulirus interruptus*), and sea stars (*Pycnopodia helianthoides*), provided functional redundancy and likely buffered against these large-scale ecological changes. It was only after fishing pressure on sheephead and lobsters increased in the 1940s that kelp deforestation was observed along the Channel Islands (37), whereas deforestation along the mainland coast was triggered by a combination of stressors, including fishing and pollution (38). Previous research has shown that

the recovery of sheephead populations, and maintenance of a size structure composed of large individuals capable of preying on invertebrates that consume kelp (for example, urchins), may play a key role in ensuring the resilience of kelp forest ecosystems in southern California (23, 39).

Modern fishing records

The historical exploitation of California sheephead probably began with the first arrival of Europeans in coastal California and Mexico. Commercial harvest did not begin until the late 1800s when Chinese fishermen arrived in California after the discovery of gold in the Sierra Nevada Mountains. Pushed out of or marginalized from the Gold Rush economy, many immigrant Chinese fishermen turned to the bounty of the seas and established markets and trade routes for fish and shellfish to local Chinatowns and mainland China (40–42). By the early 20th century, racist laws and ethnic hostility against Chinese immigrants caused a wane in the Chinese fishing industry, and Euro-Americans filled the void [see the study by Braje (42)].

California sheephead were not the target of heavy commercial or recreational fisheries for much of the 20th century, although brief commercial harvest spikes occurred between 1927 and 1931 (peaking at more than 167,000 kg) and between 1943 and 1947 (peaking at 121,000 kg) (Supplement 1) (43). Through the late 1980s, during most years, the annual average landings were relatively low at around 45,000 kg, with prices hovering around 10 cents per pound. By the late 1980s, the commercial fishery for sheephead markedly increased, fueled by the live seafood market for Asian commerce and restaurants, both domestic and abroad. By 1990, the commercial catch quadrupled and, by 1997, was at 166,000 annual kg with a market value of over \$840,000 (43). At about the same time, spikes in the recreational sport fishery markedly increased, reaching an estimated maximum peak of 203,500 kg in 1986 (43). Today, the sport fishery outpaces the commercial fishery, and sheephead, once considered a trash fish, are now a targeted species by anglers and spearfishers for their large sizes and tasty flesh.

In response to the largely unregulated live fish trade and increasing commercial pressures in the 1990s, the average sizes of sheephead and size at which sex changes from females to males occurred significantly decreased in southern California (27, 43). By the late 1990s, resource managers responded with minimum catch sizes of 30 cm (total length, ~12 inches) for the commercial and recreational fisheries. Tighter regulations followed in 2001, with minimum commercial harvest sizes set at 33 cm (~13 inches) and recreational bag limits reduced from 10 to 5. Today, the recreational fishery for sheephead is open year-round to divers and shore anglers, but only from March 1 to December 31 to boat anglers. Fishing is restricted to water depths <360 feet deep, and the daily bag limit is currently set at five fish, at least 12 inches (~30 cm) in total length (California Department of Fish and Wildlife, www.wildlife.ca.gov/Fishing/Ocean/Regulations/Fishing-Map/southern, accessed 3 June 2016).

With increasing fishing pressure over the past several decades, especially in southern California, California sheephead are considered a vulnerable species by the International Union for Conservation of Nature. One of the unique challenges of fisheries management for hermaphrodites is that commercial and recreational fisheries target the largest individuals, a process that is also driven by minimum harvest sizes. Because most of these large fish are males, size-selective fishing can cause shortages in males, triggering the morphogenesis of the largest females to males. As this process accelerates, smaller and younger

females convert to males at increasingly smaller sizes (27). This creates a deficiency in the number of eggs produced over the lifetime of a fish and can trigger overall reductions in the population structure (27). In addition, fishing can alter predator-prey interactions and the ecological role of sheephead in kelp forest systems by removing the large fish that disproportionately consume sea urchins, large crabs, and gastropods (23, 39).

Management of California sheephead populations continues to pose serious challenges for state management agencies. One of the major challenges is the lack of data on the size and abundance of sheephead in the centuries to millennia before the arrival of Europeans and the establishment of commercial fisheries. Because little is known about the fishery before the early 20th century, setting appropriate restoration baselines that consider the effects of heavy commercial and recreational catches is problematic when only consulting historical catch records. Zooarchaeological data from the northern Channel Islands can provide the long-term ecological records necessary for better understanding what a healthy population of California sheephead should look like, predating the heavy historical fishing that began in the late 1920s and accelerated in the late 1980s.

Environmental and cultural background

The northern Channel Islands consist of four offshore islands, from east to west: Anacapa, Santa Cruz, Santa Rosa, and San Miguel (Fig. 1). Nearshore marine ecosystems surrounding the islands are exceptionally productive and diverse (44). Intensive local upwelling, a mix of cold northerly and warm southerly currents, and high primary productivity combine to create marine ecosystems that are home to diverse plants and animals, including kelps, shellfish, birds, fishes, and marine mammals.

Maritime hunter-gatherers in boats first settled the northern Channel Islands at least 13,000 years ago (45, 46). Over the ensuing millennia, these small colonizing groups transformed into the large, sedentary populations of Chumash Indians that were first contacted by Spanish explorers in 1542 CE. Zooarchaeological analyses detail a general shift from early subsistence systems focused on low-trophic level shellfish to an increasing reliance on higher-trophic level finfish and pinnipeds after about 1500 calibrated years before the present (cal B.P.) (47–49). The Chumash protein economy shifted to an intensive focus on finfishes during the time interval that archaeologists have labeled the Late Period (650 cal B.P. to 1542 CE), a cultural subdivision of the Late Holocene. By this time, the Chumash had developed a sophisticated set of maritime hunting and gathering technologies; occupied large, year-round villages; and created a complex sociopolitical system. Spanish explorers marveled at the large-scale harvest of local marine resources and the shell bead trading network that formed the basis of geopolitical connections from the islands to coastal and even inland mainland areas (50, 51). Although archaeologists have identified a gradual process of subsistence shifts due to natural climatic changes, growing populations and human predation pressure, and technological innovations, the bulk of the Island Chumash protein diet came from nearshore and kelp forest fishing by the time the Spanish arrived in the Santa Barbara Channel. Zooarchaeological evidence suggests that California sheephead were an important component of Chumash fisheries for more than 10,000 years (52).

