

Where were the northern elephant seals? Holocene archaeology and biogeography of *Mirounga angustirostris*

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Abstract

Driven to the brink of extinction during the nineteenth century commercial fur and oil trade, northern elephant seal (NES, *Mirounga angustirostris*) populations now exceed 100 000 animals in the northeast Pacific from Alaska to Baja California. Because little is known about the biogeography and ecology of NES prior to the mid-nineteenth century, we synthesize and analyze the occurrence of NES remains in North American archaeological sites. Comparing these archaeological data with modern biogeographical, genetic, and behavioral data, we provide a trans-Holocene perspective on NES distribution and abundance. Compared with other pinnipeds, NES bones are relatively rare throughout the Holocene, even in California where they currently breed in large numbers. Low numbers of NES north of California match contemporary NES distribution, but extremely low occurrences in California suggest their abundance in this area was very different during the Holocene than today. We propose four hypotheses to explain this discrepancy, concluding that ancient human settlement and other activities may have displaced NES from many of their preferred modern habitats during much of the Holocene.

Keywords

historical ecology, human–environmental interactions, marine conservation, Pacific Coast, pinniped, Phocidae

Introduction

Northern elephant seals (NES hereafter, *Mirounga angustirostris*) were nearly driven to extinction by commercial and recreational hunters during the nineteenth century fur and oil trade (Scammon, 1874: 119; Stewart et al., 1994). Despite limited genetic diversity (Bonnell and Selander, 1972; Weber et al., 2000, 2004), NES along North America's Pacific Coast are now thriving, with some 124 000 animals in the California stock alone (Carretta et al., 2009: 28). The recovery of NES populations is one of the success stories of marine conservation, demonstrating resilience despite decades of intensive slaughter (Stewart et al., 1994). Because of rapid decimation from commercial hunting, little is known about NES prior to the mid-nineteenth century, however, leaving a substantial gap in our understanding of their natural history, biogeography, and historical ecology.

In this paper, we synthesize all known occurrences of NES in northeastern Pacific Coast archaeological sites, including analysis of previously reported materials and new unpublished data (Figure 1). Other archaeological studies of seal and sea lion (pinniped) remains from Pacific Coast archaeological sites have noted the dearth of NES relative to other pinnipeds (e.g. Hildebrandt and Jones, 2002; Lyman, 2011). Our study is the first to focus solely on NES and to place these data within the context of ancient DNA analyses and modern behavioral data. Similar to earlier archaeological studies of northeastern Pacific pinnipeds (Braje et al., 2011; Etnier, 2007; Gifford-Gonzalez et al., 2005; Hildebrandt and Jones, 1992, 2002; Lyman, 1988, 2003; Moss et al., 2006;

Newsome et al., 2007; Rick et al., 2009), our goal is to document long-term trends in NES biogeography and abundance that can help inform their contemporary status.

Historical and modern NES distribution and behavior

NES are the largest pinnipeds in the northeastern Pacific, with males weighing up to 2300 kg and females 800 kg (Stewart and Huber, 1993). Formally described as a species by Gill (1866), NES were thought to be extinct by the late 1870s (Townsend,

