

# Historical Ecology and Biogeography of North Pacific Pinnipeds: Isotopes and Ancient DNA from Three Archaeological Assemblages

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## ABSTRACT

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*Zooarchaeology has the potential to make significant contributions to knowledge of pinniped biogeography of import to both archaeologists and environmental scientists. We analyzed northern fur seal remains found in three archaeological sites located along the outer coast of the Northeast Pacific Ocean: Cape Addington Rockshelter in southeast Alaska, Ts'ishaa on the west coast of Vancouver Island, and the Netarts Sandspit site*

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*on the Oregon Coast. These three sites occur along an 850 km stretch of coastline between 45° to 55° N. and 123° to 134° W., far southeast of the primary breeding area for northern fur seals today, located on the Pribilof Islands at 57° N. 170° W. We use ancient DNA (aDNA) and carbon ( $\delta^{13}C$ ) and nitrogen ( $\delta^{15}N$ ) isotopes to investigate whether northern fur seal remains from these archaeological sites originated with migratory Pribilof Islands populations. For sites located in Oregon and points north, the isotope values are not distinct from those of the Pribilof fur seals. Although aDNA was recovered from three pinniped species (northern fur seal, Steller sea lion, and Guadalupe fur seal), the paucity of published genetic data from modern northern fur seals prevents us from distinguishing the archaeological specimens from modern Pribilof seals.*

**Keywords** zooarchaeology, marine mammals, carbon and nitrogen isotopes, ancient DNA, northern fur seals, historical ecology

## INTRODUCTION

Worldwide, there currently exist 33 pinniped species, not counting the Caribbean monk seal, which was driven to extinction in the twentieth century (Reeves et al. 1992:8–9). Maritime peoples have hunted pinnipeds for millennia, but harvesting intensified in recent centuries with the emergence of global markets for furs, oil, meat, and other products (Allen 1880; Busch 1985; Scammon 1968 [1874]). In the North Pacific, hunting during the nineteenth and twentieth centuries radically altered the biogeography of pinnipeds, driving several species to the brink of extinction. As various pinniped species recovered under programs of government protection, some late twentieth-century populations now are thought to represent more “natural” conditions. Archaeological data make it clear that human populations have been interacting with pinniped populations for thousands of years, however, and the biogeography and behavior of North Pacific pinnipeds have fluctuated through space and time. Archaeologists and marine ecologists are

using new analytical tools in their efforts to reconstruct the historical ecology of pinnipeds, including studies of isotopes and DNA (both ancient and modern).

Over the last 30 years, zooarchaeologists working on faunal assemblages from across the North Pacific Coast have identified pinniped bones at numerous sites spanning much of the Holocene. The occurrence and relative abundance of different species at various localities have helped document the importance of marine mammals to coastal and island communities over time. For specific sites, archaeologists have used marine mammal assemblages to infer: 1) human use of particular littoral, nearshore, and offshore habitats; 2) hunting methods, butchering patterns, and storage techniques; 3) seasonality of site occupation; 4) degree of economic reliance on marine mammals vis à vis other animals; and 5) technological, demographic, and social changes over time (e.g., Carlson 2003; Colten 2002; Erlandson et al. 2004:57–61; Hildebrandt 1981, 1984a; Huelsbeck 1988, 1994; Lefèvre et al. 1997; Lyman 1991; Stewart and Stewart 1996). Beyond specific sites,

investigators have compiled data for sub-regions of the North Pacific to argue for geographically more extensive patterns of changing resource use through time. Such changes have been variously attributed to technological evolution, adaptations to changing environments, resource intensification by growing human populations, over-exploitation of some species and subsequent prey-switching, or some combination of these (see Etnier 2002a; Hildebrandt and Jones 1992, 2002, 2004; Jones and Hildebrandt 1995; Lyman 1989, 1991, 1995, 2003; Niimi 1994; Porcasi et al. 2000; Walker et al. 1999; Yamaura 1998; Yesner 1988).

Gretchen Lyon (1937) was probably the first scientist working along the Pacific Coast to recognize discrepancies between the content of archaeological samples and then contemporary patterns of marine mammal abundance. Years later, Gustafson (1968a, 1968b), Walker and Craig (1979), and Calvert (1980) noted the presence or relative abundance of species in precontact assemblages that were rare or absent in the modern habitats surrounding the sites they studied. Hildebrandt (1984b), Clark (1986), and Lyman (1988) also detected zoogeographic discrepancies between the past and present. Recently, investigators have focused more intently on demonstrating the utility of studying pinniped remains for understanding long-term changes in the biogeography of key species prior to the industrial era (Burton and Koch 1999; Burton et al. 2001, 2002; Crockford et al. 2002; Gifford-Gonzalez et al. 2005).

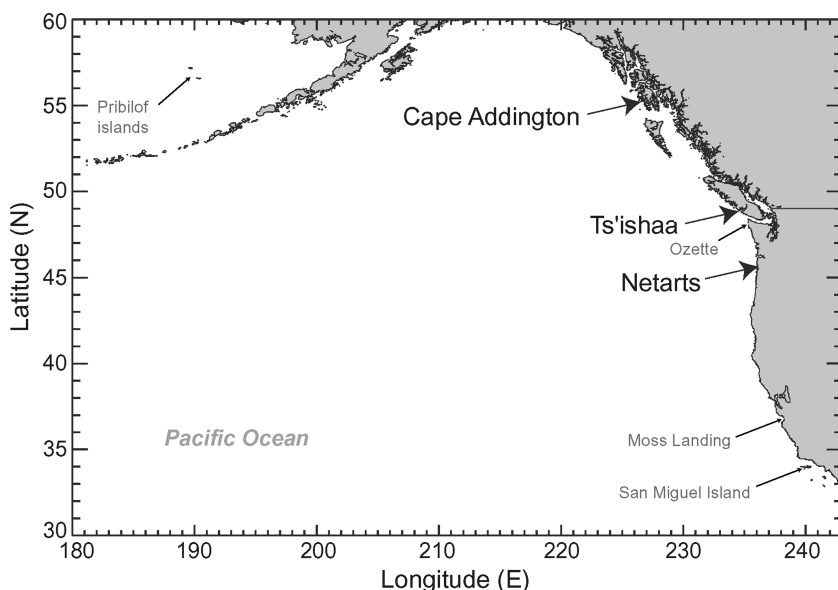
Jackson et al. (2001:629) pointed out that most ecological research is based on local field studies of short duration, conducted some time after the 1950s. Yet some pinniped populations were the focus of massive commercial hunting in the nineteenth and twentieth centuries, primarily for their oil and hides (e.g.,

Allen 1880; Sims 1906; Starks 1922). Even after pinniped numbers sharply declined, some species were subject to continuing hunting pressure because they were perceived to compete with humans for declining fisheries. For example, all the Pacific Coast states and British Columbia had predator control or eradication programs for harbor seals, some that continued into the 1960s. Such programs included open seasons, government-paid hunters, and bounty systems (Mate 1981:440). It was not until the 1994 amendments to the 1972 Marine Mammal Protection Act that intentional lethal take of any marine mammal was made illegal in U.S. waters, except for subsistence hunting by Alaska Natives or where necessary to protect human life. Illegal shootings, entanglement in commercial fishing gear and marine debris, and collisions with boats continue to cause pinniped mortality, as evidenced in stranding records (e.g., NOAA 2001:15, 2003b:5). In British Columbia, harbor seals (*Phoca vitulina*), California sea lions (*Zalophus californianus*), and Steller sea lions (*Eumetopias jubatus*) can still be legally shot if they take fish held or reared in sea cages (Fisheries and Ocean Canada 2001). Despite this, some pinniped populations are rebounding and even extending their ranges, including northern elephant seals (*Mirounga angustirostris*), California sea lions, and the eastern stock of Steller sea lions (e.g., Hodder et al. 1998; LeBoeuf 1996; NOAA 2003a; Pitcher et al. in press). In contrast, other pinniped populations are in serious decline, including the Pribilof Islands stock of northern fur seals and the western stock of Steller sea lions (Gentry 1998; O'Harra 2005; Trites and Larkin 1996). Since modern patterns of pinniped abundance, distribution, and ecology reflect the distinct histories of each population or stock (e.g., Cooper and Stewart 1983; Howorth 1993;

Stewart et al. 1993), they cannot be projected onto the more ancient past. Gifford-Gonzalez et al. (2005) have shown how studies of the historical ecology of human-pinniped interactions can contribute not just anthropological insights, but biological understandings of precontact marine environments. Zooarchaeological records therefore have the potential to contribute to improved wildlife conservation and resource management (e.g., Etnier 2004; Lyman 1996, 2006; Lyman and Cannon 2004).