Collectively, these data provide a cultural and environmental context for our analysis, with a focus on five general time periods. The Early and Middle Holocene were intervals when the bulk of maritime proteins for humans were generally derived from shellfish (53). The Early/Middle Period (3500 to 650 cal B.P.) was an interval of increased reliance on

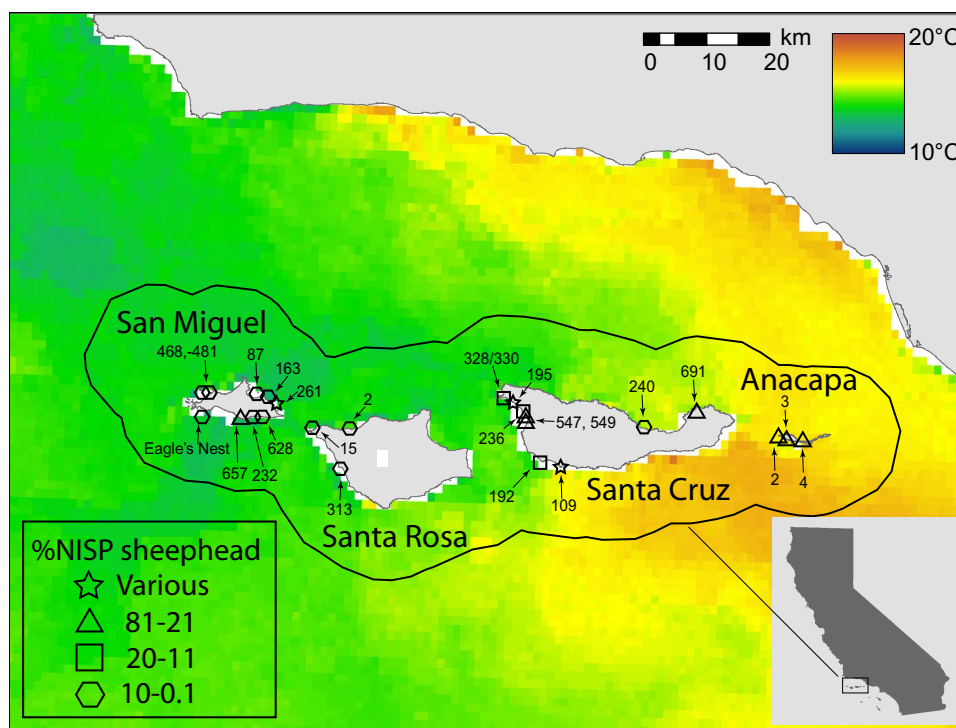


Fig. 1. Location of northern Channel Island archaeological sites with sheephead remains identified to species. Sea surface temperature (SST) gradient represents mean SST for a 10-year period from June 2006 to June 2016 (93). Relative abundances of sheephead are reported as a percentage of the total fish NISP (base map courtesy of L. Reeder-Myers). Note that site locations are approximate due to confidentiality concerns of Channel Island National Park.

nearshore and kelp forest fishing. The Late Period is marked by intensive marine fishing economies and the zenith of Chumash population densities. The Historic Period is a time of transition from Chumash occupations through the 1820s to Chinese and Euro-American fisheries of the 19th and 20th centuries. The Modern Period is characterized by recent recreational and commercial fisheries.

RESULTS AND DISCUSSION

California sheephead populations through time and across space

California sheephead remains are distributed across the northern Channel Islands (Fig. 1), including 16 assemblages (42.9%) from nine sites on Santa Cruz Island, 11 assemblages (31.4%) from nine sites on San Miguel Island, 6 assemblages (17.1%) from three sites on Santa Rosa Island, and 3 assemblages (8.6%) from three sites on Anacapa Island. In 10 of the assemblages (28.6%), sheephead rank first in abundance by NISP (number of identified specimens), and in 8 assemblages, sheephead rank between second and fourth (Table 1), indicating that this species was likely both highly abundant in the environment and an important target of fishing activities by native peoples in kelp forests around the Channel Islands. Although sheephead rank relatively low (that is, 14 of 35 rank lower than fifth) in some of the assemblages, there is evidence for long-term continuity in the ancient fishery because of the evidence of exploitation during all time periods from about 10,200 years ago until historical times.

There are strong geographic differences in %NISP of sheephead among the northern Channel Islands that are relatively consistent across time periods (Fig. 1 and Table 1). Sheephead were more abundant in the samples from Anacapa (mean %NISP = 48.2%) and Santa Cruz (mean %NISP = 30.2%) islands than in the samples from Santa Rosa (mean %NISP = 1.2%) and San Miguel (mean %NISP = 7.6%) islands across multiple time periods. However, there are some important chronological gaps in the record that require some caution in interpreting the geographic patterns of abundance. Because of Anacapa Island's small size and limited occupational history, only three sites dating to the Early/Middle Period (3500 to 650 cal B.P.) of the Late Holocene produced sheephead remains, although ANI-2 yielded the third largest number of sheephead bones in any assemblage. Early and Middle Holocene assemblages with sheephead bones are missing from Santa Rosa Island, and Late Period (650 cal B.P. to 1542 CE) assemblages are absent from San Miguel Island. Although natural environmental changes could have differentially influenced sheephead populations on different islands, the most parsimonious explanation for the geographic cline in abundance is that sheephead were less abundant at the western islands in ancient times, not that the Chumash targeted them less in that region. Higher sheephead densities in the eastern than the western islands align with modern biogeographic distributional trends (34, 39, 54), likely driven by the strong gradient in temperatures and environmental conditions that exist across the northern Channel Islands (Fig. 1) (55, 56). In addition, San Miguel and Santa Rosa are near the purported historical species range boundary of sheephead at Point Conception, where water temperatures around San Miguel Island and into central California are likely too cool to sustain breeding populations. The current extension of the sheephead range up to Monterey is likely a relatively modern phenomenon in response to strengthening El Niño Southern Oscillation events and the influence of climate change on larval dispersal and survivorship (30).

Table 2 summarizes the chronological distribution of California sheephead remains along the northern Channel Islands. Given a number of geographic gaps in this sequence, we pooled the data channel-wide to examine broad-scale temporal trends in fishing pressure. The relative abundances of sheephead remained reasonably consistent through time, with sheephead contributing between about 10 and 50% of the fish NISP over much of the past 10,000 years (Fig. 2). However, declines in the relative importance of sheephead to the finfish diet of Chumash people are evident during the Late Holocene (3500 cal B.P. to 1542 CE), especially during the Late Period (650 cal B.P. to 1542 CE) of the Late Holocene. This is likely due to intensified fishing activity during this interval as the Chumash focused their protein subsistence on finfishes to feed growing populations in swelling coastal villages (47, 49, 50). It is during this interval that large-scale net fishing in kelp forests accelerated along the Santa Barbara Channel (57, 58); although sheephead likely remained an economically important resource, their importance is overshadowed by the increased reliance of mass-harvested, netted fish species, such as surfperch.

