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Holocene changes in the ecology of northern fur seals: insights from stable isotopes and archaeofauna

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Abstract The remains of northern fur seals (*Callorhinus ursinus*) are among the most abundant of pinniped elements recovered from mainland coastal archaeological sites in both California and Oregon. This is surprising as all contemporary northern fur seals breed exclusively on offshore islands, primarily at high latitudes, and the species is otherwise pelagic. The vulnerability of these animals to human predation suggests that either humans were foraging much further offshore than has been presumed or alternatively that the ecology of these animals has shifted during the late Holocene. We used isotopic and archaeofaunal analysis of the remains of pinnipeds from the middle to late Holocene of central and northern California to clarify the breeding and foraging behavior, and migration patterns of these ancient animals. The carbon and nitrogen isotope compositions of ancient northern fur seals reveal that these animals fed as far offshore as they do today, and that they remained at middle latitudes throughout the year. From an archaeological site at Moss Landing, California, we identified 16 skeletal ele-

ments from at least 12 very small northern fur seal pups. From another site near Mendocino, California, we identified the remains of at least 6 pups. We estimate the size and age of 5 of the young animals using sex-specific regressions of body length on the short dentary length derived from measurements of modern specimens. Our estimates indicate these ancient pups were substantially smaller, and therefore younger, than modern 3-month-old northern fur seal pups from similar latitudes and their nitrogen isotope compositions suggest they had not been weaned. As present-day northern fur seals do not leave their rookeries until they are at least 4 months old, we consider it highly unlikely that these ancient pups swam to these mainland locations from some distant island rookery. While there are numerous nearshore rocky outcrops along the Mendocino Coast, which may have supported small breeding colonies, the Moss Landing site is centered on a 40-km-long sandy beach, and is more than 120 km from what at the time were the nearest offshore islands. We conclude that northern fur seal adult females, subadults, and pups whose remains were recovered at the Moss Landing archaeological site must have been taken at a mainland rookery. Evidence that northern fur seals once bred on the mainland at this central California location suggests that the abundant remains of these animals at numerous other archaeological sites along the California coast also reflect the presence of nearby mainland rookeries. Based on the relative abundance of their remains in ancient human occupation sites and the widespread distribution of sites where their remains have been found, it appears that northern fur seals were once the predominant pinniped throughout a region where they now only rarely occur. Furthermore, their presence along the central and northern California coasts appears to have once severely limited the distribution of other pinnipeds, which are now common to the region.

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Introduction

Recent observations may offer an incomplete view of the true range of behaviors and ecological roles available to extant organisms. Human harvesting and habitat alteration have affected many species, and observations of modern populations are too brief to encompass response to climatic cycles on decadal, centennial, and longer time scales. The fossil record can be a valuable source of information on the behavior and ecology of contemporary species that have experienced recent declines in abundance (Lyman 1996).

This study was stimulated by the surprising observation that the remains of northern fur seals (*Callorhinus ursinus*) are common at mainland archaeological sites from coastal California and Oregon, often comprising more than 50% of the identified pinnipeds (Table 1). At present, all extant populations of northern fur seals breed on offshore islands, primarily at high northern latitudes ($>54^{\circ}\text{N}$), and they do not otherwise regularly haul out on land (Gentry 1998). After the 4-month breeding season, females and juveniles from the Alaskan rookeries range as far south as Baja California, but typically remain more than 75 km offshore where they forage over the shelf/slope break (Kajimura 1980). The males from Alaskan rookeries also forage offshore but remain at high latitudes throughout the year (Gentry 1998).

In recent decades, small rookeries have formed off California on San Miguel Island (Peterson et al. 1968) and on the Farallon Islands (Sydeman and Allen 1999). Several historic offshore rookeries along California and the Pacific Northwest have been attributed to this species but it appears that these rookeries were decimated by fur traders during historic times (Starks 1922). Today, these animals are extremely uncommon on the California

mainland, so their ubiquity in middle Holocene coastal archaeological sites is enigmatic, as noted by prior workers (Hildebrandt 1984; Schwaderer 1992).

We evaluate three explanations for this enigma. First, most middle Holocene northern fur seals may have bred at high latitudes, as they do today, and were merely foraging at middle latitudes. If so, their abundant remains suggest either that humans hunted them far offshore, or that they were hunted while foraging nearshore or while hauled out on land. Second, middle Holocene northern fur seals at mainland California sites may have come from rookeries on the few offshore islands in the region (e.g. the Channel Islands – Walker et al. 2000), and again been vulnerable while foraging near shore or while hauled out on land. Finally, the abundant remains of northern fur seals that have been found at mainland sites, may be evidence that humans were exploiting mainland rookeries unknown to the region historically.