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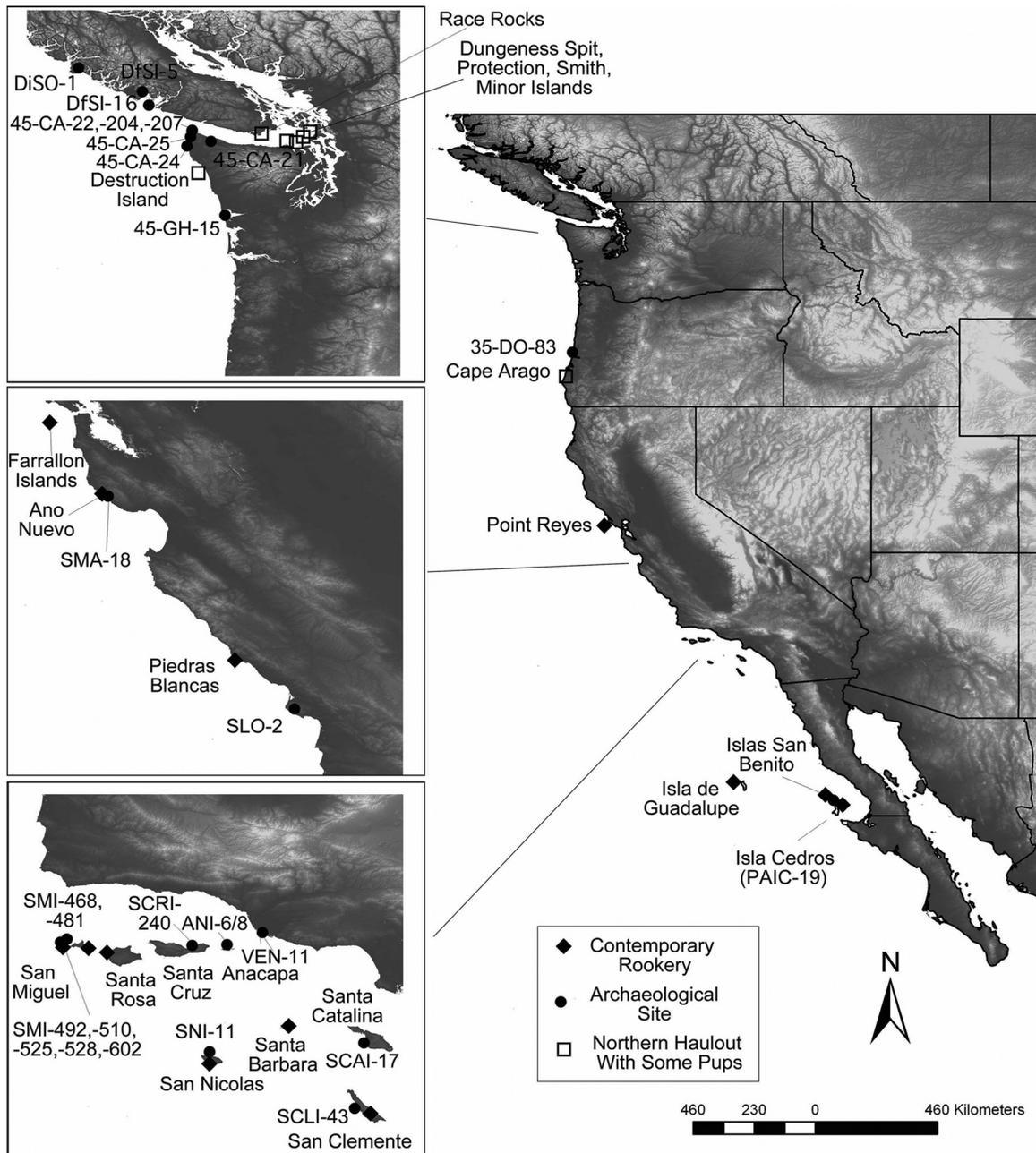


Figure 1. Western North America with inset of Channel Islands, central California, and Washington/Southern British Columbia showing the location of archaeological sites with NES remains and modern breeding colonies

1885) until a series of expeditions found and killed individuals on Isla de Guadalupe between 1880 and 1884 (Stewart et al., 1994: 30–31). They were again thought to be extinct until 1892 when Townsend and Anthony identified nine animals on Isla de Guadalupe and killed seven of them for the Smithsonian Institution’s collections (Anthony, 1924; Townsend, 1912). Through 1911 NES populations increased and ‘museum collectors continued to kill them’ (Stewart et al., 1994: 32), including 4 in 1904, 14 of 40 in 1907, and 10 of ~135 in 1911 (see also Bartholomew and Hubbs, 1960).

The population continued to grow as NES established breeding populations on San Miguel, San Nicolas, and Santa Barbara islands by the 1950s, at Año Nuevo Island in 1961, at the Farallones in 1972, on Point Año Nuevo in 1975, at Point Reyes in 1981, and on Santa Rosa Island in 1985 (Stewart and Huber, 1993; Stewart et al., 1994). The largest mainland colony was