California sheephead size through time

A modest sample size ($n = 202$) of ventral pharyngeals provides information on the average sizes of sheephead between about 3200 cal B.P. and 1820 CE. For the entire archaeological sample, data indicate a mean sheephead total length of 458.4 ± 111.4 mm, a minimum of 265.1 mm, and a maximum of 836.0 mm. During the Middle Period on Anacapa, the mean sheephead total length is 422.8 ± 91.8 mm. During the Historic Period on Santa Cruz Island, the mean sheephead total length was 542.5 ± 110.5 mm (Supplement 2). The average size of sheephead caught off the northern Channel Islands in the past was ~154 mm (33.6%) larger than modern minimum size requirements (305 mm) mandated by recreational fishing regulations.

The ancient sheephead fishery on the northern Channel Islands can be compared with fish collected in 2007–2008 from Anacapa, Santa Cruz, and Santa Rosa islands in waters outside of marine protected areas (MPAs), which had a mean total length of 391.4 ± 101.7 mm ($n = 151$), with a maximum size of 869 mm and a minimum size of 253 mm. The mean modern sheephead sample is 67.0 mm smaller than our total ancient sample. Our modern sample is 31.4 mm smaller than the average size of our Late Holocene sample (422.8 ± 91.8 mm) from Anacapa Island and 151.1 mm smaller than the average of our Historic Period sample from Santa Cruz Island (see Fig. 3 and Supplement 3). There is a statistically significant difference between the average size of ancient sheephead (458.4 ± 111.4 mm) and modern sheephead (391.4 ± 101.7 mm, $n = 151$) ($t_{351} = 5.81$, $P < 0.001$), which represents a 14.6% reduction in size in modern sheephead relative to their ancient counterparts; Cohen's d for effect size (59) is 0.62, which is moderate. When sheephead length frequency is paired with size spectra analysis and compared between ancient and modern samples, both analyses demonstrate that ancient populations skew toward larger sheephead (Fig. 4). The highest frequencies from the ancient sample are between 400 and 449 mm, whereas the highest frequencies of the modern population are between 300 and 349 mm. Every size class above 400 mm in total length was represented disproportionately more in ancient samples, whereas size classes of less than 350 mm in total length were more greatly represented in the modern samples. For the size spectra analysis, sheephead abundance declines with standardized body mass size class [analysis of covariance (ANCOVA); $F_{1,12} = 10.3$, $P = 0.0076$] because larger fish are less commonly observed in the population. The rate of decline of large fish (that is, the slope) is more negative for the modern [$y = -0.28x +$

Table 1. California sheephead remains in northern Channel Island archaeological sites, arranged by island west to east. MNI, Minimum Number of Individuals.

Site	Provenience	Age (cal B.P.) $\pm 1\sigma$	NISP	%NISP	MNI	%MNI	NISP rank	Reference
San Miguel Island								
SMI-261	Stratum F	10,150–8980	126	7.7	25	14.0	4	(52)
SMI-261	Stratum E	9030–8480	27	12.3	8	14.5	3	(52)
SMI-657	Col. 1, Unit 1	6750–6280	35	47.3	2	18.2	1	(49)
SMI-628	Col. 1, Unit 1	4520–3830	11	6.6	1	2.4	5	(49)
SMI-87	West Unit	3200–2860	2	1.1	2	7.1	6	(50)
SMI-232	Col. 2, Unit 1	1290–1070	36	1.0	10	5.8	9	(49)
SMI-481	Unit 1b	1260–1070	12	0.8	5	6.3	8	(50)
SMI-468	Unit 2	1150–1040	9	3.5	2	8.7	6	(50)
SMI-468	Unit 1	910–720	14	1.3	2	2.7	9	(50)
SMI-163	Unit 2	Historical	7	0.6	3	4.8	9	(50)
Eagle Nest	Unit 1	Historical	55	1.4	3	3.3	6	(60)
Santa Rosa Island								
SRI-15	Unit 1, 2	1190–480*	1	0.1	—	—	13	(94)
SRI-2	Unit 2, Str. 3	1030–880	17	4.0	2	10.5	5	(50)
SRI-313	Col. 1	775–565*	5	0.8	—	—	8	(94)
SRI-2	Unit 2, Str. 2	480–410	1	0.1	1	2.1	12	(50)
SRI-2	Unit 2, Str. 1	Historical	9	1.6	1	5.3	6	(50)
SRI-2	Unit 1	Historical	14	0.8	3	6.5	6	(50)
Santa Cruz Island								
SCRI-691	Unit 1, 2 and Col. 1, 2	10,090–8860	13	81.3	—	—	1	(72)
SCRI-547	Unit 1	8520–8415	4	66.7	—	—	1	(72)
SCRI-549	Col. 2	8530–8100	3	42.9	—	—	1	(72)
SCRI-109 [†]	South, Str. II	8060–7550	48	90.6	—	—	1	(71)
SCRI-109	South, Str. III	7625–5835	72	43.9	—	—	1	(71)
SCRI-109	North, Str. C	6395–4840	144	11.6	—	—	3	(71)
SCRI-109	North, Str. D	5680–5565	20	12.3	—	—	3	(71)
SCRI-109	South, Str. V	5430–5250	111	24.9	—	—	1	(71)
SCRI-109	South, Str. VI	2115–1915	21	27.3	—	—	2	(71)
SCRI-195	Col. 1, 2	Middle Period [‡]	55	2.0	—	—	10	(73)
SCRI-195	Col. 1, 2	Late Period [‡]	2	0.7	—	—	12	(73)
SCRI-192	Houses 4/8	Historical	1650	15.8	—	—	3	(74)
SCRI-236	Houses 5/9	Historical	338	10.7	—	—	3	(74)
SCRI-240	House 1	Historical	400	7.1	—	—	5	(74)
SCRI-328/330	Houses 1/5/10/13	Historical	124	15.0	—	—	3	(74)

continued on next page

Site	Provenience	Age (cal B.P.) ± 1σ	NISP	%NISP	MNI	%MNI	NISP rank	Reference
Anacapa Island								
ANI-2	Unit 1/2	3200–2740	342	42.0	—	—	1	This study
ANI-3	Unit 1	3300–3160	46	54.1	—	—	1	This study
ANI-4	Unit 1	3230–3080	87	48.6	—	—	1	This study

*Radiocarbon date reported as a 2σ cal B.P. range by Jazwa (94). †Additional Early Holocene sheephead data available from SCRI-109 in the study by Gusick (72); however, these data were not included here. ‡See Gusick *et al.* (73) and Table 2 for radiocarbon chronology.

