

Toward a Prehistory of the Southern Sea Otter (*Enhydra lutris nereis*)

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It's clear that within the sea otter's stabilized foraging range there can be virtually no human harvest of abalones (*Haliotis* spp.) (except for a few taken intertidally).

D.J. MILLER, 1974, CALIFORNIA DEPARTMENT OF
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THE SOUTHERN SEA OTTER (*Enhydra lutris nereis*) is one of the mostly widely recognized and highly cherished marine mammals on the coast of California. In seaside communities up and down the state, images of sea otters are ubiquitous on T-shirts, coffee mugs, and bumper stickers. Tourists flock in droves to watch otters from cliffs and jetties, and to peer at them underwater at the Monterey Aquarium. Not surprisingly, scientific research on sea otters has been commensurate with this interest, and much is known about their basic biology, behavior, and ecology.

The prehistory of sea otters, however, is much less well understood and has been the subject

of longstanding speculation by fishermen, biologists, and California Fish and Game representatives. Sea otters are a keystone predator in kelp forests along the central California coast, and they are voracious consumers of shellfish. Since their return from the brink of extinction early in the 20th century, their impact on shellfish populations has been obvious, and the most robust populations of abalone are found only in areas where otters have not reestablished their populations. This pattern prompted the statement by the California Department of Fish and Game quoted above.

Nonetheless, casual observations of the archaeological record and ethnohistoric accounts

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of Native people indicate that sea otters, abalone, and humans coexisted before the arrival of Euro-Americans in California in 1769 (Davis 1981; Walker 1982). Along the central coast (between San Francisco Bay and Point Conception) where sea otters have reestablished their populations, archaeological research was not sufficiently advanced in the 1970s (with some key exceptions [e.g., Greenwood's 1972 study at Diablo Canyon]) to allow for anything other than informed speculation about the relationships between abalones, sea otters, and humans. In the last 2 to 3 decades, however, hundreds of archaeological sites have been excavated in this region, including many that contain the remains of abalone and sea otters (for a history of this work see Jones et al. 2007). A regional culture history extending back to 8000 cal BC is now well established based on over 1000 radiocarbon dates. Here we rely on this dataset to develop a preliminary outline of sea otter prehistory for the central California coast that emphasizes the ecological relationships between key predators and their prey. First, we summarize some of the important traits of this animal with respect to its suitability as a prey item. We then summarize the spatial and temporal distribution of archaeological otter remains with particular regard to diachronic variability. Finally, we've supplemented this basic historical and biological information with the results of two specialized studies on otter remains: DNA analysis that reveals the sex of the otters that were exploited by Native Californians, and isotope analysis that provides insights into their diet.

THE SOUTHERN SEA OTTER (*ENHYDRA LUTRIS NEREIS*) AS PREY • *Biology, Ecology, History*

The sea otter is the smallest marine mammal on the planet, and its unique characteristics and history of near extinction and reemergence make it particularly interesting. Sea otters are members of the Mustelidae family, which bear and nurse live young. Three geographically segregated subspecies are generally recognized

within *Enhydra lutris*: *E. lutris lutris*, *E. lutris gracial*, and, *E. lutris nereis* (Kenyon 1981; Nickerson 1984; Riedman and Estes 1990). *E. lutris lutris* (the Asian sea otter) is found in the western Pacific, and *E. lutris gracial* (also *E. lutris kenyoni*), the Alaskan sea otter, is found in the Aleutian Islands and along the Alaskan mainland coast. The focus of this paper, *Enhydra lutris nereis* (the California or southern sea otter), inhabits the central coast of California.

BIOLOGY

According to Riedman and Estes (1990), adult male sea otters weigh 34% more than their female counterparts, and males are 8% longer than females. An average sea otter pup weighs about 5 pounds and is 22 to 24 inches long; fully mature male sea otters weigh 60 to 85 pounds and are about 58 inches in length, whereas females only weigh 35 to 60 pounds and are 55 inches long (Kenyon 1981). Their forelimbs have retractable claws and sensitive pads that allow the animal to accurately find and consume prey. The sea otter swims slowly compared to other marine mammals and travels through the water at 1.5 nautical miles per hour (Kenyon 1981).

The sea otter's coat is unlike that of any other marine mammal, as it is unusually dense. The denseness creates a layer of trapped air that provides warmth for the animal, which is essential because sea otters lack the fatty blubber that most other marine mammals depend on (Kenyon 1981; Riedman and Estes 1991). This layer of trapped air also provides the sea otter with extra buoyancy. The pelage of an adult can range in color from light brown to nearly black, and pups are born with a "woolly" coat that is replaced within the first few months (Kenyon 1981). It was the otter's pelt that was the object of commercial exploitation in the 18th and 19th centuries. It was also a main focus of indigenous hunting before that; ethnohistoric accounts of both the Costanoan (Levy 1978:493) and Chumash (Greenwood 1978:523) describe use of otter skins for blankets and robes, and as important trade items. Their use for these purposes is in

fact much more heavily attested to than their exploitation as a food source, but it is unlikely that California Indians did not also take advantage of the animal's meat.

REPRODUCTION

Sea otters can breed throughout the year; however, Riedman and Estes (1991:59) suggest that "the general yearly reproductive pattern in California . . . consists of a winter pupping season and a summer-fall breeding season." Males and females often form pair bonds, but this is not necessary for breeding and is often not observed in California (Riedman and Estes 1991; Woodhouse et al. 1977). The mating male and female spend one to three days participating in daily activities together, and the female often retreats ending any subsequent interactions (Kenyon 1981; Riedman and Estes 1991; Woodhouse et al. 1977). It should be noted that the reproduction patterns of Alaskan sea otters are better understood because most information gathered on otters in California is based on a limited number of occurrences.

Californian male sea otters likely reach sexual maturity around 5 years, but territoriality occurs around 8 years; males pursue females in estrus and copulation takes place in the water (Riedman and Estes 1991). Males appear to be able to reproduce until death (Riedman and Estes 1991). A male's territorial boundaries change seasonally depending on food resources, security of coastline (e.g., storm protection and available kelp), and the number of reproductive females (Riedman and Estes 1991). Although males have been observed interacting with pups, they do not participate in rearing the young (Kenyon 1981; Riedman and Estes 1991).

Californian female sea otters reach sexual maturity at approximately 4 to 5 years, with estrus lasting about 3 to 4 days, but information on the frequency of estrus is limited (Riedman and Estes 1991). Sea otters have single-pup births (mostly in the water, but land births have been observed), and California sea otters typically give birth to one offspring per year (Kenyon 1981; Riedman and Estes 1991). Gestation

length is still under investigation, as Kenyon (1981) asserts gestation lasts for 8 months, while Riedman and Estes (1991:66) cite several sources that indicate gestation requires only 4 to 6 months. Sea otter pups are raised solely by the female and are dependent on their mother for survival for several months (Kenyon 1981). After giving birth, sea otters temporarily separate themselves from other females; after a few days, they accompany other females with dependent pups (Riedman and Estes 1991).

BEHAVIOR

Sea otters often spend time in groups commonly referred to as rafts. When in rafts, sea otters mostly rest, groom, and tend to pups. Foraging, mating, and parturition all occur away from rafts, and once these activities are completed, otters return to their group. Female rafts are smaller than male groupings; female rafts have been observed to typically contain two to a dozen members, whereas male rafts are typically larger, with hundreds of otters having been observed grouped together (Riedman and Estes 1991). Otters are relatively social mammals and engage in a variety of close interactions.