In this paper, we use isotopic and genetic data from three archaeological sites on the Northwest Coast of North America to assess the biogeography of one species, the northern fur seal, *Callorhinus ursinus*. Today, northern fur seals range from Japan to the Bering Sea to southern California (Gentry 1998). Their breeding sites in the United States include the Pribilof Islands in the Bering Sea, Bogoslof Island in the eastern Aleutians (since 1982), and San Miguel Island

in southern California (since 1968; Peterson et al. 1968; See Figure 1). The bulk (74%) of the world's *Callorhinus* population breeds on the Pribilof Islands, a series of major colonies (NOAA 2005a). These islands were the primary target of industrial-scale commercial sealing until an international treaty was reached in 1911 (Gentry 1998:24; Loughlin et al. 1994). Modern Pribilof fur seals give birth from late June to late July, females nurse their pups until weaning, and then migrate south in November (Gentry 1998:22). Females and juveniles of both sexes migrate offshore, following "the general patterns of water flow of the North Pacific Current and the southern boundary current of the Alaska Gyre" (Ream et al. 2005:838-839). Some females and juveniles travel as far south as Baja California, while others spend the winter foraging offshore along the coasts of California, Oregon, and Washington. Adult males spend the winter in the high latitudes, foraging around the



**Figure 1.** The location of archaeological sites discussed in the text in relation to Pribilof Islands and San Miguel Island northern fur seal breeding areas (prepared by Iain McKechnie).

Aleutian Islands and western Gulf of Alaska (Gentry 1998:36; Kajimura 1984). Northern fur seals occur across the outer coast of the North Pacific between November and June, and can be locally abundant (as described for the outer coast of Washington by McConnaughey and McConnaughey 1994 [1985]:405).

If one were to rely exclusively on a limited, normative view of twentieth century northern fur seal biology, the presence of these seals in archaeological sites on the islands and coastlines of the North Pacific would most likely indicate the presence of northern fur seals migrating to and from the Pribilof Islands. Yet Burton et al. (2001) noted the marked abundance of northern fur seals in archaeological assemblages dating from the Middle and Late Holocene in Oregon (citing Lyman 1988, 1989) and in California. Their study of the isotopic composition of archaeological fur seal bones led these investigators to infer that northern fur seals foraged as far offshore in the distant past as they do today, but remained in the vicinity of California year-round. Burton et al. (2001) proposed that northern fur seals were the predominant pinniped in California prehistorically, and that they were hunted at mainland colonies. This argument heavily relied on data from northern fur seal pup remains found at the Moss Landing site (CAMNT-234) in central California. Burton et al. (2001, 2002) clearly showed that northern fur seals had different breeding and migration patterns in the ancient past than they did during the first half of the twentieth century. Working on other assemblages, Etnier (2002a) inferred the presence of previously unidentified fur seal colonies in the Aleutian Islands and off the coast of the Olympic Peninsula in Washington through the osteometric analysis of northern fur seal pup bones in archae-

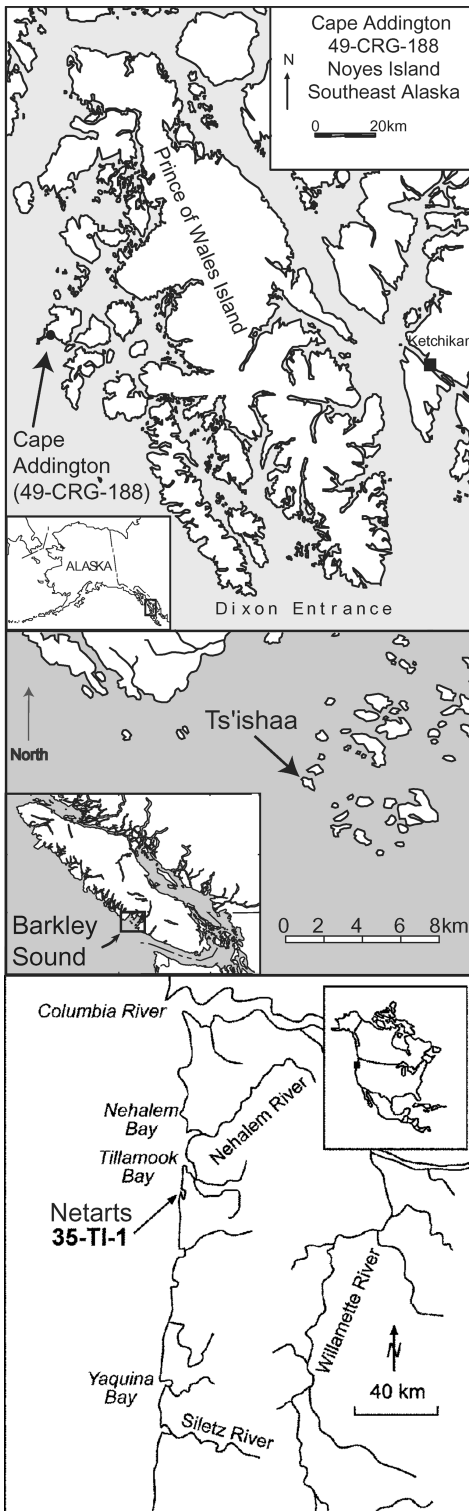
ological sites. Based on the presence of pre-weaning age pups, Crockford et al. (2002) also presented a case for a locally breeding, non-migratory population of northern fur seals along the central Northwest Coast, between Cape Flattery, Washington, and Barkley Sound on the west coast of Vancouver Island.

The questions we address here relate to whether or not northern fur seal remains found at three recently investigated archaeological sites on the North Pacific Coast derive from the Pribilof Islands population of northern fur seals. We attempted to use the variability in the isotopic and genetic data to assess whether more localized northern fur seal populations existed and whether this provides indirect evidence of pre-contact breeding sites in the vicinity of these archaeological sites prior to commercial sealing. The archaeological sites are the Cape Addington Rockshelter (49-CRG-188) located on Noyes Island in southeast Alaska, Ts'ishaa (DfSi-16) located in Barkley Sound on Vancouver Island, and the Netarts Sandspit site (35-TI-1) located on the Oregon Coast mainland (Figure 2). These three sites occur along an 850-mile stretch of the outer coast of the Northeast Pacific. While the previous archaeological studies challenging prevailing biological tenets relied on isotopic studies of pinniped bones, our analyses include both isotopic and genetic data. The sites represent widely separated points on both geographic and cultural spectra, providing an extensive framework within which to assess the isotopic and genetic results.

#### THE ARCHAEOLOGICAL SITES

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Cape Addington Rockshelter (49-CRG-188) underwent limited excavations (9.5 m<sup>3</sup>) in 1996 and 1997 (Moss 2004). The site is located near the southern end of Tlingit territory, not far from the Haida frontier. It is situated on



Noyes Island, one of the outer islands of the Prince of Wales Archipelago, about 130 km west of Ketchikan, Alaska. The occupations represented at the Cape Addington Rockshelter are dated to cal AD 50-1680, apparently pre-dating the Haida incursion into what is now Alaska. Of 8,918 vertebrate remains recovered from the site, 74% were fish and 9% were marine mammals. The latter include 292 pinniped bones, with harbor seal, Steller sea lion, and northern fur seal represented, in order of abundance (Table 1). Among the 20 northern fur seal specimens, 10 elements were from pups (Moss 2004:183).