Table 2. Temporal distribution of California sheephead remains from northern Channel Island archaeological sites. The complete fish bone assemblage from CA-ANI-2, Unit 1/2 was not analyzed, but additional ichthyological analysis is unlikely to change the general patterning.

Time period	Age range	n of sites	n of assemblages	ΣNISP of sheephead	%NISP of sheephead
Early Holocene	10,200–7500 cal B.P.	5	6	221	11.2
Middle Holocene	7500–3500 cal B.P.	3	6	393	17.5
Early/Middle Period	3500–650 cal B.P.	12	13	647	4.8
Late Period	650 cal B.P.–1542 CE	2	2	3	0.2
Historic Period	1542–~1825 CE	7	8	2597	9.4

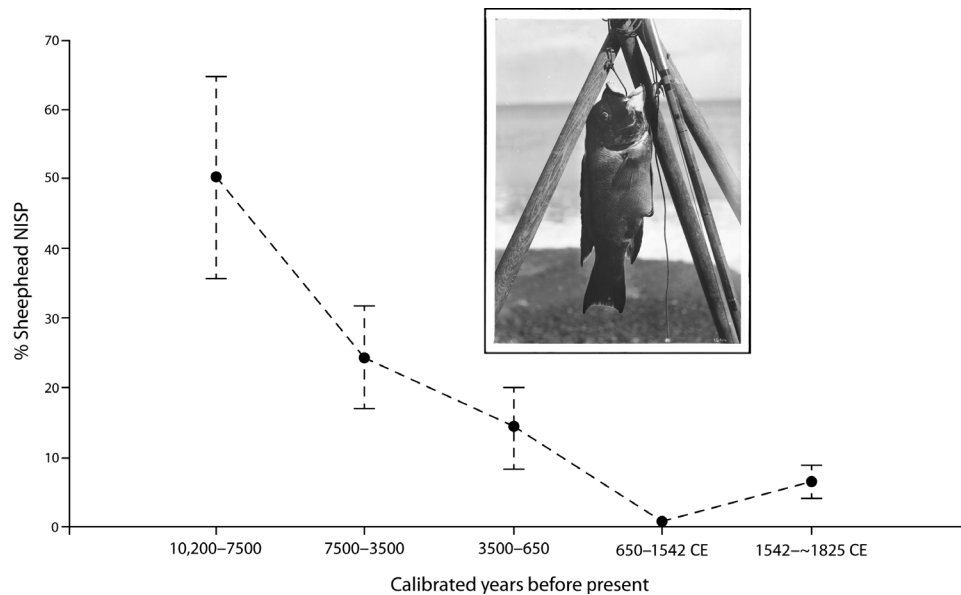


Fig. 2. Change in relative abundance of sheephead remains in archaeological sites on the northern Channel Islands through time. Sheephead abundance is represented by average %NISP with SE per time period from Table 2. Inset: Image of a male California sheephead likely captured from southern California in ca. 1910 CE (open access image via Wikimedia Commons).

0.79 ($r^2 = 0.87, P < 0.0001$) versus archaeological samples [$y = -0.22x + 1.14 (r^2 = 0.96, P < 0.0001)$]. These results indicate that large fish drop out of the population more quickly in the modern samples, although the relationship is not statistically significant (ANCOVA; time period*size class: $F_{1,12} = 1.1, P = 0.31$). However, the midpoint (intercept) is significantly lower in the modern sample (ANCOVA; time period: $F_{1,12} = 108.8, P < 0.001$), indicating that medium- to large-

sized fish are underrepresented compared to smaller size classes, likely the result of intensive fishing pressure.

California sheephead ecology through the lens of stable isotopes

Bone collagen $\delta^{13}C$ and $\delta^{15}N$ values of sheephead from archaeological sites on San Miguel and Anacapa islands are presented in Fig. 5 and