Male and female sea otters spend most of their time separated and segregated into single-sex areas; however, Riedman and Estes (1991:53) suggest that in "California, differences in the degree of exposure to rough sea conditions and availability of food resources characterizing established male and female areas are less pronounced than they are in Alaska." Juvenile females may occupy areas near or in male rafts, and juvenile males maintain independence and isolation farther offshore for most of their activities. Territorial adult male otters remain near the periphery of female rafts, and contact is sought for mating. Within the sea otter's habitat range, females and dependent pups occupy the center area and males occupy the fringe to take advantage of "unoccupied habitat" to expand their territory; however, throughout the season territorial males travel from the periphery to the center in search of a mate (Riedman and Estes 1991:53).

All sea otters exhibit haul-out behavior in which the sea otter takes refuge on exposed rocks or beaches. Common haul-out locations are composed of "low-relief, algal covered rocks" and, less frequently, "sand and cobble beaches" (Riedman and Estes 1991:24). Otters usually haul out in small groups of up to six, and during estrus females frequently haul out (Riedman and Estes 1991). Southern sea otters haul out less often than their northern counterparts, a result of near-shore human contact (Riedman and Estes 1991; Woodhouse et al. 1977).

ECOLOGY

HABITAT

California sea otters predominantly occupy areas with rocky bottoms, less frequently inhabiting soft sandy bottom areas (Riedman and Estes 1991; Woodhouse et al. 1977), including estuaries. It seems that sea otters prefer areas with dense kelp, but it is not a habitat requirement. California sea otters play a complex role in their environment, influencing many other species, and thus are known as a keystone species (Riedman and Estes 1991). Sea otter predation can stabilize nearshore ecological communities by limiting invertebrate species (e.g., sea urchins, *Strongylocentrotus* spp.) that, void of limitation, would destroy marine plants (e.g., kelp), which provide habit for benthic fish species (Riedman and Estes 1991; Simenstad et al. 1978; Woodhouse et al. 1977). Sea otters do not migrate, but rather maintain residence within a 5-to-10-mile territory along the coastline (Kenyon 1981).

PREDATION AND PREDATORS

While most carnivorous animals have sharp teeth, sea otter teeth are flat and blunt, and are ideal for crushing the shells of their invertebrate prey (Kenyon 1981). Sea otters typically specialize on about three species (sea urchins, abalones, and rock crabs); as these species become sparse, otters prey on turban snails, kelp

crabs, mussels, and other intertidal species (Riedman and Estes 1991; Woodhouse et al. 1977). A sea otter's diet may also include fish, with pursuit of fish usually limited to males who possess the required strength to catch and kill this prey (Kenyon 1981). The sea otter's dexterity and collection techniques allow them to adapt and exploit a changing environment. An average adult sea otter must eat 23 to 33% of its body weight daily (Riedman and Estes 1991).

California sea otters dive to depths of 25 m while foraging for food, and, on average, each dive lasts for around a minute, but they can dive to greater depths and stay underwater longer when they are being hunted. Males and females maintain different foraging strategies; subadult males forage with deeper and lengthier dives farther from shore, while females with pups foraged closer to shore with quicker and shallower dives (Riedman and Estes 1991).

Food stealing among sea otters is commonplace. Adult females (mostly females with dependent pups) are the most frequent targets. When a female enters a foraging area near a territorial male, the male often steals her catch; the female easily complies (Riedman and Estes 1991). Pair-bonded males frequently steal food from females, and the female is known to offer prey to the pair-bonded male (Riedman and Estes 1991). Worthy of note is a male tactic termed "hostage behavior" in which a male seizes an otter pup while the female is diving, and essentially the pup is exchanged for the female's collected prey (Riedman and Estes 1991). Males are not the only perpetrators, as females also occasionally steal from one another. Female thieves use a different strategy. Males steal any prey that is caught, but females are more selective and target one species at a time (Riedman and Estes 1991).

Killer whales and great white sharks prey upon sea otters, and otter pups sometimes fall victim to bald eagles, but all occur relatively infrequently. Humans are the only known population-limiting species (Riedman and Estes 1991; Walker 1982; Woodhouse et al. 1977).

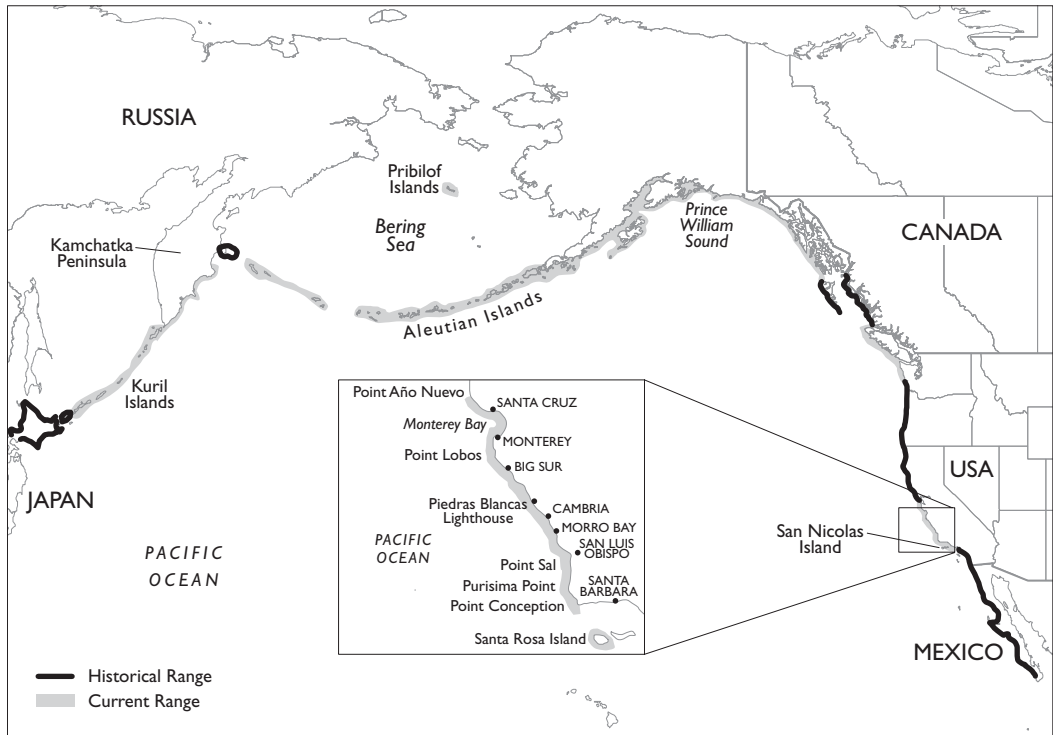


FIGURE 11.1. Distribution of sea otters in the Pacific (current range was part of the historic range).