established in 1991 on the extensive beaches south of Point Piedras Blancas in central California (Brian Hatfield, personal communication, 2009). Small breeding colonies, limited in size by the amount of rookery and haul-out habitat, now occur at Cape Arago, Oregon (Hodder et al., 1998). A few pups also have been born in the Strait of Juan de Fuca, on Protection and Smith-Minor islands and Dungeness Spit in Washington (Jeffries et al., 2000) and at Race Rocks in British Columbia (Steve Jeffries, personal communication, 2009). Since not all age and sex classes are ashore at the same time, estimating contemporary NES populations is difficult. Carretta et al. (2007: 28) estimated that the California NES population was around 101 000 in 2001 and by 2005 had grown to 124 000 (Carretta et al., 2009: 28). There is an additional population of NES breeding on islands of the Pacific Coast of Baja California, Mexico. The Mexico population was estimated to number about 32 000 animals in 1992 (Stewart et al., 1994), and

in 2003 Gallo-Reynoso et al. (2005: 181) estimated the population on Isla de Guadalupe at 14 965.

Despite their large size, several behaviors make NES susceptible to human hunting, especially females and young individuals. Although their annual migrations span some 18 000–21 000 km (Stewart and DeLong, 1993), NES come ashore two to three times yearly to breed and molt (Stewart and Huber, 1993). NES breed on land in reproductive territories featuring one or more large bull(s) and an aggregation of females. Pups, generally born in January and February, are nursed for about 30 days when they are weaned and left helpless on land for <4 months while they develop swimming skills. The weaned pups would have been the age group most susceptible to hunting by early humans. NES yearlings, immatures and adults also spend most of their molt period, lasting ~4 to 6 weeks in spring/summer, on land. Non-pregnant females and young individuals may haul-out again briefly in October (Stewart and Huber, 1993). Unlike Pacific Coast otariids, NES prefer sand and gravel beaches, which they use for thermoregulation, and do not use rocky areas for haul-outs or breeding. This significant time spent ashore, pups left alone, and propensity to use sand and gravel beaches made NES susceptible to human hunting during the historic fur and oil trade and prehistorically for Native American subsistence. Vulnerability to large non-human predators (grizzly bears, mountain lions, etc.) may have restricted the onshore activity of NES primarily to island settings (Erlandson et al., 1998) or isolated mainland locations.

Assuming humans would have hunted/scavenged prehistoric NES and other pinnipeds in direct proportion to their natural abundance, we can predict the following from modern and historical records: (1) Holocene NES should occur in archaeological sites from Baja California to Alaska; (2) the greatest numbers of archaeological NES specimens should come from Baja and Alta California where >124 000 NES now breed and reside; (3) in archaeological sites on the offshore islands of California, NES remains should be one of the most abundant of the six pinniped species documented in the area; and (4) since NES are found mostly offshore in northern waters (Stewart and DeLong, 1993), archaeological specimens north of California should be comparatively rare.

Materials and methods

Along with our own analyses of NES remains from California archaeological sites, we systematically searched the literature for reports of archaeological NES remains recovered from Baja California to Alaska. To determine more specific age and sex data, DeLong and Rick also re-analyzed collections from CA-ANI-6 and CA-ANI-8 on Anacapa Island (Sanderfur, 1978; Walker, 1978), CA-SMI-481 and CA-SMI-525 on San Miguel Island (Rick, 2007; Walker and Craig, 1979), and CA-SCLI-43B on San Clemente Island (Porcasi et al., 2000). These analyses resulted in some slight differences between our data and the original studies. We were unable to relocate NES bones from CA-VEN-11 (Lyon, 1937), so we relied on the data presented in the original report. In our experience working with pinniped remains from the Channel Islands, NES – especially their cranial remains, teeth, and long bones – are relatively easy to distinguish from those of other northeastern Pacific pinnipeds, resulting in a fairly high degree of confidence in their identification.

We report archaeological NES as the number of identified specimens (NISP), a total count of all bones, teeth, or fragments identified from each archaeological site, relying on this measure to evaluate ancient NES abundance (Lyman, 2008). To investigate NES abundance in ancient and modern times we constructed an abundance index that quantifies archaeological NES remains as $\sum \text{NES NISP} / \sum \text{Total Identified Pinniped NISP}$ for all samples with greater than 30 NISP. To quantify modern abundance, we relied on population estimates from San Miguel Island in 1997 (DeLong and Melin, 2002) and the California stock (the US stock estimate was used for California sea lion abundance) in 2005 (Carretta et al., 2009), where $\sum \text{NES Population} / \sum \text{Total Pinniped Population}$ from San Miguel Island or California. Because we only have one bone from Baja California we have not included estimates for Mexico.