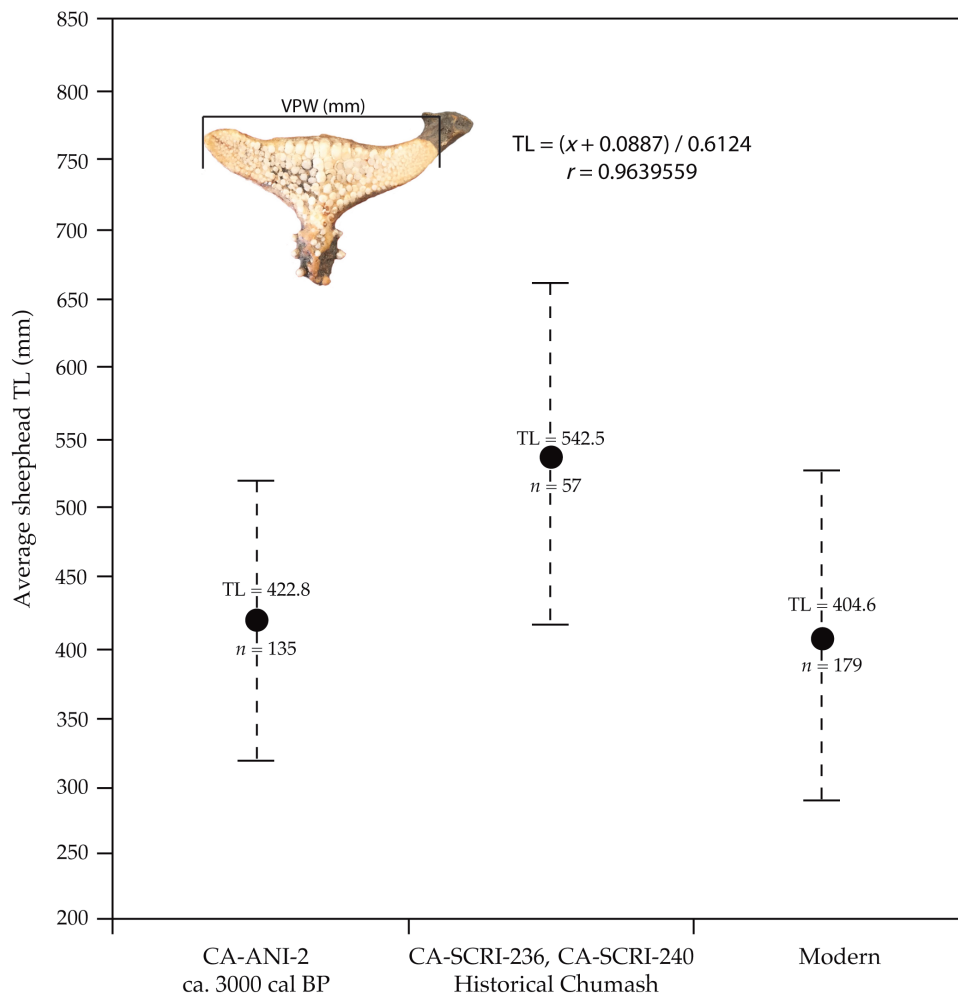


Fig. 3. Change in mean total length (TL) of sheephead through time. Dots represent means, and error bars represent SDs. Inset: Image of a California sheephead pharyngeal showing the measurement used to obtain these data. Data are derived from Supplement 2 (table S1).

summarized in table S7, along with modern sheephead from Anacapa Island collected in 2007 and historical (early to mid 20th century) sheephead from San Miguel Island (60). Because we are analyzing the same tissue type (bone collagen) from sheephead over time, our approach constrains any possible effects from differences in isotopic incorporation (turnover) rates and trophic discrimination factors among tissues (61, 62). $\delta^{15}\text{N}$ values of the sheephead from ANI-2 ($+14.3 \pm 0.8\text{‰}$) and SMI-232 ($+14.7 \pm 0.5\text{‰}$) are very similar to the modern Anacapa ($+13.6 \pm 0.3\text{‰}$) and historical San Miguel ($+13.7 \pm 0.4\text{‰}$) sheephead values, suggesting that the trophic level of the species has remained similar over time. In contrast, the $\delta^{13}\text{C}$ values of the archaeological San Miguel sheephead (SMI-232) are ~ 2 to 3‰ higher than the early 20th century individuals from the same island, as well as any other modern sheephead population that has been analyzed to date (34, 39) even when one corrects for tissue-specific trophic discrimination factors between bone collagen and muscle. Overall, these data suggest that carbon derived from kelp, which is enriched in ^{13}C relative to phytoplankton (63, 64), was of greater importance to SMI-232 sheephead than to modern individuals from San Miguel Island. Specifically, sheephead from SMI-232 (~ 1200 cal B.P.) likely fed to a much greater extent on kelp grazers, such as sea urchins, rather than on filter feeders, such as clams and

barnacles. In addition, the large differences in sheephead $\delta^{13}\text{C}$ values between SMI-232 and ANI-2 suggest significant spatial variation in the importance of kelp-derived subsidies to nearshore subtidal ecosystems across the northern Channel Islands, reflecting geographic differences in the diet reported recently for modern samples (32). At this time, we cannot rule out that the observed east-west gradient in ancient sheephead $\delta^{13}\text{C}$ is driven by temporal changes in baseline carbon isotope values or sheephead diet because these archaeological sites are not coeval. The trend could also be explained by higher sheephead density and, thus, foraging competition in the warmer, easterly waters along the Santa Barbara Channel.

Although the archaeological sheephead from Anacapa (ANI-2, ~ 3000 cal B.P.) had mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that were similar to modern individuals from this island (Supplement 4), the isotopic standard ellipse area (SEA) of the ancient sample (4.1‰^2) is an order of magnitude larger than its modern counterpart (0.4‰^2), indicating that sheephead from ancient times had a broader and more diverse diet. The ANI-2 population also had a significantly larger SEA than any other sheephead population for which bone collagen isotope data are available (table S7). Hamilton *et al.* (39) reported that the dietary niche, as reflected in SEA, of sheephead from San Nicolas Island expanded markedly between 1998 and

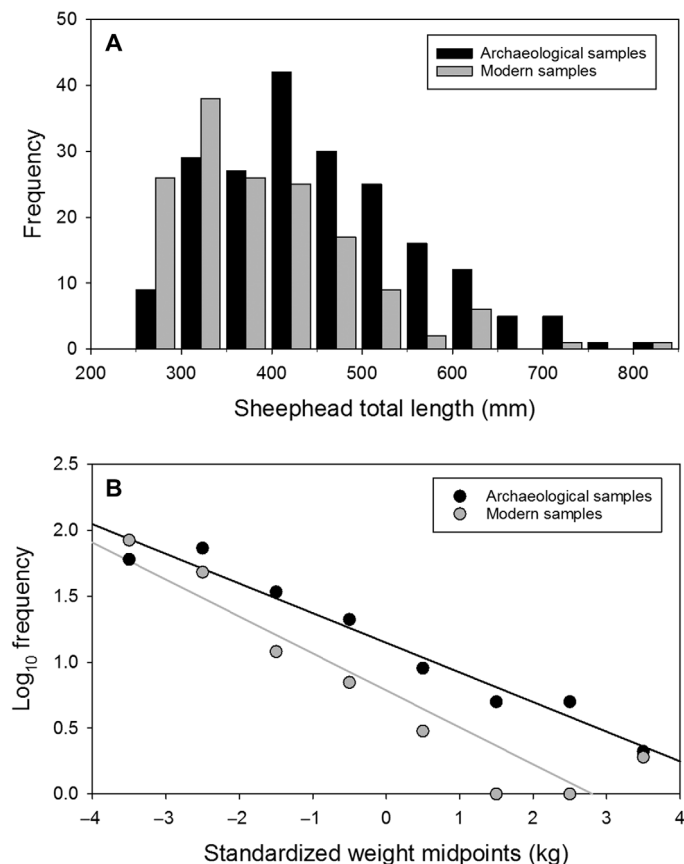


Fig. 4. California sheephead size through time along the northern Channel Islands. (A) Size distribution of California sheephead from the northern Channel Islands. Black bars are from archaeological samples, and gray bars represent modern samples collected during 2007 and 2008 (for data, see Supplements 2 and 3). (B) Size spectra analysis using the estimated weights of sheephead from archaeological and modern samples.