We consider offshore hunting unlikely, as offshore-foraging pinnipeds would have been well beyond the range of the simple boats used by aboriginal central Californians (Jobson and Hildebrandt 1980). This inference is supported by the lack of offshore fish remains from closely studied archaeofaunas that include large numbers of northern fur seals (Milliken et al. 1999). Moreover, northern fur seals occur at low densities while at sea (2–3 individuals/km²; Kajimura 1980) rendering them an energetically unrenumerative prey.

To evaluate the remaining hypotheses, which entail changes in the migration or foraging patterns of northern fur seals, we analyzed the carbon and nitrogen isotope ratios of bone collagen from the species and other pinnipeds whose remains were recovered at prehistoric human occupation sites from central and northern California. We then compared these to baseline isotope ratios for modern

Table 1 Abundance of northern fur seal remains at selected California and Oregon Holocene human occupation sites. Relative abundance estimates based on number of individual specimens (NISP)

Archaeological site	Latitude (°N)	Age of site (BP)	Abundance of <i>Callorhinus</i> (NISP)	<i>Callorhinus</i> (% of all pinnipeds)
California				
San Miguel Island ^a	34 03	8,500–800	304	71%
Monterey ^a	36 35	5,000–150	122	80%
Elkhorn Slough ^a	36 49	>5,500–1,000	18	20%
Moss Landing MNT-234 ^b	36 48	5,500–1,400	79	86%
Moss Landing MNT-234 ^c	36 48	5,500–1,400	27	79%
AŌo Nuevo Point ^d	37 00	~3,200	142	96%
San Mateo ^a	37 20	3,000–150	170	61%
Duncan's Point ^e	38 25	8,200–3,200	45	53%
Mendocino Co. ^a	39 20	1,000–100	14	5%
Shelter Cove ^f	40 00	>1,000	5	9%
Spanish Flat ^f	40 20	>1,000	16	50%
Patrick's Point ^f	41 10	>1,000	6	18%
Stone Lagoon ^f	41 15	>1,000	74	73%
Oregon				
Bandon ^a	43 00	2,300–600	8	7%
Umpqua/Eden ^f	43 40	3,000–200	31	6%
Seal Rock ^f	44 30	400–100	97	8%
Yaquina Head ^f	44 40	4,000–150	17	10%
Whale Cove ^f	44 45	3,000–2,500	19	16%
Seaside ^a	46 00	3,700–1,600	13	20%

^a Lyman (1995)

^b This study

^c Breschini and Haversat (1995)

^d Hylkema (1991)

^e Wake and Simons, (in press)

^f Hildebrandt and Jones (1992)

Table 2 $\delta^{13}\text{C}$ values of bone collagen from Modern and Middle to Late Holocene pinnipeds of the northeastern Pacific. Data for modern groups are from Burton and Koch (1999) except for the values of contemporary northern fur seals from middle latitudes

Foraging location	Foraging latitude	$\delta^{13}\text{C}$ Mean \pm SD	$\delta^{15}\text{N}$ Mean \pm SD	Groups	<i>n</i>
Modern pinnipeds from central and southern California					
Nearshore	Middle	-12.4 \pm 0.6	18.7 \pm 1.0	Harbor seal	18
Nearshore	low – middle	-13.8 \pm 1.1	18.6 \pm 0.9	California sea lion	15
Offshore	Middle	-14.4 \pm 0.8	18.1 \pm 1.3	Northern elephant seal (female)	14
Offshore	Middle	-14.5 \pm 0.4	18.4 \pm 0.4	Northern fur seal	6
Modern pinnipeds from Alaska					
Nearshore	High	-13.7 \pm 1.0	17.4 \pm 1.8	Harbor seal	37
Offshore	high – middle	-14.9 \pm 0.7	16.3 \pm 1.0	Northern fur seal (female)	9
Offshore	High	-15.7 \pm 0.7	16.5 \pm 1.4	Northern fur seal (male)	9
Middle to Late Holocene pinnipeds from central Californian Monterey Bay					
Nearshore	Middle	-11.5 \pm 0.3	18.1 \pm 0.3	harbor seal	13
Nearshore	low – middle	-12.8 \pm 0.4	18.5 \pm 1.0	California sea lion	17
Offshore	Middle	-13.2 \pm 0.5	18.5 \pm 1.4	Northern fur seal	61
Middle to Late Holocene pinnipeds from northern Californian Mendocino coast					
Nearshore	Middle	-11.9 \pm 0.5	17.9 \pm 0.5	Harbor seal	8
Nearshore	low – middle	-13.1 \pm 0.7	19.0 \pm 1.9	California sea lion	5
Offshore	Middle	-13.5 \pm 0.7	18.3 \pm 1.1	Northern fur seal	10

pinnipeds whose foraging habits and latitudinal distributions are well known (Burton and Koch 1999).