Although rarely reported, all available age at death and sex data are presented to help evaluate the composition and structure of ancient NES populations and the possibility of selectivity in human harvest strategies. The antiquity of the specimens presented here was estimated from radiocarbon dates obtained for each archaeological site. In some cases, it was difficult to determine how closely associated radiocarbon dates are with NES remains, especially for those recovered from surface contexts. In most instances, we provide age ranges for entire sites or components rather than for specific bones.

Results

Our survey of archaeological data from western North America revealed just 28 archaeological sites with NES bones, ranging from Isla Cedros, Baja California to southern British Columbia (Table 1). A total of only 96 NES bones was identified. In comparison, the remains of Guadalupe fur seals (*Arctocephalus townsendi*), which are rare in California waters today, are common in prehistoric Alta California where nearly 3500 specimens have been reported from 60 sites spanning 8000 years (Rick et al., 2009). Most of the NES bones and teeth were from the Channel Islands, where 13 sites from six of the eight islands contain NES remains. Five additional NES bones were recovered from a nineteenth to twentieth century bald eagle nest on San Miguel Island, indicating NES presence at this time (Collins et al., 2005). Along the mainland coast of California, only three sites have produced NES remains, including 21 specimens from CA-VEN-11 at Point Mugu, where they represent just 1% of the total pinniped NISP. A single NES bone was also identified from CA-SMA-18 at Point Año Nuevo and another was recovered from CA-SLO-2 at Diablo Canyon.

To the south, PAIC-19 on Baja California's Isla Cedros produced one NES bone. NES occur in 11 archaeological sites north of California, including three NES bones from 35-DO-83 in Oregon, which produced abundant remains of northern fur seals (*Calorhinus ursinus*) and Steller sea lions (*Eumetopias jubatus*) (Lyman, 1988). Seven sites in Washington have produced NES bones, but these generally constitute less than 1% of each assemblage. Finally, three sites in southern British Columbia each produced one NES bone, all of which are from the west coast of Vancouver Island, a pattern comparable with the recent distribution of NES (Campbell, 1987).

The geographic distribution of these sites suggests that ancient NES had a geographic range similar to today, from approximately

Table 1. Northern elephant seal remains in northeastern Pacific Coast archaeological sites