HISTORY

The history of market-based overexploitation of the sea otter, which nearly rendered the species extinct by the end of the 19th century, was exceptionally well documented by Ogden (1941). Before and during the fur trade, sea otters maintained an expansive, contiguous territory throughout the North Pacific that extended from the northern Islands of Japan to the southern shores of Baja California (Figure 11.1). The more restricted distribution of sea otters seen today is a direct result of the intensive hunting of the animals for pelts during the 19th century by the Spanish, Mexicans, and most significantly, the Russians, who established Fort Ross on the coast of Sonoma County in northern California as a base of operations for marine mammal hunting. The numbers of marine animals caught during the fur trade in the Pacific Ocean are staggering. The Russian-American Company reported their colonies exported

72,894 sea otters and over 1.2 million fur seals from 1797 to 1821 and another 25,899 sea otters and 372,894 fur seals from 1842 to 1862 (Tikhmenev 1978 [1888]). Gibson (1992) reports even more astronomical numbers, stating that from 1804 to 1837, American vessels alone imported 158,070 sea otter pelts to the Asian market at Canton. Of course, the California fur trade was only a portion of the overall enterprise. The sea otter fur trade was most productive between 1801 and 1819 at the height of the Russian-American partnership. During those two decades, nearly 80% of California sea otters were taken. Nonetheless, numbers of sea otters caught in California are staggering in their own right. According to Ogden (1941), fur traders caught over 45,000 sea otters along California's coast, estuaries, and islands in just over six decades. This figure serves as conservative estimate since it does not include contraband and native catches.

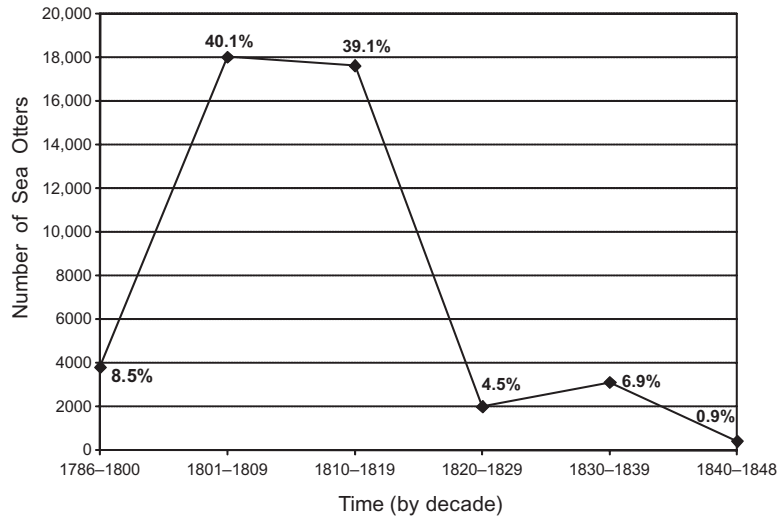


FIGURE 11.2. Total sea otters caught in California during the fur trade from 1786 to 1848 with percentages of the total harvested population (43,035) from Ogden (1941).

Today, sea otters have been extirpated south of Prince William Sound to Baja California with the exception of the central California coast, where they maintain residence from Point Año Nuevo above Santa Cruz in the north to Point Conception near Santa Barbara in the south. Riedman and Estes (1991) argue the southern range limit seems to be near the Santa Maria River in San Luis Obispo County. Sea otters also live near San Nicolas Island off the coast halfway between Santa Barbara and Los Angeles, where they are part of a conservation plan to reestablish the population.

The California Department of Fish and Game and the U.S. Fish and Wildlife Service estimate that the pre-fur trade population of otters in California was between 16,000 and 20,000 animals. Estimates for the entire population in the Pacific generally range between 150,000 and 300,000. According to Ogden (1941), historic fur trade records indicate sea otter populations were greatest in central California from San Francisco Bay to the Santa Barbara Channel Islands. Records of the fur trade exploitation show a precipitous decline in numbers of animals taken over the course of the 19th century, reflecting extreme overexploitation (Figure 11.2). By 1914, only 30 to 50 otters were

thought to remain in California waters. In 1938, approximately 50 otters were discovered off the coast of Monterey, and these have been credited with the reemergence of California's sea otter. Riedman and Estes (1991) calculate that from 1914 to 1984 the California sea otter population and range increased 5% annually. Currently, scientists conduct a census of sea otters twice a year, and California's sea otter population for 2007 was 3,026, which is the highest number recorded since the census began in 1982 (Figure 11.3).

PRE-FUR TRADE HUMAN-OTTER INTERACTION

ETHNOHISTORY

Historic records and ethnographic accounts indicate that sea otters were hunted with various techniques and technology. According to Ogden, people along the coast of California were known to hunt sea otters by the following technique:

When the parent otter left its young on the surface of the water, which it did only when it dived for food, the Indian hunter would slip up and tie a cord to the foot of the baby. Fastened to the cord, close to the body of the ani-

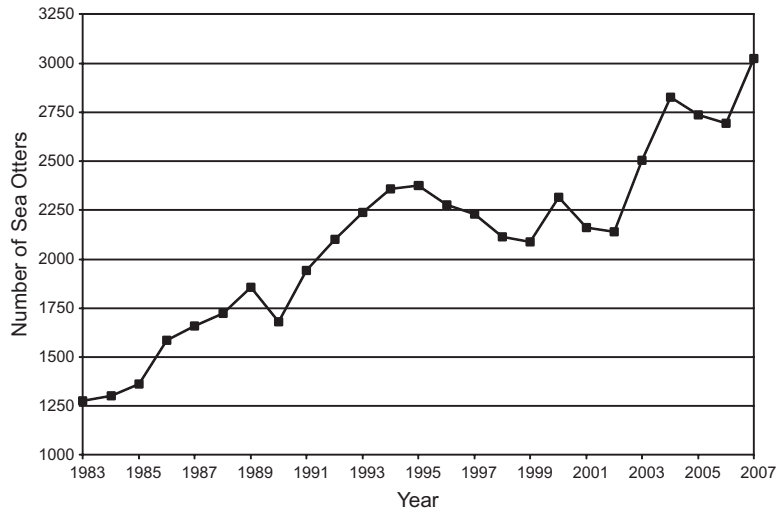


FIGURE 11.3. California sea otter census from 1983 to 2007. Source: Modified from USGS and Western Ecological Research Center 2007.

mal, would be placed a couple of fishhooks. Retiring in his canoe to a short distance, the Indian would pull his cord and thus hurt the small otter so that he would cry. The mother would rush to the rescue and could be easily approached, either because she was occupied in freeing her offspring or because she herself would become caught in the line and hooks. (Ogden 1941:14)

Woodhouse et al., citing La Perouse (1799), refer to another hunting technique employed by Native Californians:

The Indians whose boats at Monterey are only made of reeds, catch them on land with snares or by knocking them down with large sticks when they find them at a distance from the shore; for this purpose, they keep themselves concealed among the rocks, for this animal is frightened at the least noise and immediately plunges into the water. (1977:56–57)

Ogden (1941:14) also argues that hunting in California was often done without chasing the sea otter with watercraft; she states, “In California and certain places in the North Pacific, nets were spread out on the kelp beds, snares, and clubs were used.” Ogden (1941:142) even refers to an account in which three or four Native Americans caught 30 sea otters by lassoing

them while the otters were hauled out on shore. In the latter part of the fur trade, guns were used to hunt sea otters. Ogden (1941:145) reported a typical hunt included three men (two rowers and one shooter) in each of three canoes. The canoes would create a triangle formation, and, in form, the team would follow a fleeing otter and shoot at it each time it came up for air.