The carbon isotope ratio of marine consumers reflects the isotopic composition of carbon fixed at the base of marine foodwebs (Hobson and Welch 1992) with a consistent whole-body ^{13}C -enrichment of $\sim 1.0\text{‰}$ at each trophic step (Rau et al. 1983). Although animal isotope compositions vary considerably among tissue types (Tieszen et al. 1983) this pattern of ^{13}C -enrichment is consistent when similar tissues (i.e. bone, or muscle, or hair) are compared (Koch et al. 1994).

In extant marine animals, carbon isotope composition ($\delta^{13}\text{C}$) also varies with the distance from shore and the latitude at which the animal feeds (Hobson et al. 1994, 1997). A study of modern pinnipeds reveals these distinctions clearly; offshore feeders have lower collagen $\delta^{13}\text{C}$ values than nearshore feeders, and high-latitude feeders have lower $\delta^{13}\text{C}$ values than middle-latitude feeders (Burton and Koch 1999). For example, male northern fur seals from Alaska rely exclusively on high-latitude offshore foodwebs (Gentry 1998) and they have $\delta^{13}\text{C}$ values that are about 2.0‰ lower than values for harbor seals (*Phoca vitulina*) that feed in nearshore waters (Bigg 1981) at similar latitudes (Table 2). The same pattern is apparent when comparing nearshore foraging harbor seals from California to female northern elephant seals (*Mirounga angustirostris*), which are known to feed exclusively in offshore middle-latitude waters (LeBoeuf et al. 1993). When comparing animals that forage at different latitudes, those feeding at high latitudes have $\delta^{13}\text{C}$ values that are about 1.0‰ lower than values for animals feeding at middle latitudes, and this pattern is apparent in both the nearshore and offshore (Table 2). Nearshore-to-offshore $\delta^{13}\text{C}$ gradients most likely reflect differences in phytoplankton production, with higher

values in more productive nearshore waters (Falkowski et al. 1998). The meridional gradient probably reflects differences in the $\delta^{13}\text{C}$ of inorganic carbon available for photosynthesis, due to differences in vertical ocean-mixing (Kroopnick et al. 1970). These differences can also be used to identify patterns of movement over large latitudinal ranges. For example, $\delta^{13}\text{C}$ values for female northern fur seals foraging both at high latitudes and along the eastern Pacific margin at middle latitudes have $\delta^{13}\text{C}$ values intermediate between values for the males of the species and female northern elephant seals.

Nitrogen isotope ratios are strongly sensitive to trophic effects, with an average ^{15}N enrichment of 3.0‰ at each trophic step (DeNiro and Epstein 1981; Schoeninger and DeNiro 1984), but they can also be used to identify the latitude at which marine animals forage. Modern pinnipeds residing at middle latitudes of the north Pacific have higher $\delta^{15}\text{N}$ values than those from higher latitudes (Table 2; Burton and Koch 1999). Meridional gradients in pinniped $\delta^{15}\text{N}$ values track those observed at the base of the food web (Saino and Hattori 1987), which again are thought to reflect differences in the vertical mixing of “new” nitrogen into the surface ocean. These baseline carbon and nitrogen isotope gradients provide a means to study the foraging location of ancient pinnipeds, assuming that middle and late Holocene oceanographic conditions were roughly similar to today with respect to trends in primary production and vertical mixing.

Materials and methods

Isotopic analysis

We measured the carbon and nitrogen isotope compositions of bone collagen extracted from the remains of northern fur seals,

harbor seals, and California sea lions (*Zalophus californianus*) recovered at middle to late Holocene human occupation sites around the Monterey Bay, central California, and from a site on the Mendocino coast, northern California. Harbor seals and sea lions were analyzed to control for shifts in the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ of the eastern Pacific due to fossil fuel combustion or oceanographic changes. For comparison with contemporary populations from Alaska and ancient populations from California, we also measured the isotope composition of bone collagen from contemporary northern fur seals, which remain at middle latitudes year round and breed at San Miguel Island, southern California.