Site number ^a	Age (cal. BP)	Count	MNI ^b	Comment	References
<i>Baja California</i>					
PAIC-19 (Isla Cedros)	410–290	1	1	Juvenile vertebra	Des Lauriers (2005); this article
<i>California</i>					
CA-ANI-6 (Anacapa Island)	630–550	1	1	Astragulus bone in small assemblage with Guadalupe fur and harbor seals	Walker (1978)
CA-ANI-8 (Anacapa Island)	5020–540	1	1	Immature female maxilla with California sea lion, Guadalupe fur seal, and harbor seal	Sanderfur (1978)
CA-SCAI-17 (Santa Catalina Island)	5920–880	–	–	NISP and MNI not reported	Porcasi (2002)
CA-SCLI-43B (San Clemente Island)	Late Holocene	6	4	Fragmentary cranial elements and metacarpals constitute <5% of pinniped NISP	Porcasi et al. (2000)
CA-SCRI-240 (Santa Cruz Island)	Historic	1	1	Pup mandible from possible feasting context with swordfish and other species	This paper
CA-SLO-2 (Diablo Canyon)	500–200	1	1	<1% of pinniped NISP; harbor seals and California sea lions dominant	Jones et al. (2008)
CA-SMA-18 (Point Año Nuevo)	1480–1070	1	1	1 bone from Point Año Nuevo; assemblage dominated by northern fur seals and otariids	Gifford-Gonzalez and Sunseri (2009)
CA-SMI-468 (San Miguel Island)	910–720	1	1	1 of only 3 pinniped species identified in small assemblage.	Rick (2007)
CA-SMI-481 (San Miguel Island)	5980–960	4	3	~1-3% of pinniped NISP. 1 bone and 1 MNI from Walker and Snethkamp; 1 adult female mandible (all of these are ~1280-960 cal BP); 1 adult female maxilla and 1 adult female canine from ~6000 yr old shell midden	Walker and Snethkamp (1984); Colten (2002); Rick (2007); Vellanoweth et al. (2006)
CA-SMI-492 (San Miguel Island)	5580–1250	1	1	1% of total pinniped NISP identified to species	Walker and Snethkamp (1984); Colten (2002)
CA-SMI-510 (San Miguel Island)	1260–1130	1	1	4% of total pinniped NISP identified to species	Walker and Snethkamp (1984); Colten (2002)
CA-SMI-525 (San Miguel Island)	3230–520	17	5	Small portion of assemblage dominated by Guadalupe fur seals, including 3 juvenile males and 1 female	Walker and Craig (1979); Walker (1978); This paper
CA-SMI-528 (San Miguel Island)	1570–1120	1	1	<1% of pinniped assemblage, with Guadalupe fur seals most common. Possible adult female	Walker et al. (2002)
CA-SMI-602 (San Miguel Island)	540-Historic	9	4	Limited part of the assemblage dominated by Guadalupe fur seals. Includes two juveniles, a pup, and <1 year old	This paper; Walker et al., (2002)
CA-SNI-11 (San Nicolas Island)	6980–510	14	4	2% of total pinniped bones identified to species	Bleitz (1993)
CA-VEN-11 (Point Mugu)	Historic	21	5	1% of total NISP for pinnipeds and sea otters. Sex not determined, but seven adult and 14 juvenile bones	Lyon (1937)
<i>Oregon</i>					
35-DO-83 (Umpqua/Eden)	3000-Historic	3	1	Adolescent estimated to be about 3 months old	Lyman (1988)
<i>Washington</i>					
45-CA-22 (Neah Bay)	Historic	1	1	Ethnographically described village. Elephant seals limited in assemblage	Friedman (1976)
45-CA-21 (Hoko River)	1200–300	1	1	Dominated by northern fur seals with elephant seals <1% of assemblage	Wigen (2005)
45-CA-25 (Sooes)	1070-Historic	1	1	Ethnographically named village. Elephant seals limited in assemblage	Friedman (1976)
45-CA-204 (Warmhouse)	Historic	1	1	Elephant seals limited in assemblage	Friedman (1976)
45-CA-207 (Tatoosh)	930-Historic	2	2	Ethnographically known site on small island. Elephant seals limited in assemblage	Friedman (1976)
45-CA-24 (Ozette)	450–430	2	–	<1% of total pinniped NISP; assemblage dominated by northern fur seals	Etnier (2007); Huelsbeck (1994)
45-GH-15 (Minard)	950–300	1	1	Possible northern elephant seal bone	Fancher (2001); Moss and Losey (2011)
<i>British Columbia</i>					
DfSI-5 (Ma'acoah)	1200–300	1	1	Dominated by northern fur seals with elephant seals making up <1%	Monks (2006)
DfSI-16 (Ts'ishaa, Benson Island)	1870–250	1	1	Probable elephant seal bone. <1% of pinniped assemblage dominated by northern fur seal	McMillan and St Claire (2005)
DiSO-1 (Hesquiat Harbor, Vancouver Island)	650–500	1	1	Possible phalanx tentatively identified as an adult female	Calvert (1980)

^aData from SMI-602, -525, and -528 contain new and re-analyzed material from Walker et al. (2002) and Walker and Craig (1979), resulting in some differences in total counts and MNI. The NISP from SMI-525 includes four bones and two individuals identified by Walker, Kennett, and DeLong, and 13 bones and three MNI from our re-analysis of Walker and Craig's (1979) materials. A single elephant seal bone listed from Mendocino County, California (Hildebrandt and Jones, 1992) has been re-identified as a different species.

^bMNI is minimum number of individuals estimates calculated by totaling up the number of non-repetitive elements for a given site or unit (see Lyman, 2008). MNI are presented here for future work that may use this measure.