Sea otter pelts were clearly important exchange items in Native California. Driver and Massey (1957:376) documented 55 materials that were traded in California and ranked them in order of importance. Hide or furs, tied with salt, were the second-most-important commodity. Jones (1996) also argued that sea otter pelts were a valued trade commodity and noted a tentative correlation between the frequency of otter bones and obsidian in archaeological sites.

ARCHAEOLOGY AND PREHISTORY OF SEA OTTER EXPLOITATION

Although lacking a substantive dataset, some important observations were made by archaeologists in the 1970s and 80s about possible relations among humans, sea otters, and abalone during the prehistoric era. Davis (1981) noted that midden sites suggest California Indians harvested large abalones at the same

time that healthy populations of sea otters existed. She made this point specifically in reference to the view of California Fish and Game biologists that the presence of one species precluded the existence of large populations of the other. Walker (1982) discussed many of the same issues but suggested that human exploitation of otters would have changed the ecological structure of nearshore communities in that prior to the arrival of humans, otter populations would have been limited by available food (a “bottom-up” situation), but that after the arrival of humans their populations were controlled by human predation. Walker (1982) discussed some ethnographic and archaeological findings, but concluded, like Davis (1981), that significant archaeological information was not yet available.

Around the same time, findings from Alaska demonstrated the importance of archaeological data for defining the long-term ecological relationships between species. A midden site on the Aleutian Islands showed a stratigraphic sequence in which the basal layer produced abundant remains of sea otters and an overlying layer exhibited a dearth of otter remains and higher frequencies of sea urchins and remains of other shellfish (Simenstad et al. 1978). This transition suggested that hunting of otters represented in the basal layer led to near elimination of the species from the waters surrounding the island which, in turn, encouraged the expansion of sea urchin populations. The uppermost layers investigated by Simenstad et al. (1978) showed a return of otters, a renewal of their hunting, and a decrease in urchin remains. Overall, these findings clarified the keystone role of otters in kelp forest habitats: when otters are present, they reduce populations of sea urchins that compete for space on the bottom with kelp. If sea otters are overharvested, their removal from these systems can be followed by marked increases in sea urchins and reduction in kelp forests. The relationships recognized in this study establish the blueprint for investigating diachronic variability in otter exploitation elsewhere.

More recently, Hildebrandt and Jones (1992) used an optimal-foraging model to argue that

sea otters were highly elusive prey which would have been more lowly ranked than larger, less mobile marine taxa (e.g., seal and sea lions in rookeries). They argued that Native Californians would have turned to sea otters (and harbor seals) only after populations of the more vulnerable, highly ranked terrestrially breeding seals and sea lions (e.g., elephant seals, northern fur seals, Guadalupe fur seals, California sea lions and Steller sea lions) decreased as a result of overexploitation. They used faunal data from over 40 sites in California and Oregon to demonstrate this trend. For the central coast, data from 20 sites generally showed early (before 1000 BC) exploitation of terrestrial breeders (otariids and elephant seals) and later (after AD 1000) exploitation of sea otters. (Hildebrandt and Jones 1992) defined terrestrial breeders as pinnipeds who use terrestrial settings to accomplish breeding. The category included otariids (fur seals and sea lions) and elephant seals. Because these species generally migrate substantial distances and occupy breeding sites only seasonally, the term “migratory breeders” was also used to refer to this group. In central coast archaeological collections, however, remains of terrestrial breeders are almost entirely limited to otariids; only two elephant seal bones have been recovered from the region. Otariid is considered synonymous with terrestrial breeders in this chapter. The oldest evidence for sea otter exploitation in this study came from CA-MNT-229 at Elkhorn Slough, where a component dating ca. 4000 cal BC yielded 17 sea otter bones (Hildebrandt and Jones 1992).

Since then, the antiquity of sea otter exploitation has been more firmly established along the central and southern coasts based largely on findings from the Channel Islands, where Erlandson et al (2005) document sea otter exploitation as early as ca. 7000 cal BC. On the mainland, the Duncans Landing Rockshelter in Sonoma County (CA-SON-348/H; Kennedy et al. 2005; Schwaderer 1992; Simons and Wake 2000) and the Diablo Canyon site in San Luis Obispo County (CA-SLO-2; Jones, Porcasi, Gaeta et al. 2008) have produced sea otter re-

mains from contexts dating from 7000 to 5000 cal BC. Both the island and mainland records are still limited by small samples sizes, and it is likely that the antiquity of otter exploitation will eventually be pushed back coeval with the earliest exploitation of marine shellfish and fish on the islands (ca. 10,000 cal BC) and mainland (8000 cal BC). For now, the record of sea otter exploitation begins at 7000 cal B.C. Given the antiquity of unequivocal evidence for watercraft use on the Channel Islands (ca. 11,000 to 10,000 cal BC), it is reasonable to assume that boats of some type were available for the pursuit of marine animals on the mainland at this time.

Archaeological sites that have produced otter remains are fairly common on the central coast; no fewer than 46 sites have produced at least a single otter bone, and 19 have produced more than ten (Table 11.1; Figure 11.4). A total of 1194 otter bones has been reported, although only one site, CA-SMA-115 (north of Año Nuevo), produced an assemblage dominated by otter bones (57.3%). At most other sites, deer or rabbit bones tend to be most abundant. The mean representation of otters for the central coast as a whole is 8.99%. The largest collection of otter bones (NISP = 421; 14.1%) comes from CA-SLO-2 at Diablo Canyon, which also provides the longest sequence of otter exploitation (ca. 5000 cal BC to cal AD 1800; Jones, Porcasi, Gaeta et al. 2008). Putting aside small samples (mammal and bird NISP < 100), three other sites produced greater than 14% sea otter remains: CA-MNT-101, CA-MNT-391, and CA-SLO-832/1420. Overall, sites with the highest frequency of otter remains are found on exposed headlands, including the Monterey Peninsula, the Pecho Coast, and the San Simeon area. Some sites at the Elkhorn Slough estuary have also produced substantial samples of otter bones. It should be noted that middens in the San Francisco Bay area have also produced substantial quantities of otter remains (see, for example, Broughton 1999; Simons 1992), but the focus of the current study is the open coast where otters are still found today. Otter bones have also been recovered as far inland as the upper Car-

mel Valley (Breschini and Haversat 1992), but, not surprisingly, their frequency at inland sites is generally very low since there would have been no reason for bones to accompany pelts during forays to inland settlements or along exchange routes.