The prehistoric pinniped skeletal material we studied was recovered during previous archaeological investigations. Skeletal samples from contemporary northern fur seals breeding on San Miguel Island were obtained from the National Marine Fisheries Service, National Marine Mammal Laboratory, Seattle, Washington.

Cortical bone (~100 mg) was cleaned of sediment, demineralized in 0.5 N HCl (24 h at 4°C), then treated sequentially with chloroform/methanol and 1.0 M NaOH to remove lipids and humic acids, respectively. Dried samples were analyzed using a Carlo-Erba elemental analyzer interfaced with an Optima mass spectrometer (Department of Earth Science, University of California, Santa Cruz). Results are expressed as δ values, where $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$, and R_{sample} and R_{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 Pee Dee Belemnite limestone for carbon, and atmospheric N_2 for nitrogen, and the units are parts per thousand (‰). Repeated measurements of a gelatin standard yielded a $1\sigma < 0.12\text{‰}$ for both carbon and nitrogen.

Archaeofaunal analysis

The age/sex composition of the remains of these ancient populations, while potentially biased through prey selection and hunting techniques of early humans, can be used to test the interpretation of isotopic data, and can reveal whether these remains came from breeding versus non-breeding aggregations. Morphological and metric comparisons were made of taxonomically-diagnostic elements of pinnipeds recovered at archaeological sites, with collections from the Department of Ornithology and Mammalogy, California Academy of Science, San Francisco, and the Museum of Vertebrate Zoology, University of California, Berkeley. Immature northern fur seals were identified from the Moss Landing (CA-MNT-234) fauna during previous archaeological investigations (Breschini and Haversat 1995). Our analysis of a larger sample from that excavation yielded additional northern fur seal elements, including numerous very young individuals. We calculated regressions of body length on dentary short length (Woodborne et al. 1995) for 34 modern museum specimens of northern fur seals (14 males and 20 females ranging in age from pups to adults). With these regressions we estimated the body length of four small individuals from Moss Landing (CA-MNT-234), and of one small individual from the Mendocino Coast (CA-MEN-828), for which dentaries were available.

AMS radiocarbon dates were acquired for four northern fur seal specimens. Collagen was extracted with a modified Longin method (Brown et al. 1988) from skeletal elements of three infant northern fur seals from the Moss Landing site (CA-MNT-234), and one adult female from a north Monterey Bay coastal site (CA-SCR-35).

Results

Stable isotope analysis

Mean isotope values for three species of ancient pinnipeds from the Monterey Bay region and the Mendocino Coast are presented in Table 2, along with mean values

for modern northern fur seals from San Miguel Island and four species of pinnipeds from present day central California and Alaska (Burton and Koch 1999). The mean $\delta^{13}\text{C}$ value for middle Holocene-aged northern fur seals from the Monterey Bay region is -13.2‰ and the mean $\delta^{15}\text{N}$ value is 18.5‰ . The mean $\delta^{13}\text{C}$ value for ancient northern fur seals from the Mendocino Coast is -13.5‰ , slightly lower than the value for northern fur seals from central California as is the mean $\delta^{15}\text{N}$ value (18.3‰). The mean $\delta^{13}\text{C}$ value for modern northern fur seals from San Miguel Island is -14.5‰ , and the mean $\delta^{15}\text{N}$ value for this group is 18.4‰ (Table 2).

The mean $\delta^{13}\text{C}$ value of ancient California sea lions from central California (-12.8‰) is 1.0‰ higher than that of modern conspecifics. The mean value for ancient harbor seals from the same region (-11.5‰) is 0.9‰ higher than for modern specimens. The $\delta^{13}\text{C}$ values of prehistoric organisms however have to be normalized to modern values by subtracting 1.0‰ , to account for the shift in $\delta^{13}\text{C}$ of surface carbon reservoirs due to fossil fuel inputs (Quay et al. 1992; Sonnerup et al. 1999, see discussion). After the fossil fuel effect is accounted for, the differences between modern and prehistoric conspecific populations of harbor seals and California sea lions are within the limits of analytical error. The mean $\delta^{13}\text{C}$ values for ancient California sea lions and harbor seals from Mendocino are -13.1‰ , and -11.9‰ respectively (Table 2). These values are slightly lower than those for the same groups from central California, though the differences are not significant.