Extensive excavations at Ts'ishaa (DfSi-16) took place in 1999, 2000, and 2001 (McMillan and St. Claire 2005). The site is located within the territory of the Tseshah, one of the Nuuchahnulth First Nations in British Columbia. The site is a large ethnographically known village situated on Benson Island in the Broken Group islands in Barkley Sound on the west side of Vancouver Island. The main village area dates to cal AD 80-1700 (McMillan and St. Claire 2005:42-45), which is contemporaneous with the occupation at Cape Addington. From the main village area, 163 m<sup>3</sup> were excavated from several spatially dispersed, but contemporary parts of the site. The back terrace area of the site is substantially older (5320-2950 cal BP) and dates to a period when relative sea level was approximately 3-4 m higher than today in this region of the Northwest Coast (Friele and Hutchinson 1993). From the back terrace, 44.7 m<sup>3</sup> were excavated (McMillan and St. Claire 2005:72-74). Of the 48,962 vertebrate

**Figure 2.** Maps of archaeological sites discussed in the text (drafted by Iain McKechnie).

**Table 1. Pinniped bones (NISP) from Cape Addington Rockshelter, Ts'ishaa, and Netarts.**

		49-CRG-188	DfSi-16	35-TI-1
<i>Arctocephalus townsendii</i>	Guadalupe fur seal	0	0	3
<i>Callorbinus ursinus</i>	Northern fur seal	20	250 <sup>1</sup>	31
<i>Eumetopias jubatus</i>	Steller sea lion	52	19	166
<i>Mirounga angustirostris</i>	Northern elephant seal	0	1	0
<i>Phoca vitulina</i>	Harbor seal	97	43	124
<i>Zalophus californianus</i>	California sea lion	0	1	2
Otariid		31	16	175
Pinniped		92	159	141
Total		292	489	642

<sup>1</sup>Only 31 northern fur seal bones were identified from the back terrace, or older part of the site, and all others were from the main village, dating to within the past 2000 years (Frederick and Crockford 2005:180).

*Note:* Three specimens identified as northern fur seal in Moss (2004) are Steller sea lion; one specimen identified as northern fur seal in Losey (2002) is Steller sea lion. One specimen identified as harbor seal in Moss (2004) is Steller sea lion, but was labeled as northern fur seal when submitted to Newsome and later Yang. One specimen identified as northern fur seal in Losey (2002) is Guadalupe fur seal.

remains examined, fish constitute 93% and marine mammals 3%. The latter include 489 pinniped bones; the majority of those identified to species were northern fur seal (n = 250). The relative frequency of northern fur seals increased through time (Frederick and Crockford 2005:180), and fur seals of both sexes and all age groups (including seven elements from pups younger than four months) provide evidence of a fur seal breeding ground in the site vicinity according to Crockford et al. (2002) and Frederick and Crockford (2005:180-181). Fur seals dominate the mammalian assemblages at almost all excavated sites along western Vancouver Island and around Cape Flattery (Calvert 1980; Crockford et al. 2002; Gustafson 1968a; McMillan 1999:140). Harbor seal, Steller sea lion, California sea lion, and northern elephant seal are also represented in the Ts'ishaa assemblage.

The Netarts Sandspit site (35-TI-1) is located within Tillamook territory on the northern Oregon Coast, approximately

100 km west of Portland. The site was first dug during the 1940s, although work by professional archaeologists did not occur until 1952 (Cressman 1952). Extensive excavations (estimated at nearly 500 m<sup>2</sup>) continued in 1956, 1957, and 1958 (Losey 2002:193; Newman 1959). Losey recovered additional material in his small-scale excavations using intensive recovery methods in 1999, 2000, and 2001, and dated the site occupations to cal AD 1300-1800 (Losey 2002:246-259). He analyzed 5108 vertebrate specimens excavated in the 1950s (curated at the University of Oregon Museum of Natural and Cultural History) and 62,156 specimens from his 1999-2001 investigations. Of the total 67,264 vertebrate remains, over 90% were fish and 2.5% were marine mammals. Of the marine mammals, 642 specimens were pinniped bones. In order of abundance, Steller sea lion, harbor seal, northern fur seal, California sea lion, and Guadalupe fur seal are represented. Of the 31 northern fur seal

specimens, seven elements are from pups.

Despite substantial differences in excavation volume and faunal recovery, the analyzed samples of pinniped bones from the three sites are within the same order of magnitude (Table 1). Occupations at Cape Addington Rockshelter, the main village at Ts'ishaa, and at Netarts, are all dated to within the last 2000 years (i.e., they are roughly contemporaneous).<sup>1</sup>

#### CONTEMPORARY PATTERNS OF PINNIPED ABUNDANCES

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Northern fur seals spend much of their lives far offshore and are rarely seen nearshore today, except for the modern breeding sites on the Pribilof Islands in the Bering Sea and the Channel Islands off southern California. In the vicinity of Cape Addington, or almost anywhere else in southeast Alaska, northern fur seals are rare. Alaska Department of Fish and Game biologist Ken Pitcher (1998, pers. comm. to Moss) reported that several northern fur seals occasionally haul out on the Forrester Islands during the summer. The Forrester Islands are an isolated group of small islands located 68 km southwest of Cape Addington, a substantial distance by canoe. Currently, the Forrester Islands (Lowrie Island in particular) support the largest Steller sea lion breeding site in the world at approximately 7,000 animals (Isleib 1992:2; Pitcher et al. In press). The Hazy Islands, located 66 km northwest of Cape Addington, serve as another substantial Steller sea lion breeding site with about 3,000 animals counted annually (NMML 2004). Near the western tip of Cape Addington itself, only 8 km (by water) from the archaeological site, an average of 820 Steller sea lions haul out annually. Harbor seals are the most abundant

nearshore pinniped in southeast Alaska, but their absolute abundance in the vicinity of Cape Addington is not documented. Harbor seals do not migrate long distances annually. Cape Addington lies considerably north of the modern range of Guadalupe fur seals whereas the occurrence of California sea lions has increased recently (Maniscalco et al. 2004). Male northern elephant seals feed in the Aleutian Islands, but females and young generally occur south of 45°N. (NOAA 2002:1). The primary breeding sites for northern elephant seals are in California and Baja California.

With respect to the site of Ts'ishaa, northern fur seals migrate through British Columbia waters on their way north to the Pribilofs in April and on their way south in November (Kajimura 1984; MacAskie 1979). The modern populations do not come inshore, but tend to forage along the edge of the continental shelf, about 70 km from shore at this latitude (Ream et al. 2005). There are no isolated offshore islands near Ts'ishaa equivalent to the Farallon (Pyle et al. 2001) or Forrester Islands. The most accessible northern fur seals may have been those associated with a breeding site (or sites) in the vicinity of Cape Flattery, inferred by Etnier (2002a) and Crockford et al. (2002). Cape Flattery is approximately 75 km from Ts'ishaa.

Steller sea lions currently breed at three sites in British Columbia, but the closest to Ts'ishaa is the Scott Island complex (Pitcher et al. In press), located approximately 350 km north of Barkley Sound. Outside of the breeding season, Steller sea lions are widely dispersed. Today, small groups haul out near Ts'ishaa on the northeast side of Benson Island (less than a kilometer from the site, Frederick and Crockford 2005:198) and on several exposed reefs in the outer Broken Group islands in Barkley Sound (Bigg 1985). Although



California sea lions do not breed this far north (they breed mainly on the Channel Islands and off Baja California), some adult and subadult males overwinter in southern British Columbia (McTaggart Cowan and Guiguet 1965). Harbor seals are common year-round in Vancouver Island waters. Northern elephant seals are “reported rarely but sporadically” from the west coast of Vancouver Island (Banfield 1974; Frederick and Crockford 2005:199). Barkley Sound is considerably north of Monterey Bay, California, which is considered the northern limit of the range of Guadalupe fur seals prior to their nineteenth-century extirpation (NOAA 2000:1).