Of course, diachronic comparisons are ultimately more meaningful (Table 11.2; Figure 11.5). Fortunately, the corpus of available data on marine mammal frequencies is now substantial enough that such comparisons can be made with reasonable confidence. Overall, the record from the region shows clearly that sea otters were the preferred marine mammal along central coastal California throughout the Holocene contradicting the earlier assessment by Hildebrandt and Jones (1992) based on a more limited sample. While central coast middens generally exhibit a certain degree of mixing due to the impacts of small burrowing animals, diachronic trends can still be recognized with a reasonable degree of certainty. During the Milling Stone Period (5000–3500 cal BC), there was little interest in marine mammals in general; sites at Elkhorn Slough, Morro Bay, and the open coast have produced low frequencies of otter bones (5.4% of all mammals and birds) and very few remains of otariids and elephant seals (terrestrial breeders). Sea otters outnumber remains of these larger marine taxa during this period by a ratio of nearly 3:1. This situation changed significantly after 3500 cal BC with the onset of the Hunting Culture, when there was a marked increase in marine mammal hunting in general and otariids in particular. Otters were still the preferred marine prey overall (increasing to 11.1% of regional NISP), but the larger otariids show a fivefold increase to 9.9%. This trend continued through the Middle Period (600 cal BC to cal AD 1250), when the greatest number of otter (NISP = 704) and otariid bones (NISP = 560) occur. It is important to acknowledge that significant spatial variability is also apparent during this period; sites near Año Nuevo (CA-SMA-218), Elkhorn Slough (CA-MNT-234), and the Monterey Peninsula (CA-MNT-115) produced assemblages

TABLE 11.1
Archaeological Sites with Sea Otter (Enhydra lutris) Bones on the Central California Coast

TRINOMIAL	LOCATION	TOTAL NISP ^a	SEA OTTER NISP	%	REFERENCE
CA-SMA-115	Año Nuevo	96	55	57.29	Hylkema 1991
CA-MNT-391	Monterey Peninsula	241	54	22.40	Cartier 1993
CA-MNT-170	Monterey Peninsula	36	8	22.22	Dietz 1991
CA-SLO-71	San Simeon	51	11	21.60	Joslin 2006
CA-MNT-1942	Big Sur	69	13	18.84	Wolgemuth et al. 2002
CA-SLO-832/1420	Pismo Beach	124	22	17.74	D. Jones et al. 2004
CA-MNT-101	Monterey Peninsula	384	64	16.70	Dietz 1987
CA-SCR-7	Santa Cruz coast	36	6	16.66	D. Jones and Hildebrandt 1990
CA-SLO-585	Pecho Coast	49	8	16.32	T. Jones et al. 2009
CA-MNT-116	Monterey Peninsula	28	4	14.30	Dietz and Jackson 1981
CA-SLO-2	Pecho Coast	3049	431	14.13	T. Jones et al. 2008
CA-SLO-9	Pecho Coast	139	18	12.94	Codding and Jones 2007
CA-MNT-228	Elkhorn Slough	283	35	12.40	Jones et al. 1996
CA-SLO-179	San Simeon	631	70	11.10	Jones and Ferneau 2002
CA-SCR-132	Santa Cruz Coast	28	3	10.71	Hylkema 1991
CA-SLO-165	Morro Bay	307	33	10.75	Mikkelson et al. 2000
CA-MNT-234	Elkhorn Slough	365	37	10.13	Milliken et al. 1999
CA-SMA-18	Año Nuevo	683	67	9.80	Hildebrandt et al. 2006
CA-MNT-831	Monterey Peninsula	290	28	9.65	Breschini and Haversat 2006
CA-SLO-274	San Simeon (?)	94	9	9.60	Hildebrandt et al. 2002
CA-SMA-97	Año Nuevo	84	8	9.52	Hylkema 1991
CA-MNT-1765	Elkhorn Slough	11	1	9.10	Fitzgerald et al. 1995
CA-MNT-63	Big Sur	154	14	9.10	Jones 2003
CA-MNT-229	Elkhorn Slough	1013	89	8.80	Dietz et al. 1988; Jones and Jones 1992
CA-SMA-118	Año Nuevo	103	9	8.73	Hylkema 1991
CA-SCR-93	Santa Cruz Coast	71	6	8.45	Bourdeau 1986

TABLE 11.1 (continued)

TRINOMIAL	LOCATION	TOTAL NISP ^a	SEA OTTER NISP	%	REFERENCE
CA-MNT-1570	Elkhorn Slough	147	12	8.16	Jones et al. 1996
CA-MNT-115	Monterey Peninsula	74	6	8.11	Dietz and Jackson 1981
CA-SLO-273/H	San Simeon	14	1	7.14	Hildebrandt et al. 2002
CA-SLO-2357	Pismo Beach/ Halcyon Bay	65	4	6.20	Jones and Mikkelsen 2006
CA-MNT-112	Monterey Peninsula	114	6	5.30	Dietz and Jackson 1981
CA-MNT-73	Big Sur	49	2	4.10	Jones 2003
CA-SLO-267	San Simeon	308	12	3.90	Jones and Ferneau 2002
CA-MNT-238	Big Sur	862	24	2.78	Mikkelsen et al. 2005
CA-SMA-218	Año Nuevo	197	5	2.53	Hylkema 1991
CA-MNT-1277/H	Big Sur	124	3	2.41	Jones 2003
CA-SLO-175	San Simeon	49	1	2.04	Jones and Waugh 1989
CA-MNT-108	Monterey Peninsula	305	4	1.31	Breschini and Haversat 1989
CA-MNT-1233	Big Sur	238	2	0.84	Jones 2003
CA-MNT-1227	Big Sur	126	1	0.79	Jones 2003
CA-MNT-1223	Big Sur	119	1	0.84	Jones 2003
CA-MNT-1232/H	Big Sur	151	1	0.66	Jones 2003
CA-SLO-215	Morro Bay	165	1	0.60	T. Jones et al. 2004
CA-MNT-1486/H	Monterey Peninsula (inland)	485	2	0.41	Breschini and Haversat 1995
CA-SCR-9	Santa Cruz Coast	619	2	0.32	Hylkema 1991
CA-MNT-1485/H	Monterey Peninsula (inland)	646	1	0.15	Breschini and Haversat 1995
Totals		13276	1194	8.99 ^b	

^aAll nonfish animal bones except intrusive and ground-burrowing species (e.g., pocket gophers) identified to the genus level or better.

^bMean.