The differences in mean $\delta^{13}\text{C}$ values among contemporary northern fur seals from Alaska and San Miguel Island, and ancient northern fur seals from central and northern California are highly significant (one factor ANOVA, $P < 0.001$). When these individual values are normalized to account for a fossil fuel effect (by subtracting 1.0‰), the mean values of ancient northern fur seals from central and northern California and contemporary northern fur seals from San Miguel Island are statistically indistinguishable yet remain significantly different from modern male northern fur seals from Alaska (Sheffé's test, $P < 0.05$ for each group). Modern females that migrate between middle latitudes and Alaskan rookeries have lower $\delta^{13}\text{C}$ values than all three groups from California, but are only significantly different from ancient northern fur seals (for which values have been adjusted to account for the fossil fuel effect) from Moss Landing (Scheffé's test, $P = 0.02$).

The mean $\delta^{15}\text{N}$ value of ancient California sea lions from central California (18.5‰) is nearly identical to modern sea lions from the region. The mean $\delta^{15}\text{N}$ value for ancient California sea lions from Mendocino is 19.0‰ , which is $\sim 0.5\text{‰}$ higher than the value for both ancient and modern sea lions from central California (Table 2). Conversely, the mean values for ancient harbor seals from central (18.1‰) and northern California (17.9‰) are indistinguishable and are lower than the mean value for modern harbor seals (18.7‰) from central California. None of these differences are statistically significant.

Fig. 1 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm SD) for middle to late Holocene northern fur seals from California, separated by age-class: ■ adult females, ● subadults, ▲ juveniles, ○ pups

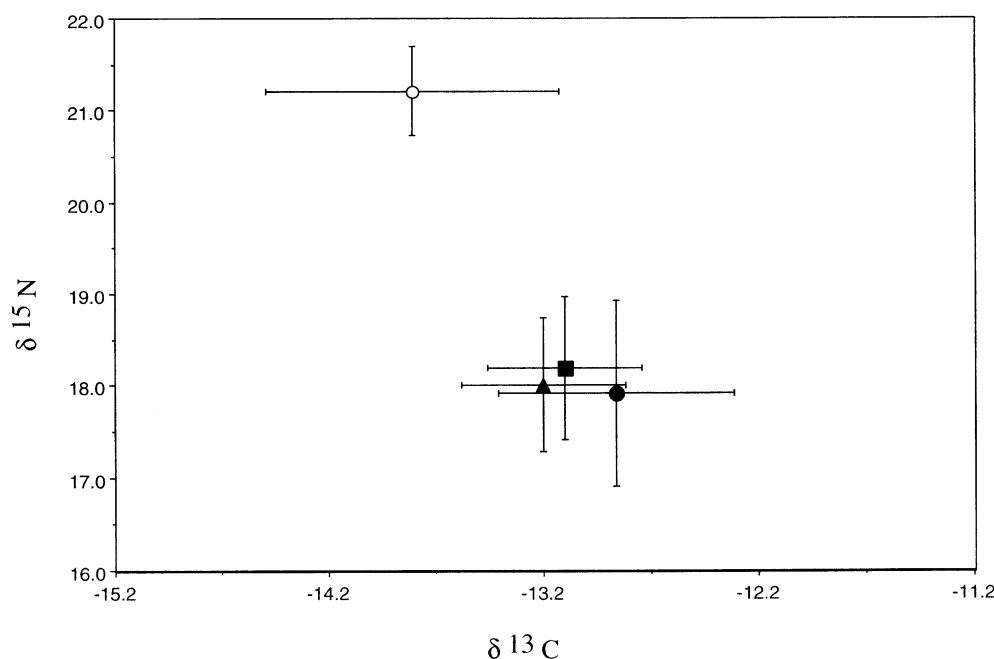
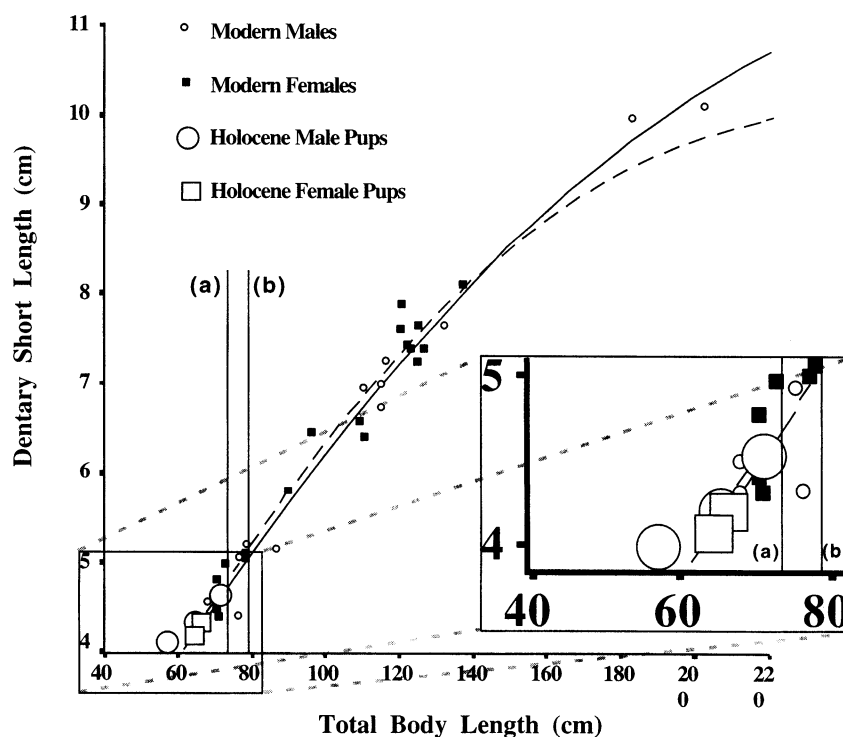