Since Netarts Bay is positioned along the northern Oregon Coast, pinniped abundances in both Washington and Oregon should be considered. Today, northern fur seals are infrequently seen along the coast except when they are stranded onshore. These tend to be females and juveniles that migrate south from the Pribilofs, so they occur in Oregon and Washington waters during the winter. In recent years, small numbers of northern fur seals have hauled out in the Shell Island—Simpson Reef area off Cape Arago (Oregon Coastal Atlas 2005), but this site is 245 km south of Netarts. Steller sea lions have no breeding sites on the coast of Washington today, but they maintain three colonies in southern Oregon (Rogue Reef, Orford Reef, and St. George Reef on the California border). Branded Steller sea lions from the Forrester Islands breeding area in Alaska (on Lowrie Island) and the Rogue Reef colony in Oregon have been observed along the Washington Coast (Pitcher et al. In press). Steller sea lion pups are born at Three Arch Rocks, located only 6 km north of the Netarts site, but biologists consider the numbers of pups too few for this site to

be classified as a breeding site (Robin Brown 2005, pers. comm. to Moss). As described above, California sea lions breed in California, and there is no evidence that they breed in Oregon today (McClenachan 2002), although Lyman (1988) suggested that they did in the past. Some adult and subadult males move north to winter in Oregon, Washington, and British Columbia. Those found in Oregon include animals moving to and from more northerly localities, as well as those that winter in Oregon. California sea lions also haul out at Three Arch Rocks and at the tip of Cape Lookout about 8 km south of Netarts. Harbor seals are year-round residents and reproduce everywhere they occur (Pearson 1968). Northern elephant seals have produced pups on Shell Island in recent years, but this appears to be the northernmost extent of their pupping range (Hodder et al. 1998). Even this site is considerably north of the contemporary range of Guadalupe fur seals in Monterey Bay.

To summarize, we list specific questions related to northern fur seals when archeological findings (as briefly presented in the previous section) are compared to contemporary patterns of abundance:

1. A few northern fur seal pup remains from Cape Addington are found in the absence of a contemporary breeding site for this species in the vicinity of the archaeological site. Are these remains from animals migrating to or from the Pribilof Islands, or was there a northern fur seal breeding area somewhere in southeast Alaska in the past?
2. Northern fur seals are the most abundant pinniped at Ts'ishaa, and fur seals of both sexes and all age groups are represented. Are these remains from animals migrating to or from

the Pribilof Islands, or was there a northern fur seal breeding area somewhere along the west coast of Vancouver Island (or the adjacent coast of Washington) in the past?

3. The northern fur seals from Netarts include males, females, and pups. Are these remains from animals migrating to or from the Pribilof Islands, animals associated with a Vancouver Island or Washington breeding area, or was there a breeding site somewhere along the Oregon Coast in the past?

#### MATERIALS AND METHODS

Moss and Losey identified the vertebrate remains from Cape Addington using comparative specimens in the Department of Anthropology at the University of Oregon. Pinniped bones from the site were also examined in reference to comparative collections in the Department of Anthropology at Oregon State University and the National Marine Mammal Laboratory in Sand Point, Washington. Losey used collections at these same institutions in his analysis of remains from the Netarts Sandspit site. From Ts'ishaa, Gay Frederick (Malaspina University-College, Nanaimo, British Columbia) and Susan Crockford (Pacific Identifications, Inc., Victoria, British Columbia) identified the vertebrate remains using the comparative collections of the Department of Anthropology, University of Victoria. It is worth noting that the DNA analyses reported below revise some of the identifications Moss (2004) and Losey (2002) reported on the Cape Addington and Netarts projects (see also Moss and Losey 2003).

Newsome measured the carbon and nitrogen isotope compositions of bone collagen extracted from archaeological specimens from Cape Addington,

Ts'ishaa, and Netarts at the Stable Isotope Laboratory in the Departments of Earth and Ocean Sciences, University of California, Santa Cruz. To gauge the feeding behavior of the northern fur seals, he also measured the isotopic composition from harbor seal bones from these same three sites for comparison. Harbor seals are well-documented nearshore resident foragers, whereas northern fur seals forage offshore. The isotopic composition from the remains of Steller sea lion and Guadalupe fur seal was also measured, as later identified by Yang and Speller through their analyses of ancient DNA (see results). The techniques used to clean and treat the samples have been described by Burton et al. (2001:110, 2002:8). The isotopic results are expressed as delta ( $\delta$ ) values where  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N} = \left( \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} \right] - 1 \right) \times 1000$ , and  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  ratios of the sample and the standard, respectively. The standards are Vienna Pee Dee Belemnite limestone for carbon and atmospheric  $\text{N}_2$  for nitrogen, and the units are parts per thousand or per mil (‰). Repeated measurements of a gelatin standard ( $n = 30$ ) yielded a standard deviation of  $<0.20$  for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. Duplicate isotopic measurements were performed on  $\sim 20\%$  of all unknown samples and yielded an absolute difference of 0.20 for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values.

Yang and Speller extracted ancient DNA from the archaeological specimens from the three sites in the dedicated Ancient DNA Laboratory in the Department of Archaeology at Simon Fraser University. The protocols used for bone preparation, bone decontamination, and DNA extraction can be found in Yang et al. (1998, 2004, 2005) and Speller et al. (2005). Both the conservative cytochrome b and the hyper-variable D-loop control region of mitochondrial DNA were analyzed to

generate genetic information for this study. The D-loop fragment of 199bp was amplified by forward primer NFS-F99-DL (5-CTCCCCCTATGTA CTTCGT GCA-3) and reverse primer NFS-R301-DL (5-GTACACTTTTCACAAGGGTTGC TG-3); a slighter shorter cytochrome b gene fragment of 180bp was targeted using forward primer NFS-F5-CtB (5-CCAACATTCGAAAAGTTCAT CC-3) and reverse primer NFS-R185-CtB (5- GCTGTGGTGGTGTCTGAGGT-3). All PCR amplifications were conducted in a Mastercycler Personal (Eppendorf, Hamburg, Germany) in a 30  $\mu$ L reaction volume containing 50 mM KCl and 10 mM Tris-HCl, 2.5 mM MgCl<sub>2</sub>, 0.2 mM dNTP, 1.5 mg/mL BSA, 0.3  $\mu$ M each primer, 3  $\mu$ L DNA sample, and 2.25 U AmpliTaq Gold™. PCR was run for 60 cycles at 94°C for 30 seconds, 55°C for 30 seconds, and 72°C extension for 40 seconds, with an initial denaturing at 95°C for 12 minutes. Five  $\mu$ L of PCR product were separated by electrophoresis on 2% agarose gel and visualized using SYBR-Green on a Dark Reader Box. PCR products were purified using Qiagen's MinElute™. For the majority of samples, both directions were sequenced with relevant PCR primers from the same PCR products or different PCR products of the same DNA sample.