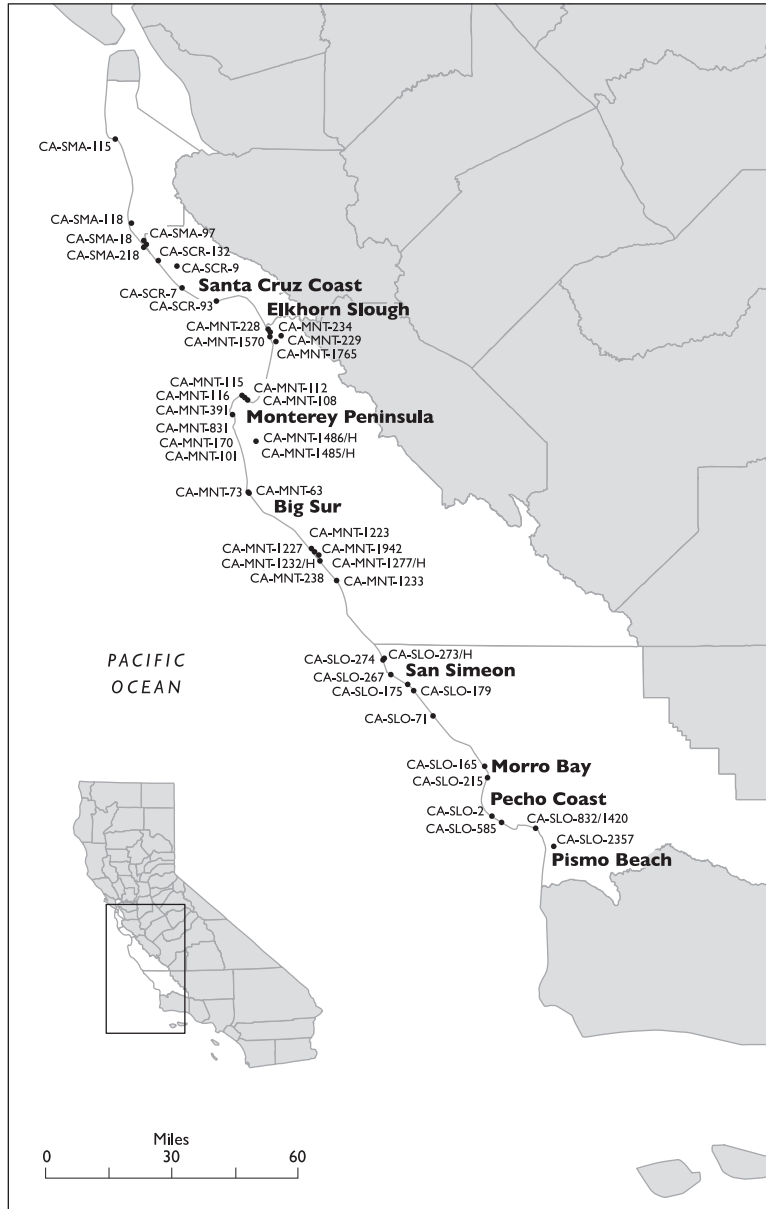


FIGURE 11.4. Archaeological sites with sea otter bones on the central California coast.

with heavy proportions (25–72%) of otariids and few otter bones, while other sites at Elkhorn Slough (CA-MNT-228) and the Pecho Coast (CA-SLO-2) show high frequencies of otters (14–17%) and few remains of the larger otariids. The bones at the majority of these sites represent northern fur seals (*Callorhinus ursinus*), and it is fairly apparent that this species had a greater onshore presence (e.g., breeding colo-

nies) during the Middle Period near Año Nuevo, Elkhorn Slough, and the Monterey Peninsula than it does today (see discussion by Gifford-Gonzalez, Chapter 10).

With the end of the Hunting Culture and the onset of the Late Period ca. cal AD 1250, trends in otter and otariid remains diverge dramatically; otter bones continue to increase, while the remains of large otariids and elephant

TABLE 11.2
Sea Otter and Other Marine Mammal Remains through Time on the Central California Coast

COMPONENT	TOTAL MAMMAL AND BIRD NISP	SEA OTTER NISP	%	OTARIIDS NISP	%
MILLINGSTONE (5000–3500 BC)					
CA-MNT-228 Area B	3	0	0.00	0	0.00
CA-MNT-229	155	17	10.96	7	4.51
CA-MNT-1232/H	31	0	0.00	2	6.45
CA-SLO-2 Component II	419	17	4.06	5	0.12
CA-SLO-165	26	1	3.84	0	0.00
CA-SLO-215	165	1	0.60	0	0.00
CA-SLO-585	45	8	17.80	1	2.22
CA-SLO-832/1420	69	5	7.25	0	0.00
CA-SLO-2357	65	4	6.20	4	6.20
Total	978	53	5.41	19	1.94
HUNTING (EARLY PERIOD: 3500–600 BC)					
CA-MNT-73	49	2	4.08	1	2.04
CA-MNT-108	305	4	1.31	16	5.25
CA-MNT-116	28	4	14.30	5	17.86
CA-MNT-170	36	8	22.22	15	41.66
CA-MNT-234	124	22	17.74	28	22.58
CA-MNT-391	241	54	22.40	32	13.27
CA-MNT-831	290	28	9.65	29	10.00
CA-SCR-7	36	6	16.66	3	0.83
CA-SLO-165	263	26	9.88	13	4.94
CA-SLO-274	94	9	9.60	5	5.32
CA-SLO-273/H	14	1	7.14	0	0.00
Total	1480	164	11.08	147	9.93
HUNTING (MIDDLE: 600 CAL BC TO CAL AD 1250)					
CA-MNT-63	154	14	9.10	21	13.63
CA-MNT-101	384	64	16.70	39	10.15
CA-MNT-115	74	6	8.11	49	66.21
CA-MNT-229	669	90	13.45	20	2.98
CA-MNT-234	97	8	8.24	25	25.77
CA-MNT-238	804	23	2.98	38	4.72

(continued)

TABLE 11.2 (continued)

COMPONENT	TOTAL MAMMAL AND BIRD NISP			OTARIIDS NISP	%
	SEA OTTER NISP				
CA-MNT-1233	238	2	0.84	2	0.84
CA-SCR-9	619	2	0.32	11	1.77
CA-SCR-93	71	6	8.45	1	1.41
CA-SCR-132	28	3	10.71	3	10.71
CA-SLO-2 Component III	1638	278	16.97	20	1.22
CA-SLO-9	139	18	12.24	2	1.43
CA-SLO-165	2	0	0.00	1	50.00
CA-SLO-175	49	1	2.04	0	0.00
CA-SLO-179	631	70	11.10	48	7.60
CA-SLO-267	308	12	3.90	19	6.16
CA-SMA-18	683	67	9.80	112	16.39
CA-SMA-218	197	5	2.53	142	72.08
Total	7030	704	10.01	560	7.96
LATE					
CA-MNT-112	114	6	5.30	7	6.14
CA-MNT-234	25	2	8.00	6	24.00
CA-MNT-1223	119	1	0.84	0	0.00
CA-MNT-1227	126	1	0.79	0	0.00
CA-MNT-1277/H	124	3	2.41	1	0.80
CA-MNT-1765	11	1	9.10	0	0.00
CA-MNT-1942	69	13	18.84	0	0.00
CA-SLO-2 Component IV	688	136	19.77	17	2.47
CA-SLO-165	4	0	0.00	1	25.00
CA-SLO-71	51	11	21.60	4	7.84
CA-SMA-97	84	8	9.52	12	14.28
CA-SMA-115	96	55	57.29	6	6.25
CA-SMA-118	103	9	8.73	6	5.82
Total	1614	246	15.24	60	3.71

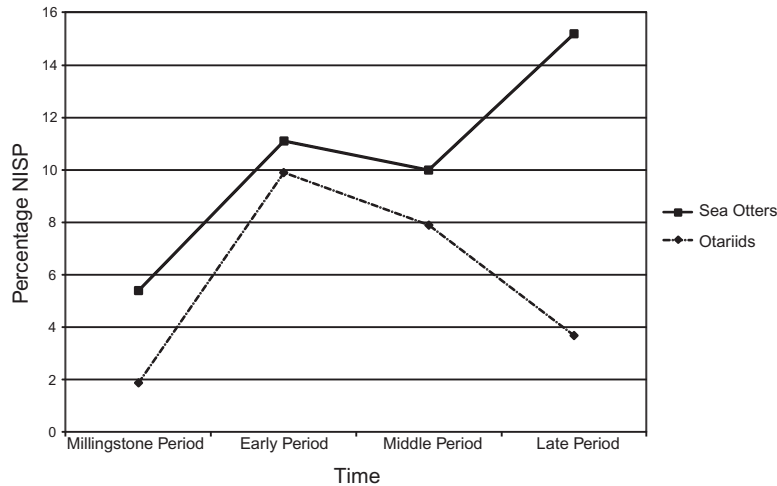


FIGURE 11.5. Sea otter and terrestrial breeder remains (northern fur seal, Guadalupe fur seal, California sea lion, Steller sea lion, and elephant seals) over time along the central California coast based on percentage of identified bird and mammal remains (NISP).