Fig. 2a,b Estimated body length of four northern fur seal pups recovered from the Moss Landing site CA-MNT-234 and of one pup recovered from the Mendocino Coast site CA-MEN-828. Sex-specific regressions of dentary short length on body length are based on measurements of 34 museum housed modern specimens. The average body length of modern 3-month-old pups, measured on San Miguel Island, is 73.2 cm for females (a) and 79.5 cm for males (b) (Melin and DeLong 1997)



The mean $\delta^{15}\text{N}$ value for ancient harbor seals from the Mendocino Coast (18.0‰) is also lower than for contemporaneous conspecifics from central California.

Differences in mean $\delta^{15}\text{N}$ values among ancient northern fur seals from central and northern California and modern conspecifics from both San Miguel Island and from Alaska are also highly significant (one factor ANOVA, $P < 0.001$). The difference however is between middle and high latitude groups. The mean $\delta^{15}\text{N}$ values for ancient northern fur seals from central and northern

California are significantly higher than the mean value for modern northern fur seals (both male and female) from the Alaskan rookeries (Sheffé's test, $P < 0.005$), as is the mean for contemporary conspecifics from San Miguel Island (Sheffé's test, $P = 0.017$). Differences among the middle latitude groups are not significant.

The mean $\delta^{15}\text{N}$ values for prehistoric adult females, sub-adults, and older juvenile northern fur seals are similar to each other, indicating they fed within a single trophic level (Fig. 1). The mean $\delta^{15}\text{N}$ value for the prehis-

toric pups is $\sim 3.0\%$ higher, which is one trophic level higher than the other groups (Schoeninger and DeNiro 1981)

Archaeofaunal analysis

This study did not include all of the pinniped skeletal elements recovered at each of the archaeological sites. Nonetheless, from the Moss Landing site (CA-MNT-234), we identified 88 skeletal elements and teeth from northern fur seals, 14 elements from California sea lions, and 6 from harbor seals. Northern fur seal skeletal elements included those of adult females, subadults and juveniles of both sexes, and 16 elements that represented at least 12 pups. From the site on the Mendocino Coast (CA-MEN-828), we identified 20 northern fur seal elements, including bones of at least 6 young pups. We also identified the remains of 8 harbor seals and 6 California sea lions.

Using the sex specific regressions of body length on dentary short length we estimate the body lengths of 4 northern fur seal pups from the Moss Landing site, for which we had mandibles, to have been 57, 62, and 71 cm for the 3 male specimens and 63 cm for the female (Fig. 2). Similarly, we estimated the body length of 1 pup from the Mendocino Coast site to have been 63 cm.

The conventional AMS radiocarbon ages were $2470 \text{ BP} \pm 60$ years (CAMS#56398), $2600 \text{ BP} \pm 60$ years (CAMS#56397), and $2700 \text{ BP} \pm 60$ years (CAMS#56399) for the three northern fur seal pup elements from Moss Landing and 2920 ± 50 years (CAMS#50787) for the adult element from CA-SCR-35.

Discussion

The mean $\delta^{13}\text{C}$ values for middle Holocene harbor seals and California sea lions from Moss Landing are $\sim 1.0\%$ higher than are values for their respective modern conspecifics (Table 2). If this difference reflected a change in feeding habits, such as a drop in trophic level over time, we would expect to see lower $\delta^{15}\text{N}$ values (by $\sim 3.0\%$) for the modern animals, relative to those from the past. In fact we see a slight trend in the opposite direction. The differences could indicate that nearshore waters along central California are less productive now than they were in the past (see Burton and Koch 1999), but there is no other corroborating evidence for this.

