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The shifting baseline of northern fur seal ecology in the northeast Pacific Ocean

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Historical data provide a baseline against which to judge the significance of recent ecological shifts and guide conservation strategies, especially for species decimated by pre-20th century harvesting. Northern fur seals (NFS; *Callorhinus ursinus*) are a common pinniped species in archaeological sites from southern California to the Aleutian Islands, yet today they breed almost exclusively on offshore islands at high latitudes. Harvest profiles from archaeological sites contain many unweaned pups, confirming the presence of temperate-latitude breeding colonies in California, the Pacific Northwest, and the eastern Aleutian Islands. Isotopic results suggest that prehistoric NFS fed offshore across their entire range, that California populations were distinct from populations to the north, and that populations breeding at temperate latitudes in the past used a different reproductive strategy than modern populations. The extinction of temperate-latitude breeding populations was asynchronous geographically. In southern California, the Pacific Northwest, and the eastern Aleutians, NFS remained abundant in the archaeological record up to the historical period ≈ 200 years B.P.; thus their regional collapse is plausibly attributed to historical hunting or some other anthropogenic ecosystem disturbance. In contrast, NFS populations in central and northern California collapsed at ≈ 800 years B.P., long before European contact. The relative roles of human hunting versus climatic factors in explaining this ecological shift are unclear, as more paleoclimate information is needed from the coastal zone.

Callorhinus ursinus | historic ecology | stable isotopes | zooarchaeology | ancient DNA

Humans, including prehistoric indigenous groups, play a major role in shaping their environment, such that some of the ecosystems we are familiar with today operated differently in the past (1). Paleocological data illuminate the natural history of species on ecologically and evolutionarily relevant timescales, providing a means of evaluating the significance of current ecological trends that is vital to the success of long-term conservation strategies (2). This perspective is especially important for species that have suffered recent declines in population size because of human disturbance. Here we use archaeometric, isotopic, genetic, and chronologic data to reveal prehistoric shifts in the ecology of northern fur seals (NFS; *Callorhinus ursinus*) and then briefly explore the factors driving these changes.

Post-Columbian explorers encountered just two NFS breeding populations along the entire margin of the northeast Pacific Ocean (Fig. 1), a small one on the Farallon Islands ($\approx 38^\circ\text{N}$) off San Francisco Bay (3) and a much larger one on the Pribilof Islands ($\approx 57^\circ\text{N}$) in the eastern Bering Sea (4). In striking contrast, NFS fossils are substantial components of archaeological sites from southern California to the eastern Aleutian

Islands (5–8) (Fig. 1). The latter finding is puzzling because the modern pattern of offshore foraging, primarily high-latitude island breeding, and a short lactation period (4) should have made NFS largely unavailable to human hunters at temperate latitudes. Even if indigenous people had the maritime technologies needed to exploit offshore/pelagic prey, regular offshore hunting of NFS, which are relatively small pinnipeds that occur today at low densities (9), would be a suboptimal foraging strategy. There are two potential explanations for the common occurrence of NFS in archaeological sites. (i) They may be the remains of individuals, largely from high-latitude breeding colonies, that accidentally stranded and were scavenged by humans. This explanation requires no major changes in NFS breeding or migratory behavior, although it might require a larger source population at high latitudes to explain the higher stranding frequency in the past. (ii) NFS may have come from nearby haul-outs or breeding colonies (5–8). This explanation requires a marked increase in the number and/or size of NFS breeding colonies at temperate latitudes. Under the second scenario, NFS would have been especially susceptible to human predation if they congregated at high densities close to shore or if they weaned their pups at an older age than modern populations. We evaluate these possible explanations using information obtained from NFS remains in archaeological sites from the western Aleutian Islands to southern California (Fig. 1).

Currently, NFS in the eastern North Pacific are in decline for unknown reasons. Population estimates are at a historic low for the Pribilof Islands stock in the eastern Bering Sea (9), where $\approx 65\%$ of the global population breeds (4). Adult females, after spending autumn through late spring at sea, return to the Pribilof Islands to breed in late June. Most pups are born between July 3rd and July 11th and are weaned in early November (4), at which time young-of-the-year (YOY) and adult females migrate as far south as California during the winter months (10). Adult males from the Pribilofs population remain in the Gulf of Alaska throughout the winter (11). Recently, migrants from the Pribilofs have established breeding colonies on San Miguel

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Abbreviations: AMS, accelerator mass spectrometry; HS, harbor seals; NFS, northern fur seal(s); SMI, San Miguel Island; YOY, young-of-the-year.

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cation kit protocol and served as templates in the sequencing thermocycling. To corroborate results and resolve ambiguous sites on single strands, fragments were sequenced in both directions.

Sequences were aligned in Sequencher 3.1.1 (Gene Codes, Ann Arbor, MI) and checked by eye for potential polymorphic sites. For tree-building, we used MEGA 3.0 (MEGA, Tempe, AZ) to perform neighbor-joining analyses and PAUP 4.0 (Sinaur Associates, Sunderland, MA) for maximum likelihood analyses and parameter estimation. We used the Akaike Information Criterion in Modeltest 3.7 (David Posada, Vigo, Spain) to select the most likely model of DNA substitution (TVM+G, using substitution code abcdbe and $\alpha = 0.3655$). *Martes* and *Procyon* were used as outgroup taxa.

Bootstrapping of the data by using both likelihood and neighbor-joining methods yielded significant support for the monophyly of ancient and modern NFS (98%) and for each of the sympatric species. This result was not affected by the inclusion of available DNA sequences from additional nonsympatric *Arctocephalus* taxa (data not shown). The clustering of most ancient sequences among modern NFS (SI Fig. 6) to the exclusion of other species further supports the notion that prehistoric temperate-latitude NFS did not form a distinct genetic unit separate from modern NFS. We also acknowledge that the genetic distinction between NFS and *A. townsendi* is based on a small sample size ($n = 2$) for *Arctocephalus*, which experienced a severe loss of genetic diversity because of a population bottleneck after historic exploitation (45). In addition to the significant support for reciprocal monophyly mentioned above, the specific distinction is strengthened by the fact

that NFS and *A. townsendi* are not in the same genus and thus are not expected to share similar haplotypes that closely related species may share with rapid molecular markers like the control region. It would indeed be possible that primitive haplotypes of one species with high intrinsic genetic variability could be misidentified if a closely related species within the same genus went through a genetic bottleneck, but it would be very unlikely to make a genetic misdiagnosis at the generic level with fast-evolving molecular markers. The phylogenetic tree shows similar intergenus distances for *Arctocephalus*–*Callorhinus* and *Arctocephalus*–*Zalophus/Eumetopias*, which are significantly larger than the largest intra-*Callorhinus* distance.

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