seals decrease. Regional variability is apparent, as some sites on the Pecho Coast (CA-SLO-2) and near Año Nuevo (CA-SMA-115) produced substantial quantities of otter remains (19–57% NISP) while others at Big Sur (CA-MNT-1223 and -1227) yielded almost none. The overall regional increase runs counter to a trend described by Jones (1996) based on preliminary findings from Big Sur where a decrease in otter bones during the Late Period (ca. AD 1250–1769 give approximate dates) was thought to reflect decreased interregional trade. A subsequent excavation in Big Sur by Wolgemuth et al. (2002) produced previously underrepresented otter bones, offsetting the earlier pattern.

Both the combined regional record and the large collection from CA-SLO-2 show the same relative pattern: otters were the most heavily exploited marine mammal over time and their exploitation increased incrementally through the Holocene. That these two datasets are mutually concordant suggests that the overall pattern is empirically legitimate and provides some justification for using data from CA-SLO-2 to represent the region as a whole. Several aspects of the patterning in these data also suggest they are the products of incremental human population growth over the course of the Holo-

cene. At CA-SLO-2, the increase in sea otter bones correlates inversely with the disappearance of the flightless sea duck (*Chendytes lawi*; Figure 11.6), which was caused by overexploitation throughout the duck's range over an 8000-year period (Jones, Porcasi, Erlandson et al. 2008). Increasing exploitation of otters likewise seems to reflect increased use of watercraft and greater presence of humans in offshore habitats over time. Importantly, the CA-SLO-2 data set also includes values for exploitation of both abalone and sea urchins over the course of the Holocene (Figure 11.7) that show no evidence of the kind of species replacement that Simenstad et al. (1978) documented in the Aleutians. Rather, sea urchins remained insignificant over time, while abalone exploitation increased concomitantly with otter exploitation. This suggests that some reduction in the nearshore populations of otters as a result of human harvest led to increased availability of abalones for Native people, with local kelp forests appearing to remain fairly stable over the long term.

One other recent archaeological finding has contributed to knowledge of sea otter hunting of a different type. Langenwalter II et al. (2001) recovered a sea otter femur embedded with a chert projectile point tip at a site in Long Beach,

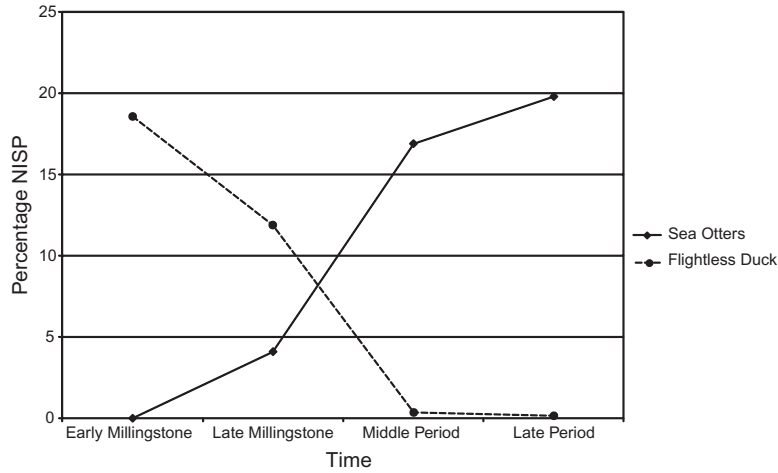


FIGURE 11.6. Remains of the sea otter and the flightless duck (*Chendytes lawi*) from CA-SLO-2 over time (percentage of NISP).

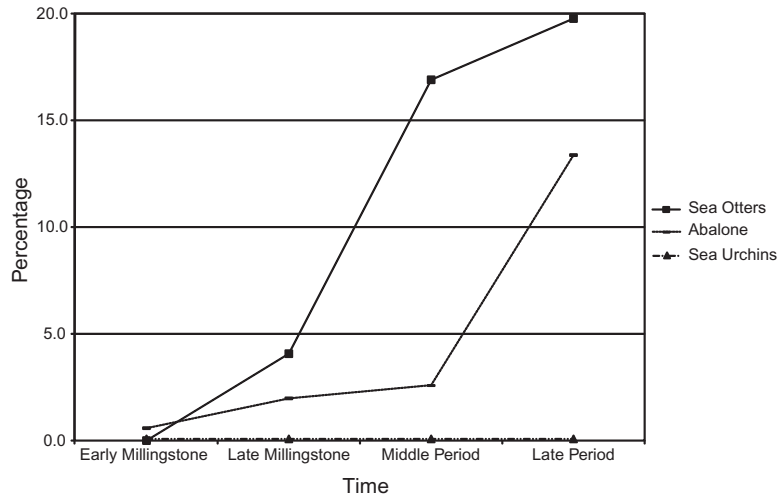


FIGURE 11.7. Sea otter, abalone, and sea urchin remains through time from CA-SLO-2 (percentage NISP for sea otters; percentage of shell weight for abalone and urchins).

California, that had been occupied from ca. AD 1420 to contact. This evidence suggests that prehistoric people hunted sea otters with stone-tipped projectiles. Langenwalter II et al. (2001) assert the otter was killed while swimming and not on land due to the projectile point's angle of entry. Erlandson and Braje (2007) have also speculated that small Channel Island Barbed Points (aka Arena points) dated to ca. 8000 to 6000 BC may have been used to hunt sea otters on the Channel Islands.

PREHISTORIC GENETICS

A sample of 41 prehistoric bones from CA-SLO-2 (Table 11.3), representing approximately 10% of the 431 sea otter NISP from this site, was analyzed genetically at the Seattle Aquarium to determine the sex of the animals. The method used focused on variation at four microsatellite loci (Mvi 57 and Mvi 87 [O'Connell et al. 1996] and Mvis 72 and 75 [Fleming et al. 1999]). Caution was used to prevent multiple sampling from the same individual and to prevent sam-

TABLE 11.3
Results of DNA and Isotopic Analysis of CA-SLO-2 Sea Otter Bones

SAMPLE	UNIT	LEVEL (CM)	µG N	δ ¹⁵ N (AIR)	µG C	δ ¹³ C (PDB)	C:N	SEX	COMPONENT
S2	N10/W17&18	50-60						Male	Late Period
S3	S1/W1	20-30						Female	Late Period
S4	N4/W1	30-40	190.5	14.01	498.2	-10.23	3.05	Female	Late Period
S5	N4/W2	20-30	79.1	13.63	216.3	-10.45	3.19	Female	Late Period
S6	N11/W14	50-60	189.6	15.31	510.1	-10.12	3.14	Female	Late Period
EL1	N1/W1	40-50						Female	Late Period
EL2	N1/W1	40-50						Female	Late Period
EL3	N1/W1	40-50	149.3	13.32	411.4	-10.92	3.21	Male	Late Period
EL4	N1/W1	60-70	163.9	14.03	444.4	-9.86	3.16	Female	Late Period
EL5	N1/W1	60-70						Female	Late Period
EL6	N10/W1	50-60						Female	Late Period
EL8	N10/W17	0-10						Female	Late Period
EL11	N10/W4	50-60						Female	Late Period
EL12	N10/W4	50-60						Female	Late Period
EL14	N4/W1	10-20						Female	Late Period
EL15	N4/W1	10-20	201.6	17.11	522.0	-10.50	3.02	Female	Late Period
EL16	N4/W1	50-60						Female	Late Period
EL17	N4/W1	50-60						Female	Late Period
EL18	N4/W1	60-70	135.6	12.91	371.3	-10.62	3.19	Female	Late Period