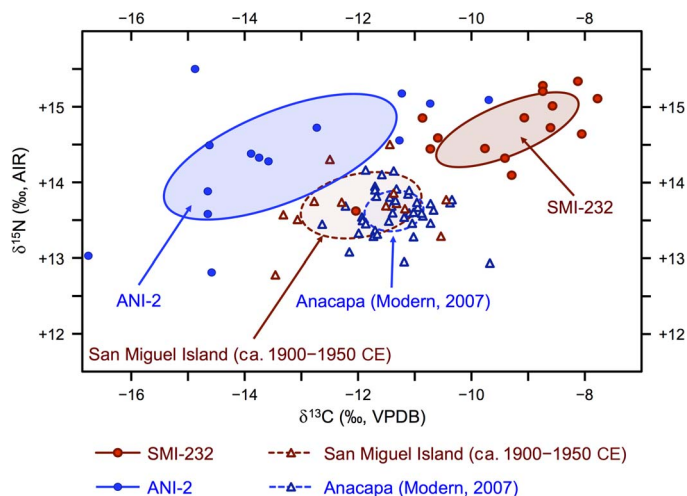


Fig. 5. Dietary shifts in California sheephead through time across the northern Channel Islands. Carbon and nitrogen isotopic compositions for archaeological sheephead bone collagen from ANI-2 (filled red circles) and SMI-232 (filled blue circles), modern sheephead bone collagen from Anacapa Island (open blue triangles), and historic sheephead bone collagen from San Miguel Island (open red triangles) (for data, see Supplement 4). The shaded ellipses represent the standard bivariate ellipse areas for each of the four groups.

2007, coincident with the recovery of size structure in that population following a period of intense size-selective harvest. In a similar fashion, the reduction in dietary niche observed at Anacapa Island through time is potentially related to fishery-induced decreases in the mean size of the sheephead or alternatively to reductions in prey diversity as a result of ecosystem-wide human impacts or environmental changes in modern times.

In contrast, the dietary niche of SMI-232 sheephead (1.4‰²) was similar to the early 20th century sheephead from San Miguel Island (1.4‰²) and much lower than the ANI-2 sample (Fig. 5 and Supplement 4). This disparity in dietary niche between ANI-2 and SMI-232 is likely driven by differences in prey availability between Anacapa and San Miguel because sheephead diets are known to be geographically variable and influenced by local prey availability (30, 32). San Miguel Island is also remote and remained lightly exploited by fishermen during the early 20th century and earlier. The much larger dietary niche of the ANI-2 sheephead relative to a modern population from the same island indicates the potential for further dietary niche expansions to occur in sheephead populations at other locations in the Channel Islands if and when they recover from recent harvesting activities. Our isotope data indicate that predator-prey interactions and the ecological role of sheephead in kelp forests have been altered by fishing activities for much longer than most resource managers realize. It is also important to note that the variation in temporal scale represented by the archaeological, historical, and modern samples may exaggerate, to some extent, the magnitude of the difference in dietary diversity between archaeological and modern populations. Additional isotopic studies of archaeological sheephead will help to determine the geographic and temporal variation in the importance of kelp-derived carbon and sheephead dietary niche throughout the Channel Islands.

CONCLUSION: THE FUTURE OF THE SOUTHERN CALIFORNIA SHEEPHEAD FISHERY

Chumash fishers captured sheephead both below and above modern minimum catch sizes during the Middle and Historic periods (see Supplement 2). At Anacapa (ANI-2), for example, the smallest sheephead measured 265.1 mm, and at Santa Cruz (SCRI-236 and SCRI-240), the smallest sheephead measured 269.7 mm, well below the modern size restrictions of 305 mm. In total, 10 sheephead (7.4%) from ANI-2 measured below current size minimums, although only a single individual measured below restrictions from historical deposits. The average size of sheephead along the northern Channel Islands today is significantly smaller than in the deep past. This may be due to the targeting of large sheephead by modern commercial and recreational anglers, which has culled many of the largest fish from the modern population. This is especially evident when the modern size population structure is compared to the population structure in the deep past. These findings are supported by our isotopic results, which suggest that the modern population of southern California sheephead has undergone demographic and dietary changes as the result of intense fishing. Consistent with the findings of several modern sheephead studies, reduced sizes (and ages) due to modern commercial fishing pressure seem to have resulted in reduced fecundity and diminished reproductive outputs (27, 39, 53, 65, 66) and an altered ecological role for this predator in kelp forest ecosystems (23, 39).

The integration of deep historical data sets stands to offer important management lessons for the future of the southern California

sheephead fishery and other at-risk nearshore fisheries around the world. Zooarchaeological and isotopic evidence for the sheephead fishery over the past 10,000 years offers hope for the restoration and sustainability of the fishery. There is considerable evidence for the long-term continuity and stability of sheephead populations in the northern Channel Islands, in terms of both relative abundances and average sizes. Relative abundances and mean sizes of sheephead fluctuated through time, suggesting that there are multiple baselines that might be applied to modern management and that the true baseline extends beyond 10,000 years. The general pattern is that the ancient fishery was relatively sustainable and productive through time despite intensive and sustained indigenous fishing pressure. Technological limitations may have facilitated the ecological resilience of this species because Chumash fishers likely captured sheephead by hook and line from indigenous watercraft or through spearing (67). Broad-based Chumash fishing economies that targeted a range of finfish species and shellfish, seals and sea lions, and other organisms may have also lessened the pressure on sheephead. Their fishery practices were not biased toward the largest males (as is the modern sport fishery) and probably allowed refugia populations of older, more fertile females in deeper waters and more remote and exposed locations that were not accessible with their fishing techniques.

An essential component of building effective restoration baselines involves looking into the past and consulting archaeological data. Zooarchaeological and isotopic data suggest that ancient sheephead populations were larger and may have had broader dietary niches, affecting predator-prey interactions in kelp forests. These findings suggest that it may be time to rethink minimum size limits for sheephead and other fishes with hermaphroditic mating systems and skewed sex ratios. A strategy that mirrors Chumash fishing practices that is based on hook-and-line fishing, targets a broader array of sheephead sizes, allows for refugia populations, and maintains a more balanced population structure of fish that are young and old or male and female may be more sustainable. This may lend support for MPAs, which, in many ways, help create these deep historical ecological conditions and now protect ~15% of the southern California coastline (www.wildlife.ca.gov/Conservation/Marine/MPAs/Network/Southern-California). However, such a determination will require continued study that increases the sample sizes of archaeological sheephead remains. Thus, these data may help to further elucidate the dietary patterns and population structure of ancient sheephead and can then be compared against modern data to help us more effectively assess sheephead stocks and build more accurate management baselines. These findings provide broader lessons to fisheries and other environmental management, demonstrating the power of archaeological and deep historical perspectives as well as indigenous knowledge in helping develop sustainable approaches to conservation and restoration (68–70).