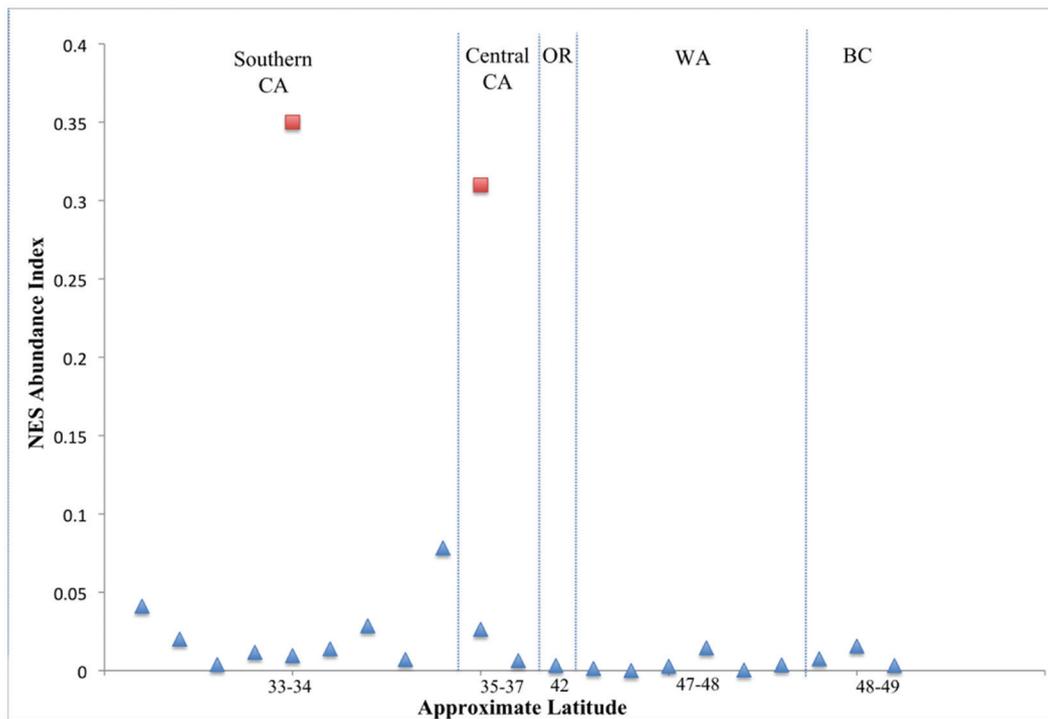


Figure 2. Abundance index of ancient and modern NES by approximate latitude. Values are between 0 and 1 where 1 is the highest possible abundance. Archaeological sites noted with a triangle. San Miguel Island (left) and California stock (right) population abundance noted with a square. CA, California; OR, Oregon; WA, Washington; and BC, British Columbia

28°N to 49°N latitude (Figure 2) (see also Lyman, 2011). Roughly 85% of the NES bones identified from Pacific Coast archaeological sites come from between ~33° and 35°N, but most of these are from the Channel Islands. Although the Channel Islands contain the most archaeological sites in western North America with NES bones and large modern breeding colonies, NES are extremely rare in archaeological assemblages, generally making up only about 0.7–7.8% of the total identified pinniped NISP and always ranking much lower than other pinnipeds. The highest percentage is recorded at CA-SMI-602 (located within the huge contemporary Point Bennett rookery), where they are significantly outnumbered by remains of Guadalupe fur seals and California sea lions (*Zalophus californianus*) (Walker et al., 2002). In contrast to these archaeological data, DeLong and Melin (2002) noted that in 1997 some 50 000 NES were present on San Miguel Island, second only to California sea lions at ~80 000.

On the central California coast, where there are currently four substantial rookeries, a single NES specimen is reported from each of two sites, CA-SMA-18 and CA-SLO-2. Extensive excavations at a site immediately adjacent to the largest modern rookery on the mainland at Piedras Blancas failed to produce a single NES specimen (Jones and Ferneau, 2002); where California sea lions instead dominate the archaeological pinniped assemblage. At sites currently being damaged by NES breeding activities at Point Año Nuevo, excavations produced dozens of northern fur seal bones, but just one NES bone (Gifford-Gonzalez and Sunseri, 2009; Hildebrandt et al., 2006; Hylkema, 1991).