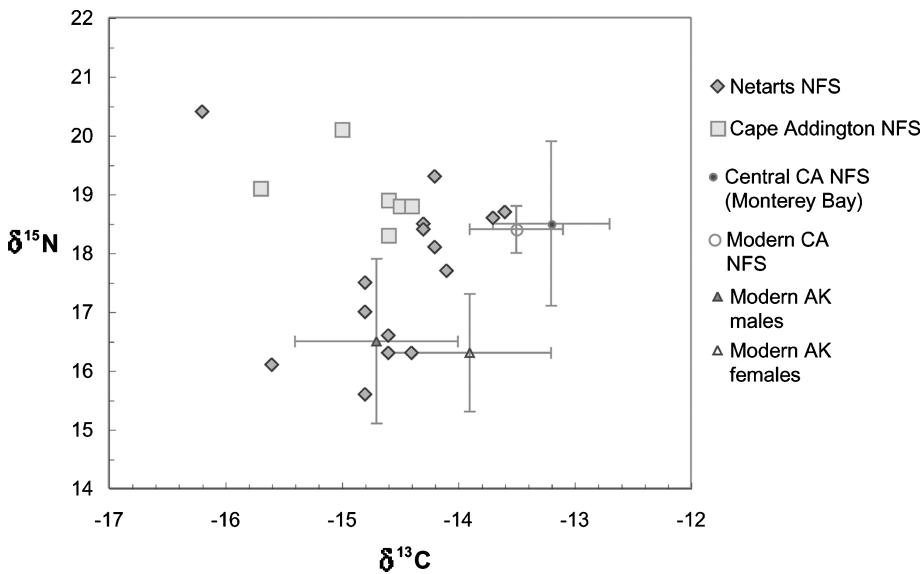
## RESULTS

Carbon and nitrogen isotope compositions of bone collagen were measured from 19 archaeological specimens from Cape Addington and 29 from Netarts (identified as northern fur seals and harbor seals). Of these same specimens, the 10 identified as northern fur seal from Cape Addington and the 16 identified as northern fur seal from Netarts underwent genetic analysis. From Ts'ishaa, 10 specimens underwent genetic analysis.

## Isotopic Measurements

A host of biological and physical variables interact to produce the isotopic composition of pinniped bones. Stable isotope values of plants and animals in marine ecosystems vary along a number of gradients, including latitude, nearshore versus offshore, proximity to upwelling, etc. (Aurioles et al. 2006; Kelly 2000; West et al. 2006). These isotopic differences cascade up food webs modified by fractionation at each successive trophic level (Kelly 2000; Kurle 2002; Newsome et al. 2006; Wu et al. 1999). Burton and Koch (1999) and Burton et al. (2001, 2002) have pioneered interpretation of isotopic values of pinniped bones. They have demonstrated how comparison between species and across different localities can be used to detect changes in patterns of foraging and migration over the millennia, specifically of northern fur seals. Age and sex are also key variables; adult male and adult female northern fur seals have different foraging patterns, and nursing pups feed on their mother's tissues at a trophic level higher than nursing females, exhibiting enriched nitrogen isotope values.

One complication that arises when comparing data from modern animals to archaeological specimens is that the isotopic composition at the base of marine food webs may have shifted due to anthropogenic perturbations. The best known of these is the Suess effect. The combustion of fossil fuels, which are relatively rich in <sup>12</sup>C, has caused the  $\delta^{13}\text{C}$  value of many Earth surface carbon reservoirs, including the atmosphere and surface ocean in some regions, to drop by  $\sim 1\text{‰}$  relative to values in the Late Holocene (e.g., Indermuhle et al. 1999; Quay et al. 1992). There is debate about the extent to which this effect would impact vertically



**Figure 3.** Carbon and nitrogen isotope ratios from Cape Addington, Netarts, and Monterey Bay archaeological sites compared to values for modern specimens.

well-mixed surface waters in high-latitude regions, such as the Bering Sea (Schell 2001). Here, however, we assume the effect is uniform throughout the North Pacific, and add 1‰ to  $\delta^{13}\text{C}$  values from modern pinnipeds.

Table 2 shows the isotopic values for individual pinniped specimens from Cape Addington and Netarts. Table 3 shows mean isotopic values from pinniped remains from these sites along with those from the Moss Landing site in Monterey Bay (CA-MNT-234, Burton et al. 2001) and two modern samples (one from the Pribilof Islands, one from San Miguel Island; see also Figure 3). First we compare the harbor seal values to those of adult female northern fur seals. Burton and Koch (1999) have shown that the bone collagen  $\delta^{13}\text{C}$  values in modern harbor seals as nearshore feeders are ~2‰ higher than those of offshore feeders such as northern fur seals. At Moss Landing, the difference is 1.7‰ and at Netarts the difference is 1.3‰, roughly

consistent with expectations. No adult female northern fur seals from Cape Addington are available for comparison with harbor seals.

The  $\delta^{15}\text{N}$  values of the Moss Landing harbor seals are not significantly different from that of the northern fur seals from that site. In contrast, the Cape Addington harbor seal mean  $\delta^{15}\text{N}$  values are 1.1‰ lower than that of northern fur seals. In this case, the high values for the Cape Addington fur seals are probably due to the age of the animals whose remains were tested; young fur seals are represented, but no adults. Previous investigators have shown that because nursing pups feed at a higher trophic level than adults, their  $\delta^{15}\text{N}$  values will be enriched (Newsome et al. 2006). At the Netarts site, while the harbor seal  $\delta^{15}\text{N}$  values are 0.4‰ lower than that of the adult male northern fur seals from the site, they are 2.4‰ higher than the female northern fur seals. There are several possibilities to explain this

**Table 2. Carbon and nitrogen isotope values from Netarts and Cape Addington.**

Provenience	Species	Element	Sex/Age	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	SFU #NF-
NETARTS 35-TI-1						
House 12 brown sand and shell layer	<i>Arctocephalus</i>	L tibia	Juvenile	-15.9	21.4	11
House 13 rim	<i>Callorbinus</i>	R mandible	Adult male	-13.7	18.6	2
House 10 fill	<i>Callorbinus</i>	R calcaneous	Adult male?	-14.2	19.3	14
House 13, upper occupation	<i>Callorbinus</i>	ilium	Adult male	-14.3	18.5	16
House 13 fill	<i>Callorbinus</i>	L femur	Adult male	-14.3	18.4	4
House 12 fill	<i>Callorbinus</i>	L femur	Adult male	-14.8	17.5	15
House 1 carbon stratum	<i>Callorbinus</i>	R femur	Adult male	-16.2	20.4	6
House 13, sand lens below outside	<i>Callorbinus</i>	L mandible	Subadult male	-14.1	17.7	9
House 13 fill	<i>Callorbinus</i>	L femur	Adult female	-14.8	17.0	10
House 13 shell layer gray sand	<i>Callorbinus</i>	R femur	adult female	-14.2	18.1	5
House 12 fill	<i>Callorbinus</i>	R femur	Adult female	-14.8	15.6	3
House 13 fill	<i>Callorbinus</i>	L femur	Adult female	-14.6	16.6	12
House 2	<i>Callorbinus</i>	L femur	Adult female	-15.6	16.1	7
House 12 fill	<i>Callorbinus</i>	L ulna	No estimate	-14.6	16.3	1
House 12 fill	<i>Callorbinus</i>	L ulna	Adult female	-14.4	16.3	8
House 10 fill	<i>Eumetopias</i>	R astragalus	Adult female	-13.6	18.7	13
CAPE ADDINGTON 49-CRG-188						
Unit 2/Stratum VI	<i>Callorbinus</i>	Ulna	Juvenile	-15.0	20.1	34
Unit 7, 23-35 cm	<i>Callorbinus</i>	Premaxilla	Pup	-14.6	18.9	32
Unit 7, 25-35 cm	<i>Callorbinus</i>	Maxilla	Pup	-14.5	18.8	37
Unit 7, 15-25 cm	<i>Callorbinus</i>	Maxilla w/canine & 1 post-canine	Pup	-14.4	18.8	30
Unit 2/Stratum IVB	<i>Callorbinus</i>	Pubis, ischium, part of acetabulum	Pup	-14.6	18.3	35
Unit 7/ SE bulk sample	<i>Callorbinus</i>	Calcaneous	Juvenile	-15.7	19.1	33
Unit 7, 65-75 cm	<i>Eumetopias</i>	Scapula	Adult	-13.4	21.2	36
Unit 6, 15-25 cm	<i>Eumetopias</i>	Scapula	Adult	-14.8	20.3	31
Unit 6-7 slough	<i>Eumetopias</i>	Femur	Juvenile	-14.6	19.6	29
Unit 7, 40 cm	<i>Eumetopias</i>	Auditory bulla and zygomatic	Adult	-14.3	20.0	28

**Table 3.** Mean carbon and nitrogen isotope values from three archaeological sites and two modern populations. The modern  $\delta^{13}\text{C}$  data have been corrected for the Suess effect by adding 1.0 per mil to the mean  $\delta^{13}\text{C}$  values.