MATERIALS AND METHODS

Zooarchaeological samples and methods

We conducted a systematic literature review of published and unpublished sources to synthesize the zooarchaeological record of California sheephead fishing along the northern Channel Islands; sources are listed in Table 1. This resulted in data from 35 temporally distinct ichthyofaunal assemblages recovered from 24 northern Channel Island archaeological sites, including one historical bald eagle's nest on San Miguel Island. The largest trans-Holocene sample of sheephead

remains comes from Santa Cruz Island, where Glassow *et al.* (71) analyzed Early (10,000 to 7500 cal B.P.), Middle (7500 to 3500 cal B.P.), and Late (3500 cal B.P. to 1542 CE) Holocene samples from the Punta Arena site on the island's southwest coast. Gusick (72) and Gusick *et al.* (73) analyzed Early and Late Holocene deposits, respectively. Noah (74) analyzed historical age deposits (~1542 to 1825 CE) from a series of large coastal Chumash villages. Research on San Miguel Island has produced smaller sample sizes but similar temporal coverage from sites spanning ~10,000 years ago to historical times, including the remains from a bald eagle's nest dating from the early to mid 20th century (60, 75). Santa Rosa and Anacapa island data sets are relatively small, with three sites on each island producing Late Holocene to historical samples. Despite some temporal and spatial gaps, the California sheephead fishing record spans 10,000 years and the entire breadth of the Santa Barbara Channel.

Radiocarbon (^{14}C) ages were reported in calibrated years before the present (cal B.P.) as calendar ages, with the present defined as 1950 CE. Age ranges were reported at 1 SD from the mean. Because the amount of atmospheric ^{14}C has not remained constant through time, radiocarbon years are not equivalent to calendar years. Thus, all radiocarbon dates use the calendar age either reported by the cited authors or calibrated using Calib 7.1 (76).

In general, California sheephead remains are highly distinctive and relatively easy to identify by trained zooarchaeologists, especially cranial elements. All sheephead bones come from shell midden sites, most of which contain dense concentrations of faunal remains. Like all archaeological deposits, a variety of taphonomic processes, mostly wind and marine erosion, have affected Channel Island archaeological sites and faunal assemblages (77). However, archaeological sites on the Channel Islands are generally well preserved and lack pocket gophers and other primary burrowing animals and major construction activities that have mixed and fragmented shell middens from many sites on the California mainland.

We provide the site number and age for all known archaeological localities with sheephead remains and the total NISP (Table 1). We also determined the percentage that sheephead contributed to the total fish NISP of all taxa identified to family, genus, or species, as well as the rank abundance of sheephead compared to all other fish taxa. To investigate the changes in sheephead abundance through time, we grouped assemblages by culturally important time periods and determined the %NISP of sheephead within the total fish assemblage by time period. When available, we provide the Minimum Number of Individuals (MNI) sheephead and the %MNI relative to other species identified in a given assemblage. However, many zooarchaeologists rely on NISP in zooarchaeological analyses and do not report MNIs. Therefore, our meta-analysis relies on NISP as a proxy for sheephead abundance.

After controlling for the volume of excavated material, we assume that an increase in the relative abundance of sheephead remains through time signals an increase in human harvesting pressure. To assess the degree of harvest pressure and the size of sheephead through time, we used a sheephead-specific regression (78, 79) to estimate total fish length from measurement of the ventral pharyngeal maximum width. Because the ventral pharyngeal is a dense bone, it tends to preserve well in archaeological deposits, and only one such element is found in each sheephead, ensuring that individual fish are not included in our analysis more than once.

Measured sheephead pharyngeals were available for deposits on Anacapa (ANI-2; $n = 135$) and Santa Cruz (SCRI-109, SCRI-236,

SCRI-240, and SCRI-823; $n = 67$) islands and for Middle Holocene ($n = 2$), Late Holocene ($n = 143$), and Historic Period ($n = 57$) assemblages. Total sheephead length was calculated using the formula

$$TL = (x + 0.0887)/0.6124$$

where TL is the total sheephead length (in centimeters) and x is the ventral pharyngeal maximum width (in millimeters) [see the work by Salls and Bleitz-Sanburg (79) and also the studies by Blick (80) and Carder *et al.* (81)]. Boyer-Sebern (78) found a strong relationship between pharyngeal width and total length ($r = 0.96$). A t test was used to examine whether sheephead size structure shifted during the ancient Chumash and modern fishery. Data on modern sheephead size were collected in 2007 and 2008 from waters surrounding Anacapa ($n = 59$), Santa Cruz ($n = 76$), and Santa Rosa ($n = 44$) islands outside of MPAs, mostly by spearfishing and some by hook and line and trapping. During spearfishing, all sheephead encountered were targeted in an effort to collect an unbiased modern size sample. For the size spectra analysis, we used the length-weight equation for sheephead

$$\text{Weight (g)} = [0.0144 \times \text{TL (cm)}]^{3.04}$$

to convert the length of each sample into a weight (82–85). Then, the samples were binned into 1-kg weight bins, and the frequency was counted. The log of the frequency of each size bin was plotted against the standardized weight class. The slopes of the size spectra were calculated from linear regressions of $\log_{10}(x + 1)$ frequency per size class versus the rescaled (that is, standardized) midpoint of each weight class. Centering of the independent variable gives a value for midpoint height as opposed to the intercept (83), which removes the correlation between slope and intercept. The midpoint height is effectively an index of abundance, whereas the slope is an index of how quickly numbers decline with increasing size/age in the population (83). Size spectra for the two time periods were compared statistically using ANCOVA, with time period as a fixed factor and standardized weight class as the covariate.