The majority of NES specimens come from late-Holocene (3500 yr ago–present) sites. This includes all sites from mainland California, Oregon, Washington and British Columbia, and nine from the Channel Islands. The oldest specimens may come from San Nicolas Island where 14 bones from CA-SNI-11 were reported from a large, multi-component site dated between about 7000 and 500 cal. BP (Bleitz, 1993). Two specimens from CA-SMI-481

come from a discrete component securely dated to ~6000 years ago (Vellanoweth et al., 2006). Specimens from CA-SCAI-17, CA-ANI-8, and CA-SMI-492 may also be middle Holocene in age, but could date to the late Holocene. Collectively, these data suggest sporadic human exploitation of NES for at least 6000 years, with most evidence from sites dated to the last 1500 years.

Eleven of 28 sites had age at death or sex data reported. On Isla Cedros, the single bone is from a juvenile of unknown sex. Seven sites from the Channel Islands produced sex and/or age at death data. These include a juvenile female from CA-ANI-8, a pup from CA-SCRI-240, two adult females from CA-SMI-481, five immature individuals, including at least four males and one female from CA-SMI-525, a possible adult female from CA-SMI-528, and two juveniles, one of which is 1–2 years old, a pup, and an immature specimen less than 1 year old from CA-SMI-602. Six fragmentary NES bones from CA-SCLI-43B are difficult to age or sex, but include a juvenile and either an adult female or juvenile male. The bones of seven adults and 14 juveniles were recovered from CA-VEN-11, but no sex data were reported. At Oregon's 35-DO-83, all three bones are thought to be from an approximately three-month-old animal. Finally, Calvert (1980) tentatively identified the DiSO-1 specimen from Vancouver Island as an adult female. These data suggest that Native Americans exploited primarily juveniles and smaller numbers of adult females, but no adult males. Although two pups are represented, the data are too few to be certain whether or not breeding colonies were exploited, but if they were, the small number of archaeological bones suggests they were likely small in size and limited in distribution.

The high incidence of juveniles (75%) raises the possibility that Native Americans exploited mostly stranded NES. Colegrove et al. (2005) found that between 1992 and 2001, 1277 NES stranded on beaches in central California, of which 420 died or were euthanized. Of these, 99% ($n=1266$) were pre-weaned pups,

molted weanlings, and yearlings, with just six subadults and five adults. Malnutrition, disease, and human intervention were the primary causes of strandings. Native Americans probably harvested some stranded NES, but given the vulnerability of younger animals we would also expect a high proportion of young animals if they were actively hunted. Regardless of whether they were scavenged, hunted, or both, the data provide a proxy of the relative abundance of NES in the area.

Discussion and conclusion

Archaeological NES data document geographic distributions similar to modern populations, but substantial differences with contemporary NES abundance compared with those of other pinnipeds. North of California the data generally meet our test expectations and are similar to modern times, with very small numbers of ancient NES in Oregon, Washington, and British Columbia. However, the limited occurrence and abundance of NES in California, including absence from most sites located near modern rookeries and low numbers on the Channel Islands, suggest a very different pattern from the modern hyper-abundance of NES in central and southern California. The limited archaeological data available from Baja California, including an apparent absence of prehistoric human occupation on Isla de Guadalupe, currently prevent a comparison of abundance in modern and ancient NES populations in Mexico.

Analysis of ancient and modern NES DNA provides further insight into changes in NES abundance and distribution. With a drastic historic population bottleneck, modern NES show extremely limited genetic diversity. Weber et al. (2000, 2004) and Hoelzel et al. (2002) analyzed pre- and post-bottleneck NES samples from modern, late nineteenth century, and late-Holocene archaeological specimens from San Miguel and San Nicolas islands. Not surprising given the historical population decline, the archaeological samples of pre-bottleneck age were more diverse genetically than the post-bottleneck specimens (Hoelzel et al., 2002; Weber et al., 2000, 2004). The contrast between large modern NES populations with very low genetic diversity and ancient populations with apparently lower abundance (at least in areas where they are common today) and higher genetic diversity raises the question: Why are there not more NES bones in California archaeological sites?