Site/Locality	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		Species	N	Source
	Mean	SD	Mean	SD			
Pribilof (modern)	-12.7	1.0	17.4	1.8	Harbor seal	37	Burton et al. 2001
	-13.9	0.7	16.3	1.0	Northern fur seal (female)	9	Burton et al. 2001
	-14.7	0.7	16.5	1.4	Northern fur seal (male)	9	Burton et al. 2001
	-13.3	—	17.9	—	Northern fur seal	19	Hirons et al. 2001
Cape Addington	-12.0	0.7	17.9	1.1	Harbor seal	9	This study
	-14.8	0.5	19.0	0.6	Northern fur seal (pup-juvenile)	6	This study
	-14.3	0.6	20.3	0.7	Steller sea lion	4	This study
Netarts	-13.3	0.9	19.1	0.8	Harbor seal	13	This study
	-14.6	0.5	16.7	0.8	Northern fur seal (female)	8	This study
	-14.6	0.9	19.5	1.3	Northern fur seal (male)	6	This study
	-13.6	—	18.7	—	Steller sea lion	1	This study
Moss Landing	-15.9	—	21.4	—	Guadalupe fur seal	1	This study
	-11.5	0.3	18.1	0.3	Harbor seal	13	Burton et al. 2001
	-12.8	0.4	18.5	1.0	California sea lion	17	Burton et al. 2001
San Miguel (modern)	-13.2	0.5	18.5	1.4	Northern fur seal	61	Burton et al. 2001
	-13.5	0.4	18.4	0.4	Northern fur seal	6	Burton et al. 2001

pattern. The Netarts harbor seals appear to be somewhat  $^{15}\text{N}$ -enriched relative to conspecifics at other sites in California and the Pacific Northwest. Harbor seal values of  $\sim 18\text{‰}$  are common in this region, but values up to  $19\text{‰}$  are anomalous, suggesting greater access to a higher trophic level food resource (possibly salmon).<sup>2</sup> The values for female northern fur seals at Netarts, in contrast, are similar to values for females from the Pribilofs and other sites along the Pacific Coast. Finally if the male northern fur seals from Netarts fed offshore, as we suspect from their  $\delta^{13}\text{C}$  values, then they either fed at a trophic level higher than females, or they fed further south, off the California Coast, in waters similar

to those used by animals from Moss Landing.

At Cape Addington, the  $\delta^{15}\text{N}$  values of Steller sea lion are  $1.3\text{‰}$  and  $2.4\text{‰}$  greater than that of northern fur seal and harbor seal respectively. For the  $\delta^{13}\text{C}$  values, the Cape Addington Steller sea lions are  $2.3\text{‰}$  lower than the harbor seals, but  $0.5\text{‰}$  higher than the northern fur seals. This suggests that the Steller sea lion foraging pattern more closely resembles that of the northern fur seals at the site than it does that of the harbor seals (i.e., more offshore than nearshore). From Netarts, isotopic values are available from only one Steller sea lion. For this specimen, the  $\delta^{13}\text{C}$  values are closer to that of the harbor

seals ( $-0.3\text{‰}$ ) than to the northern fur seals ( $+1.0\text{‰}$ ). The  $\delta^{15}\text{N}$  values of Steller sea lion fall within the wide range between the male and female northern fur seals (2.0‰ more than females, 0.8‰ less than males). The small sample size precludes further discussion.

To summarize, the high  $\delta^{15}\text{N}$  values appear to confirm the presence of northern fur seals less than 1 year old at Cape Addington. We say “appear to confirm” because bone collagen takes as much as 10 months to turnover, and young-of-the-year could still have high nitrogen isotope values for several months as the weaning signal is diluted out of the system (Newsome et al. 2006). At both Cape Addington and Netarts, northern fur seals were feeding offshore, as indicated in their lower  $\delta^{13}\text{C}$  values when compared to harbor seals, conforming to predictions (Burton and Koch 1999; Burton et al. 2001). Yet the isotope values do not allow us to distinguish the northern fur seals of Cape Addington or Netarts from those of the modern Pribilof Islands.

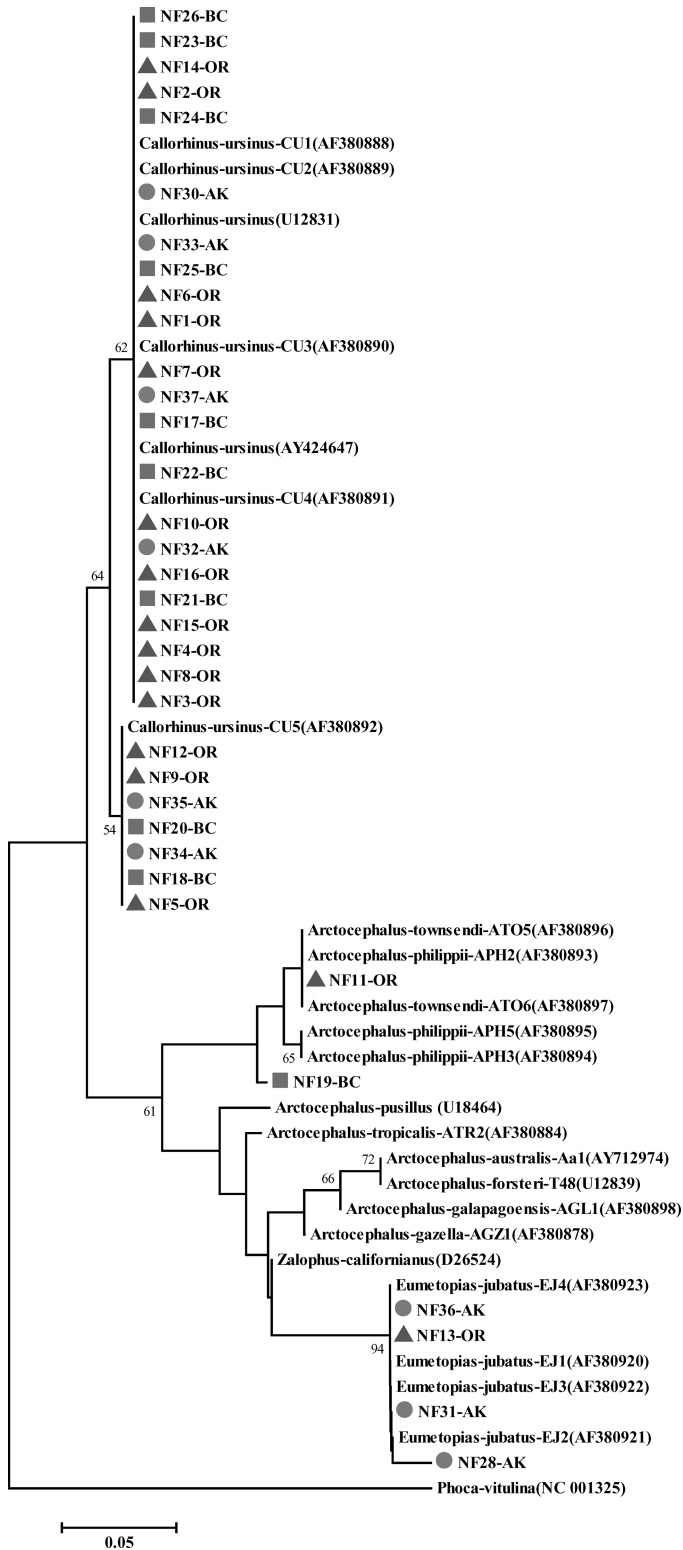
#### Ancient DNA

Yang and Speller analyzed 37 bone samples: 16 from Netarts (sample numbers NF1-NF16), 10 from Ts’ishaa (NF17-NF26), and 11 from Cape Addington (NF27-NF37). The specimens from Netarts and Cape Addington used for isotopic analysis were also used for genetic analysis. The results show that the analyzed samples contain good quality DNA. Of 37 samples, 35 yielded positive PCR amplifications for the cytochrome b fragment and only one sample failed for the D-loop amplification. When the amplified DNA sequences are compared with those from GenBank (Wynen et al. 2001) through phylogenetic analysis, the obtained trees reveal that the cytochrome b fragment clearly affiliates

the ancient DNA samples with available modern reference DNA sequences, allowing for confident species identifications (Figure 4). The D-loop fragment, on the other hand, reveals a significant amount of variation within the ancient sequences, although the same species identifications can also be determined (Figure 5).