Stable isotope samples and methods

To assess changes in diet between modern and ancient sheephead populations, we measured carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values of collagen extracted from sheephead bones from ANI-2 ($n = 14$) and SMI-232 ($n = 15$). $\delta^{13}\text{C}$ values provide information about the sources of primary production in nearshore marine ecosystems, which, in this region, is derived from a combination of macroalgae (including kelp) and phytoplankton (64, 86). Nitrogen isotopes provide information about trophic level because $\delta^{15}\text{N}$ values increase by ~ 3 to 5‰ per trophic level (87). We quantified the isotopic niche of ancient and modern sheephead using SEAs (‰²) with the R package Stable Isotope Bayesian Ellipses (SIBER) (84), which are robust measures of isotopic niche for sample sizes of ≥ 10 (88). For comparisons between modern or historical and archaeological isotopic data, $\delta^{13}\text{C}$ values were adjusted to account for changes in the carbon isotope composition of ocean dissolved inorganic carbon from the burning of fossil fuels. The rate of change in $\delta^{13}\text{C}$ values has increased markedly in recent decades relative to the early 20th century (89), and accordingly, historical (early 20th century) sheephead $\delta^{13}\text{C}$ values were adjusted by +0.4‰ and modern (ca. 2000s) values were adjusted by +1.5‰ (90).

Bone collagen was extracted and purified using a modified version of the method presented by Beaumont *et al.* (91). Chunks of bone weighing ~ 0.5 g were removed using a dental drill equipped with a diamond-tipped cutting wheel. The exterior surface of the sample was cleaned with a toothbrush and Millipore water (18.2 megohm-cm). The bone samples were then sonicated three times in 2:1 chloroform/methanol for 30 min, with the solution changed each time. Samples were air-dried and then treated with 0.5 M HCl at 4°C until the bone was fully demineralized. After demineralization, the samples were rinsed to neutrality with type II water and then sonicated in 0.1 M NaOH for successive 1-hour treatments (solution refreshed every 1 hour) until the solution no longer changed color. After these treatments, the samples were rinsed to neutrality with type II water and then heated at 75°C for 48 hours in 10^{-3} M HCl (pH ~ 3) to gelatinize the collagen. The solution containing the water-soluble collagen was then filtered with 60- to 90- μm EZ filters (Elkay Laboratory Products) to remove sediments and other large, insoluble particulates. This solution was filtered using 10-kDa molecular weight cutoff filtered centrifuge tubes (Microsep, Pall Corporation) to remove low-molecular weight contaminants (92). The remaining >10 -kDa fraction was freeze-dried, and the collagen yield was calculated. Collagen samples were analyzed in duplicate with an IsoPrime continuous flow isotope ratio mass spectrometer coupled to a Vario Micro elemental analyzer (Elementar) at the University of British Columbia; see Supplement 4 for additional details on measurement calibration, analytical accuracy, and precision.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/3/2/e1601759/DC1>

Supplement 1. Sheephead commercial landings summary

fig. S1. Commercial landings of California sheephead from 1916 to 1999 [adapted from Stephens (43)].

Supplement 2. California sheephead sizes from archaeological samples

table S1. Sheephead ventral pharyngeal maximum width measurements and derived total length from Channel Island archaeological sites.

table S2. Raw data for measurements of ventral pharyngeal widths.

Supplement 3. Modern California sheephead measurements

table S3. Modern California sheephead total lengths collected by S.L.H. in 2007 and 2008 from waters surrounding Anacapa, Santa Cruz, and Santa Rosa islands.

Supplement 4. Stable isotope summary data, calibration, analytical accuracy, and precision

table S4. Summarized stable isotope and dietary niche results for SMI-232 and ANI-2 sheephead, modern and historical sheephead from Anacapa (2007 CE) and San Miguel (ca. 1900 to 1950 CE) islands, and modern sheephead from San Nicolas Island.

table S5. Standard reference materials used for calibration of $\delta^{13}\text{C}$ relative to VPDB and $\delta^{15}\text{N}$ relative to AIR.

table S6. Standard reference materials used to monitor internal accuracy and precision.

table S7. Mean and SD of carbon and nitrogen isotopic compositions for all check standards, as well as the SD for all calibration standards.

table S8. Duplicate sample carbon and nitrogen isotopic compositions and absolute difference between measurements.

table S9. All isotopic and elemental data for sheephead included in this study.

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Acknowledgments: We thank R. Galipeau, L. Kirn, A. Huston, and K. Minas (Channel Islands National Park) and C. Boser, D. Dewey, S. Morrison, and L. Laughrin (The Nature Conservancy and the University of California Santa Cruz Island Reserve) for their continued support of our research. H. Thakar provided sheephead size data for CA-SCRI-236 and CA-SCRI-823, and A. Gusick shared data on sheephead abundances for CA-SCRI-195, CA-SCRI-547, CA-SCRI-549, and CA-SCRI-691. **Funding:** This research was funded by the National Park Service (to T.C.R. for Anacapa Island archaeological fieldwork), the National Science and Engineering Council of Canada (to P.S. for isotopic analysis), California Sea Grant and the Ocean Protection Council (to S.L.H. for R/OPC-FISH05 modern sheephead collections), the National Oceanic and Atmospheric Administration (to S.L.H. for NA04OAR4170038 modern sheephead collections), and the San Diego State University (to T.J.B. for collections research). **Author contributions:** T.J.B. took the lead on conceptualizing the manuscript and writing the initial draft. All junior authors contributed data and data analysis: zooarchaeological data and analysis (T.C.R., J.M.M., and M.G.), isotopic data and analysis (P.S., S.D.N., E.A.E.S., and S.L.H.), and modern sheephead size data (S.L.H.). All authors helped draft the manuscript and assisted with multiple rounds of editing. T.C.R., J.M.M., and M.G. made major contributions to the archaeology, and P.S., S.D.N., E.A.E.S., and S.L.H. made major contributions to the isotopic work and fisheries science details. All authors have approved the final version of this manuscript and agree to be accountable for all aspects of the work. **Competing interests:** The authors declare that they have no competing interests. **Data and materials and availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data are available from authors upon request.

Submitted 28 July 2016

Accepted 18 December 2016

Published 1 February 2017

10.1126/sciadv.1601759

Citation: T. J. Braje, T. C. Rick, P. S. Zpak, S. D. Newsome, J. M. McCain, E. A. Elliott Smith, M. Glassow, S. L. Hamilton, Historical ecology and the conservation of large, hermaphroditic fishes in Pacific Coast kelp forest ecosystems. *Sci. Adv.* **3**, e1601759 (2017).

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Sci Adv 3 (2), e1601759.
DOI: 10.1126/sciadv.1601759

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