Four hypotheses might explain the limited abundance of NES remains in coastal California: (1) preservation bias; (2) human food preferences or hunting capabilities; (3) climatic changes; and (4) human settlement strategies/habitat displacement and predation. The first hypothesis – NES bones are found in low abundance because they preserve poorly compared to other pinnipeds – can be dismissed because 96 bones were found and even juvenile elephant seal bones are large and robust. Did human hunters not pursue elephant seals because they were too large and difficult to capture or the flesh was not palatable? While large male elephant seals may have been difficult to hunt, this is not the case for the much smaller females and young. Ancient peoples also extensively hunted/scavenged other pinnipeds using a variety of technologies, including large California and Steller sea lion males (Lyman, 2003). NES contain rich sources of protein, fat, and oil that would have been attractive to ancient peoples. The Makah in Washington hunted NES possibly incidental to their offshore hunting of northern fur seals and described the NES flesh as good to eat (Cowan and Carl, 1945). Southern elephant seals (*M. leoni*)

were also hunted prehistorically elsewhere in the world (e.g. Tasmania, Bryden et al., 1999). Given these factors, hypothesis (2) seems unlikely.

A third hypothesis is that environmental and climatic variables during the Holocene reduced NES populations. The small number of archaeological specimens and limited chronological resolution make it difficult to identify specific paleoclimatic events that may have influenced NES abundance. While marine climatic conditions during the Holocene were variable, including periodic El Niño events and periods of warmer and colder sea surface temperature than today (Kennett, 2005; Kennett et al., 2007), NES were present during the generally warm period of the middle Holocene, but are most common in the last 1500 years or so when marine climatic conditions were highly variable and include periods of cool and warm water conditions (Kennett and Kennett, 2000). Climatic factors likely influenced the biogeography of ancient NES populations, but there are no clear correlations in the Holocene climatic or archaeological data that point to climate as the primary reason for the dearth of NES bones in archaeological sites.

The fourth hypothesis is that Native American settlement and possibly predation by large carnivores influenced the ancient abundance and distribution of NES, especially in coastal California, resulting in the displacement of NES from many of their favored habitats. As humans colonized the Pacific Coast, including the California Channel Islands by about 13 000 calendar years ago (Erlandson et al., 2008), they likely found an abundance of pinnipeds, including NES, particularly on offshore islands where they were protected from predation by bears and other large terrestrial predators (Erlandson et al., 1998: 165). Native American occupation or settlement near or on current haul-outs and rookeries, the presence of Native American dogs, and possibly direct predation may have displaced NES from their preferred habitats and driven them to haul-out, breed, and give birth to their young elsewhere. One important variable that affects NES differently than otariids (which often haul-out on rocky shores) is their reliance on sandy beaches, and to a lesser extent gravel or cobble beaches, for haul-outs and rookeries. Many of the primary beaches used by NES as breeding sites today also have archaeological sites nearby. The presence of Native American peoples near these preferred beaches – especially during the late Holocene when human populations were relatively high – would have likely driven NES to increasingly remote pocket beaches and islands without human occupation. In contrast, otariids had options for using nearby offshore rocks and more extensive isolated rocky shores not utilized by NES. Isla de Guadalupe, the Farallones, and possibly other isolated and difficult-to-access islands or coves may have provided ancient refugia for breeding, birthing, and molting. These islands and pocket beaches may have allowed NES populations to remain viable throughout the Holocene, acting as a source of animals that would swim northward to forage as they do today and maintain the genetic diversity seen in prehistoric samples.

Hypothesis four is the best supported by the current archaeological and contemporary NES data. Given the small sample of NES bones currently available, however, questions remain about the effects of ancient human activities and predation, as well as environmental variables on NES, leaving important avenues for further research.

The current abundance and distribution of breeding NES is a testament to their resilience, persistence, and adaptability in the wake of millennia of interactions with Native Americans

and the onslaught of Euro-American hunters during the eighteenth and nineteenth century fur and oil trade. In the absence of human predation, these animals appear to do exceptionally well and to maintain fitness despite low genetic diversity (Weber et al., 2004). The archaeological data presented here suggest that the abundance of Holocene NES in California was considerably different than today. The modern abundance of NES on islands off California may provide a glimpse of what their populations were like during the Pleistocene prior to human arrival, but bears, saber-tooth cats, and other large terrestrial predators may have restricted their distribution and numbers along the mainland coast before humans arrived. In the absence of human disturbance and predation, as well as major disease, climate change, pollution, or food source disruptions, modern NES populations may continue to expand and thrive. We should be cautious in interpreting their current abundance as a natural or ancient phenomena, however, as it appears to be a pattern not seen in portions of the northeastern Pacific for at least 10 000 years.

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