Several bone samples previously identified morphologically as northern fur seal were determined to be from other species through DNA analysis. These include four specimens from Cape Addington and one specimen from Netarts identified through genetic analysis as Steller sea lion.<sup>3</sup> This discrepancy may reflect intrinsic difficulties associated with morphological identification of some fragmentary and juvenile skeletal remains. Although Steller sea lion remains were identified in both assemblages, without comparative specimens representing the full range of morphological variation among pinniped species, identification errors were made. An additional specimen from Netarts was identified genetically as Guadalupe fur seal (*Arctocephalus townsendi*). This specimen can be added to two Guadalupe fur seal bones previously identified by Losey (2002) from the site. This result is consistent with Etnier’s (2002b) study identifying Guadalupe fur seal at Ozette, showing that this species ranged further north at the time these sites were occupied than it does today. Ideally, the species identifications reported here should be confirmed with more reference DNA sequences.

Analyses of both the D-loop and cytochrome b fragments indicate that sample NF19 from Ts’ishaa cannot easily be assigned to either the Guadalupe fur seal (*A. townsendi*) or the southern fur seal (*A. philippii*) based on its position in the trees and its low bootstrap values (below 50%). Genetic analyses of





modern southern fur seal populations have revealed a very close genetic relationship between *A. philippii* and *A. townsendi* (Wynen et al. 2001), and *A. townsendi* has also experienced a loss of genetic diversity (Weber et al. 2004). This makes it difficult to distinguish the two species based on limited fragments of mtDNA.

The phylogenetic analysis currently shows 23 haplotypes of the D-loop present within the 29 samples identified as northern fur seal, representing a high diversity of haplotypes. Because the same haplotype is found among both the Ts'ishaa and Netarts samples (NF21 and NF14), the minimum number of individual northern fur seals represented at the three sites (based on aDNA) is 24, with a MNI of four individuals from Cape Addington, nine from Ts'ishaa, and 11 from Netarts. At this stage of the analysis, we cannot use the aDNA data alone to distinguish between the same individual, the same maternal family, or a closely related maternal lineage. Based on morphology and provenience, however, samples NF37, NF32, and NF30 from Cape Addington could be the same individual. This would mean that at least two pups and two juvenile northern fur seals are represented among the samples tested from Cape Addington (Table 2). From Ts'ishaa, all nine specimens have different haplotypes (i.e., they represent

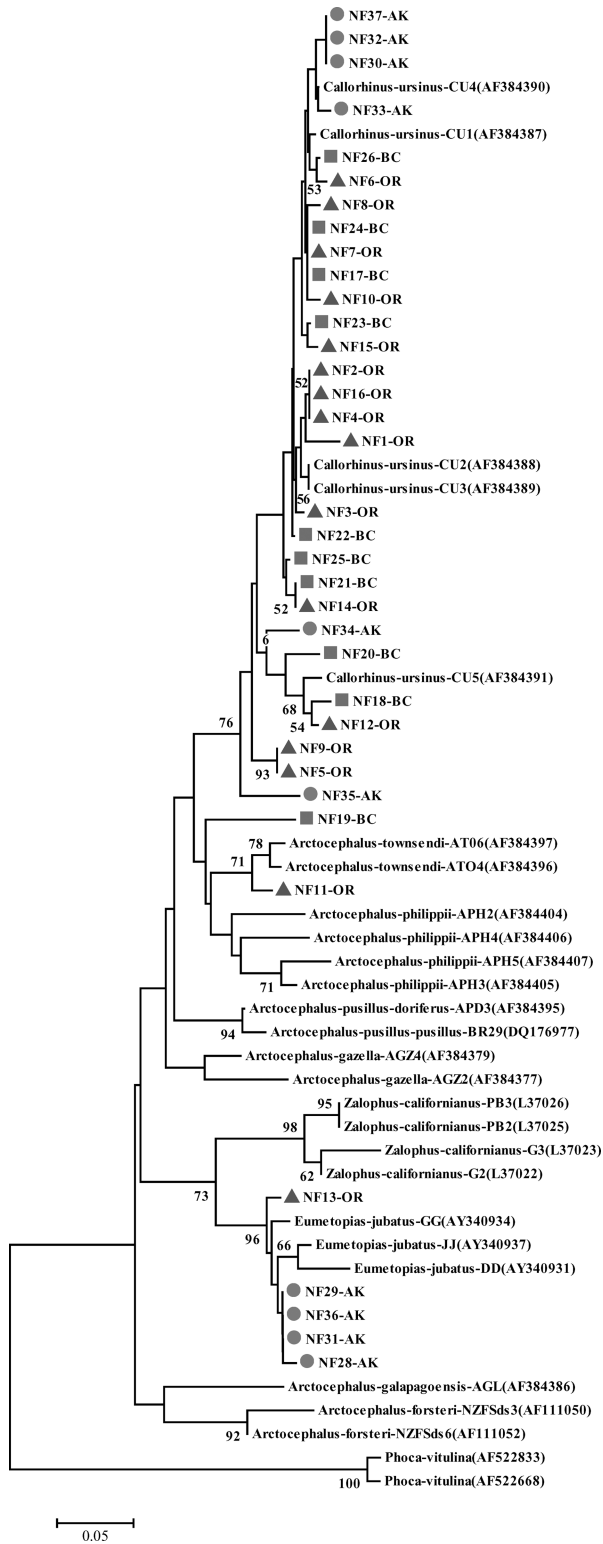
nine individual animals), with a mix of adults, possibly two subadults and two juveniles represented (McKechnie, unpublished data). From Netarts, two sets of samples are the same haplotype (NF2, NF16, NF4 and NF9, NF5). Considering the morphological and provenience data, NF2, NF16, and NF4 could be from the same individual, but NF9 and NF5 cannot, resulting in an MNI value of 12 northern fur seals from Netarts.

The large number of haplotypes (23 from the 29 samples) suggests a much higher genetic variability in the precontact populations, although the relatively small number of modern DNA haplotypes used in this study prevents us from drawing firm conclusions regarding the extent of recent genetic bottlenecks. The phylogenetic trees do not reveal distinctive clades within the archaeological DNA sequences. These sequences are scattered across the five available modern northern fur seal DNA sequences from GenBank. The archaeological samples do not cluster into site groupings (i.e., there is no correlation between the DNA haplotype and geographic location).

The lack of strong geographic association fails to confirm the presence of local northern fur seal breeding sites along the Pacific Coast of Oregon, British Columbia, and southeast Alaska. Yet the

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**Figure 4.** Results of phylogenetic analysis of northern fur seals from Cape Addington (circles), Ts'ishaa (squares), and Netarts (triangles) archaeological sites inferred from partial cytochrome *b* sequences. The phylogenetic tree displays the cytochrome *b* gene haplotype diversity of the 35 archaeological samples (NF27 and NF29 failed to yield DNA) based on the amplified cytochrome *b* gene fragment. The tree (NJ with Kimura 2-parameter) was composed using Mega3 software (Kumar et al. 2004) with harbor seal (*Phoca vitulina*) as the outgroup. The numbers at the nodes indicate those bootstrap values above 50% after 2000 replications. As expected, less haplotype diversity was observed when compared to that of the D-loop fragments (Figure 5) and the tree is consistent with those built by longer cytochrome *b* gene fragments revealing the evolutionary histories of Otariidae (Wynen et al. 2001). For some reference sequences, the code after the species name in the sequence label is the haplotype code listed in GenBank.