The differences in the carbon isotope compositions of harbor seals and California sea lions most likely reflect a recent drop in the $\delta^{13}\text{C}$ of surface carbon reservoirs resulting from fossil fuel and biomass burning (Quay et al. 1992; Sonnerup et al. 1999). Similar $\delta^{13}\text{C}$ shifts have been detected in time series from plants, ice cores, and mammals (Bada et al. 1990; Marino and McElroy 1991; Indermuhle et al. 1999). Taking this shift into account, bone collagen $\delta^{13}\text{C}$ values indicate that these species' foraging and migratory behaviors have been constant

from the middle Holocene to the present. On the other hand, after adjusting for the fossil fuel effect, middle Holocene northern fur seal $\delta^{13}\text{C}$ values are still significantly different than values for modern conspecifics from Alaska. Their values are most similar to values for contemporary northern fur seals from San Miguel Island and for female northern elephant seals, both of which feed offshore and remain at middle latitudes throughout the year. The carbon isotope ratios thus strongly imply that during the middle Holocene northern fur seals from California foraged far offshore, as they do today, and were year-round residents.

This conclusion is supported by our measurements of nitrogen isotopes, which vary with both trophic level and latitude (Burton and Koch 1999). The $\delta^{15}\text{N}$ values of contemporary pinnipeds from Alaska and both ancient and modern pinnipeds from California show considerable similarity between groups, indicating they all fed at approximately the same trophic level (Table 2). Nonetheless the $\delta^{15}\text{N}$ values of middle Holocene northern fur seals from central and northern California are significantly higher than values for modern northern fur seals from high latitudes and they are indistinguishable from values for contemporary northern fur seals now breeding on San Miguel Island.

Based on these results we conclude that ancient northern fur seals preyed on by early Native Californians were not seasonal migrants from high-latitude rookeries, nor were they regularly foraging near enough to shore to be accessible to human hunters. In fact the isotope compositions of ancient northern fur seals suggest that these animals were as pelagic in the past as they are today. If they remained at middle latitudes throughout the year during the middle Holocene, as indicated by their isotope compositions, they must have bred in the region and therefore may have been vulnerable at local rookeries.

The isotopic data do not reveal breeding locations, but the composition and location of archaeofaunas can. Northern fur seals comprise $\sim 80\%$ of the identified pinniped remains from the Moss Landing site, representing a broad spectrum of age classes, including pups. Although the relative abundance of northern fur seals from the Mendocino Coast archaeological site is far lower (White, unpublished data), the presence of bones of adult females, subadults of both sexes, and pups suggest the presence of a nearby rookery there as well.

Modern northern fur seal pups from high latitudes do not leave their natal rookeries until they are weaned at 4 months of age (Gentry 1998). A short lactation period is typical of high latitude pinnipeds that are exposed to extreme seasonality but is atypical of middle latitude and equatorial populations (see Boness and Bowen 1996). It is unlikely that the length of lactation would have been less than 4 months for ancient northern fur seals from California. This inference is supported by the observation that northern fur seals now breeding on San Miguel Island have extended lactation to 5 months (Sharon Melin, personal communication).

The average body length of modern 3-month-old pups, measured on San Miguel Island, is 79.5 cm for males and 73.2 cm for females (Melin and DeLong 1997). Our estimates of the body lengths of four pups from the Moss Landing site (57–71 cm) and the one pup from the Mendocino site (63 cm), suggest that at least some of the pups were substantially smaller, and therefore younger, than modern 3-month-old pups from similar latitudes (Fig. 2). The very small size, and therefore young age, of some of the pups strongly suggests they had not been weaned at the time they were killed.

The nitrogen isotope composition of the pups supports this conclusion. Preferential loss of ^{14}N as urea leads to ^{15}N -enrichment of the mother's amino acid pool available for protein synthesis, and hence leads to ^{15}N -enrichment of the milk she produces, resulting in higher $\delta^{15}\text{N}$ values for pups relying exclusively on their mother's milk for nutrition (DeNiro and Epstein 1978). The mean $\delta^{15}\text{N}$ values of adult females, sub-adults, and older juveniles from the archaeological sites are very similar, indicating they fed within a single trophic level, yet the mean $\delta^{15}\text{N}$ value for the ancient pups is 3.0‰ higher, indicating they were feeding one trophic level above the older animals (Fig. 1).