DNA results cannot be used to reject the hypothesis that such breeding sites existed at some time in the past. If the northern fur seal had at least two groups according to their behaviors (one or more “residential” or “non-migratory” at mid-latitudes and the other migratory from the Pribilofs), we should see genetic difference between the groups only if: 1) they were reproducibly isolated from each other for a significant amount of time; and 2) there was no emigration/immigration between one group to the other. Unless populations are geographically circumscribed (like some terrestrial species), opportunistic switchover cannot be ruled out. Our limited aDNA data are consistent with a migratory mode of behavior for northern fur seals.

Archaeologists have used the purported distinction between pinnipeds that are resident or migratory breeders to debate the nature of technological and cultural evolutionary change (e.g., Hildebrandt and Jones 1992; Jones and Hildebrandt 1995; Lyman 1995). Yet Lyman (1995:50–51) pointed out that the categories of resident breeder and migratory breeder “are founded on the historic behaviors of these species,” and that these categories might not adequately characterize the past. Even though northern fur seals are generally labeled as “migratory,” the San Miguel northern fur seals are now considered

a separate stock that is essentially non-migratory (NOAA 2003b). This contemporary behavior, as well as evidence accumulating from archaeological studies (e.g., Crockford et al. 2002; Gifford-Gonzalez et al. 2005), show that it is a mistake to consider long-distance migrations as characteristic of all northern fur seals throughout the Holocene, when even today this species exhibits significant behavioral flexibility.

The DNA variation observed from our phylogenetic analyses does not confirm the hypothesis of long-term and/or isolated breeding sites used by non-migratory populations. Alternately, the DNA data do not allow us to reject the hypothesis that such breeding areas existed, even if not in total isolation. At this point in time, due to the limited length of the analyzed ancient DNA fragments and the lack of an adequate number of modern DNA samples against which to compare, we cannot use this analysis to confirm the presence of colonies at locations near the three archaeological sites under consideration. With the addition of more northern fur seal data points to GenBank, our results will be worth re-visiting in the future.

#### DISCUSSION AND CONCLUSIONS

Study of ancient DNA along with morphological analyses have allowed the identification of a minimum of four

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**Figure 5.** Results of phylogenetic analysis of northern fur seals from Cape Addington (circles), Ts’ishbaa (squares), and Netarts (triangles) archaeological sites inferred from partial D-loop sequences. The phylogenetic tree displays the D-loop haplotype diversity of the 36 archaeological samples (NF27 failed to yield DNA) based on the amplified mtDNA control region fragment. The tree (NJ with Kimura 2-parameter) was composed using Mega3 software (Kumar et al. 2004) with harbor seal (*Phoca vitulina*) as the outgroup. The numbers at the nodes indicate those bootstrap values above 50% after 2000 replications. Although the DNA fragment analyzed may not be sufficiently informative to reflect Otariidae species evolutionary histories (Wynen et al. 2001), the fragment is useful for assessing haplotype relationships within species. For some reference sequences, the code after the species name in the sequence label is the haplotype code listed in GenBank.

individual northern fur seals from Cape Addington, nine from Ts'ishaa, and 12 from Netarts among our samples. From Cape Addington, the presence of two young-of-the-year and two juvenile northern fur seals was confirmed. The Netarts sample we tested contains northern fur seal adults of both sexes and one subadult. Unfortunately, none of the seven northern fur seal pup bones found at the site (Losey 2002) were included in the sample that underwent isotopic or aDNA analyses. The Ts'ishaa sample we tested includes a mix of adults, possibly two subadults, and two juveniles. Only one of the bones we tested is included among the seven northern fur seal bones (representing seven individuals) Crockford et al. (2002:162) identified as "rookery age animals."

Until we better understand the variables involved in producing the isotopic signatures in bone, and until more DNA data on modern northern fur seals have been published, the best evidence for a breeding area may be morphological age estimates that show that more than a few pups are present. Of the three sites reviewed in this paper, the sample from Ts'ishaa presents the strongest case for a breeding area somewhere in the vicinity of this site. Crockford et al. (2002:162) identified the remains of seven individual "rookery-age" northern fur seals, arguing that it is not possible that these young animals migrated from the Pribilof Islands. Even from Tsi'ishaa, however, the number of pups is relatively small. The numbers of northern fur seal pups from Cape Addington and Netarts are even smaller. Greater numbers of all the age and sex groups present will be necessary to generate robust harvest profiles. The isotopic values of young fur seals from Cape Addington are suggestive of "rookery age," although because the weaning signal persists for so long, and because of the small sample size, we

cannot rule out the possibility that these are stragglers or stranded animals.

For archaeological sites located along the Pacific Coast from Oregon north to Alaska, it appears that available isotopic data are hard to use as direct evidence to support a case for or against the presence of local northern fur seal breeding areas. Isotopic values from northern fur seals in California are distinct from those in the Pribilofs, but once animals are foraging north of the North Pacific Current (which flows west to east between 40° N. to 50° N.), they appear to have values similar to the modern Pribilof population. One goal of the ancient DNA analysis was to provide data complementary to the isotopic results to better understand the relationship between prehistoric and modern northern fur seals. At this time, our genetic data have not allowed us to answer the question of local breeding areas, partly because of the limited modern northern fur seal DNA data available through GenBank. As Mulligan (2006:368) stated, a "sufficiently comprehensive and representative dataset on modern individuals" must exist to answer research questions such as those posed in this study.

Nevertheless, this is one of the first archaeological studies to report successful extraction and amplification of ancient DNA from three pinniped species: northern fur seal, Steller sea lion, and Guadalupe fur seal. As more genetic data become available, we may be able to answer questions related to how humans interacted with northern fur seals in the past. If ancient breeding areas of the northern fur seal can be identified (or inferred), we might better understand archaeological site seasonality and human settlement patterns within subregions of the outer North Pacific Coast. Alternatively, if northern fur seals harvested at these sites exhibited the same migratory behavior as that of

the Pribilof population today, it would appear that people were venturing considerable distances offshore in ocean-going watercraft to take northern fur seals.

With additional genetic work, the consequences of bottleneck events that occurred in the past might be identified. Understanding the genetic diversity of northern fur seals is important because this species has been listed as a depleted stock under the Marine Mammal Protection Act of 1988 (NOAA 2005b:iv). Although the size of the Eastern Pacific stock of northern fur seals appears healthy at an estimated 888,120, pup production in recent years has dropped below the 1921 level on St. Paul Island and below the 1916 level on St. George Island (NOAA 2005b:16). From their 2004 field survey, Towell et al. (2006:489) estimated that pup production on the Pribilof Islands is less than half of what it was in 1968. Archaeological data suggest, moreover, that northern fur seals were more widely distributed in the past, when they may have been less vulnerable to catastrophic collapse. A loss of genetic diversity since the eighteenth and nineteenth centuries has been documented for other marine mammals (Larson et al. 2002; Weber et al. 2004), and the same may be true for northern fur seals.

To a great extent, the distribution and abundance of many of the 33 pinniped species extant today has been shaped by human activity over the past 250 years. Eventually, we hope that archaeological research can help us establish a baseline from which to evaluate the rapid changes that have occurred during the era of industrial and commercial northern fur seal exploitation. Clearly, more study of larger samples of northern fur seal remains from other Pacific Coast archaeological sites is warranted.

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#### END NOTES

1. Of the 250 northern fur seal bones identified from Ts'ishaa, 219 are from the main village, and 31 are from the older back terrace.
2. Ideally one should control for sex among the harbor seal values also. Although adult male harbor seals are somewhat larger than adult females, faunal analysts generally do not distinguish them osteologically.
3. The isotopic composition of only one of the four Steller sea lion specimens from Cape Addington fell outside the range exhibited by the northern fur seal specimens at this site.

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