The numerous nearshore rocky outcrops along the Mendocino Coast could have supported small rookeries, but there are no offshore rocks in the vicinity of the Moss Landing site. In fact, the Moss Landing site is located near the midpoint of a 40 km long sandy beach, far from cliff-backed pocket beaches, and >120 km from the Farallons, which at the time were the nearest offshore islands. The Moss Landing pups would have been too young to have swum from the Farallon Islands or some other distant offshore rocks and human import of fur seals en masse from these distant offshore islands is implausible. The animals from Moss Landing must have come from a rookery located on the mainland.

Mainland breeding represents a dramatic departure from the current reproductive strategy of this species. It has been argued that northern fur seals breed on offshore islands because they require rookery sites with temperatures moderated by oceanic winds, and because islands provide ready access to productive continental margins during foraging excursions while providing protection from terrestrial predators (Gentry 1998). The first two conditions are met at many locations along the California and Oregon coast, but terrestrial predation, especially by grizzly bears (*Ursus arctos horribilis*) has been viewed as an impediment to the establishment of pinniped rookeries on mainland eastern Pacific beaches (see Riedman 1990). As the geomorphology of the Moss Landing site offers little protection from large carnivores, we conclude that non-human terrestrial predation has been overestimated as a limit to pinniped breeding on mainland beaches.

Reanalysis of the Duncan's Point Cave fauna in Sonoma County suggests the presence of another mainland rookery (Wake and Simmons, 2000), as may the report of "fetal" northern fur seal remains from Point Mugu, in

southern California (Lyon 1937). Our results, coupled with the prevalence of northern fur seal remains in numerous prehistoric archaeofaunas' provide strong evidence that at least some of California's mainland beaches met the reproductive requirements of this species as well as do beaches on offshore islands.

This conclusion has several implications for understanding the ecology of contemporary northern fur seals. If their abundance at California and Oregon coastal sites is viewed as evidence that middle-latitude, mainland rookeries were widespread, then northern fur seals may have had a much broader distribution and a greater global abundance in the Holocene than they have today. Northern fur seals would have in fact been the predominant pinniped in central California waters, as California sea lions appear to have been less abundant in the past and Steller sea lions (*Eumetopias jubatus*) are quite rare in central California archaeofaunas (Hildebrandt and Jones 1992). Northern elephant seals, which now breed in large numbers in central California (McGinnis and Schusterman 1981), are virtually nonexistent in archaeofaunas from north of Santa Barbara (Hildebrandt and Jones 1992; Lyman 1995; Colten and Arnold 1998). The nature of the interaction of these species with northern fur seals in these abundance shifts is an intriguing, but unexplored topic. Given potential top-down effects of carnivores on ecosystem structure and function (Estes et al. 1998), shifts in abundance among pinniped species may have had profound effects on the ecology of the California Current. With respect to conservation biology, it is essential to recognize that mainland beaches are potential rookery sites for northern fur seals, and to determine why these animals are absent from these beaches today.

The conventional AMS radiocarbon dates we obtained from the 4 fur seal bones we analyzed range from 2,470 to 2,920 BP. Using a reservoir age of ~630 years for an animal assumed to be feeding in the California Current (Ingram and Southon 1996), as indicated by their carbon isotope compositions, these fur seals were killed between 1,800 and 2,290 years ago.

Northern fur seal populations along coastal California appear to have declined sometime after ~1,000 BP (Hildebrandt and Jones 1992). Some workers attribute the decline to climate change (Glassow 1993; Colten and Arnold 1998); others blame predation by aboriginal hunters (Hildebrandt and Jones 1992; Jones and Hildebrandt 1995). If climate change were responsible, it must have been transient, as northern fur seals maintained island rookeries in the region into historic times. If aboriginal cropping focused on rookeries it could have accelerated a regional population decline. Of the three species of eared seals common to the central California coast during prehistoric times, only northern fur seals would have had breeding sites within reach of local hunters. Modern California sea lion rookeries lie on islands far to the south (Odell 1981), inaccessible to all but hunters with pelagic watercraft, and contemporary Steller sea lion rookeries are centered far north of central Califor-

nia, where they are also located mainly on offshore islands (Schusterman 1981). No remains of very young individuals of either species have been encountered in Monterey Bay archaeofaunas, suggesting their breeding has not changed substantially since the middle and late Holocene. The archaeofaunas from the central California coast indicate that humans preferentially took northern fur seal females and young from rookeries, rather than preying on bachelor male aggregations. Thus northern fur seals would have been uniquely vulnerable to local extirpation. While further research on middle and late Holocene climate in central California is needed, we suspect that the demise of mainland northern fur seal rookeries reflects prehistoric human predation.

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