(continued)

TABLE 11.3 (continued)

SAMPLE	UNIT	LEVEL (CM)	µg N	δ ¹⁵ N (AIR)	µg C	δ ¹³ C (PDB)	C:N	SEX	COMPONENT
EL19	N4/W1	60-70						Female	Late Period
EL23	N4/W2	20-30	173.3	13.36	473.4	-10.70	3.19	Female	Late Period
EL24	N4/W2	40-50	147.6	13.60	412.4	-11.60	3.26	Female	Late Period
EL25	N4/W2	40-50	131.3	13.75	375.3	-11.78	3.34	Female	Late Period
EL26	N4/W2	40-50	151.9	13.28	413.4	-10.12	3.18	Male	Late Period
EL27	N4/W2	40-50	187.9	12.63	485.3	-10.15	3.01	Female	Late Period
EL 28	N4/W2	40-50	216.2	12.94	559.6	-10.18	3.02	na	Late Period
EL29	N4/W2	50-60	182.8	14.03	473.4	-9.92	3.02	Female	Late Period
EL30	N4/W2	60-70	159.6	14.19	436.4	-10.79	3.19	Female	Late Period
EL10	N10/W17	80-90						Female	Middle Period
EL20	N4/W1	70-80						Female	Middle Period
EL21	N4/W1	70-80	262.6	14.45	675.5	-9.46	3.00	Female	Middle Period
EL22	N4/W1	70-80	166.5	16.29	454.4	-11.63	3.18	Female	Middle Period
EL9	N10/W17	80-90	102.1	13.14	280.4	-9.69	3.20	Female	Middle Period
EL13	N10/W4	70-80	140.7	13.53	378.3	-10.55	3.14	Female	Middle Period
EL31	N1/W1	180-190	167.3	14.30	447.4	-9.34	3.12	Male	Middle Period

EL33	N10/W4	190-200	110.7	17.26	306.7	-12.00	3.23	Female	Middle Period
EL40	S4/W9	230-240	185.3	15.12	511.1	-10.96	3.22	Female	Millingstone
EL41	S4/W9	230-240	175.9	15.21	471.4	-12.62	3.13	Female	Millingstone
EL44	N1/W4	240-250	170.8	18.43	473.4	-14.53	3.23	Female	Millingstone
EL45	S1/W12	250-260	22.4	15.02	87.5	-15.26	4.56*	Female	Millingstone
EL46	N4/W1	250-260						Female	Millingstone
MOD1			186.3	12.96	463.3	-12.25	2.90	Male	Modern
M-1788			227.9	14.47	572.1	-11.85	2.93	Male	Modern
M-1793			193.9	13.66	486.1	-10.82	2.92	Male	Modern
M-1797			178.4	15.06	445.2	-10.39	2.91	Male	Modern
M-1784			198.0	16.43	498.3	-11.58	2.94	Female	Modern
M-1899			175.3	15.48	439.1	-12.12	2.92	Female	Modern
M-2211			206.8	14.72	517.7	-12.48	2.92	Female	Modern

ple contamination. To minimize the chances of obtaining more than one sample per individual, three precautions were taken: (1) samples were taken from a wide array of locations on each bone; (2) a narrow range of skeletal elements (femur, humerus, mandible, maxilla) was utilized; and (3) after amplification, samples were compared for identical genotypes and if found one was removed. Control of potential contamination of the ancestral bone samples followed aspects of protocols described previously (Hagelberg and Clegg 1991; Hoss and Paabo 1993; Rosenbaum et al. 1997). All materials and equipment that could potentially come into contact with the samples (cotton gauze, tips, tubes, etc.) were treated with UV light for 10 minutes. Each bone sample was cleaned repeatedly with ethanol and 10% bleach and rinsed with RNA- and DNA-free water prior to sampling. A variable-speed Dremel rotary tool was used, with a new UV-treated drill bit for each sample, to collect bone dust. Samples were collected in a sterile 1.5 mL microcentrifuge tube and stored at ambient temperature until extraction. Bone samples were decalcified in 1 mL of 0.5 M EDTA for at least 24 hours at 37°C. Several changes of EDTA supernatant were made to remove pigmented humic acids absorbed from the sediments. Once relatively clear EDTA supernatant was obtained, the EDTA was removed and the resulting bone pellet was rinsed with sterile water, and the DNA was extracted using the DNeasy tissue extraction kit (Qiagen, Valencia, CA). Blank controls during DNA extraction, PCR, and fragment visualization were employed to determine potential contamination. Bone sexing followed the methods described in Hattori et al. (2003) and utilized pcr primers ZFX/ZFY, digested with *Nla*III and visualized on a 1.5 % agarose gel.

A determination could not be made for one specimen. Sex determinations for the remaining 40 specimens showed that 36 (90%) were female and 4 were male. Five specimens representing the Early to Middle Holocene (Millingstone) occupation (5000–3000 cal BC) were all

female. The Late Holocene samples (Middle and Late periods; ca. 1500 cal BC to cal AD 1800) included 31 (89%) females and 4 males. While the available sample is small, it suggests that prehistoric exploitation favored females over males at least at CA-SLO-2.

STABLE ISOTOPE ANALYSES

Collagen stable isotopes reflect the average isotopic composition of the protein portion of an individual's diet in the years before death. The duration over which the values are averaged depends upon the rate of collagen turnover, which varies by species, life history stage, diet quality, and skeletal element (Tieszen et al. 1983). The heavier stable isotopes of carbon and nitrogen (i.e., ¹³C and ¹⁵N) are preferentially taken up during protein synthesis, causing a widely recognized but variable trophic enrichment between diet and consumer tissues (DeNiro and Epstein 1978, 1981; Hedges and Reynard 2007; Minagawa and Wada 1984; Sealy et al. 1987). Collagen isotope values represent a proportional mixture of the isotope signatures of the various prey species consumed by an individual. In a simple system, for example, an individual eating 50% prey A and 50% prey B will have a corrected collagen value halfway between the two food sources. Organisms with relatively monotonous diets (e.g., specialized feeders) show less intraspecific variation in collagen isotope values than animals capable of foraging in multiple isotopically distinct habitats (e.g., a mixed marine-terrestrial diet) or at a variety of trophic levels (e.g., a diet including both herbivores and carnivores). Some pinniped species, as dedicated piscivores, are examples of the former, whereas sea otters are consistent with the latter, given the variety of invertebrates from different functional classes they may consume (e.g., filter feeders, grazers, scavengers, etc.).

Among contemporary central coast otter populations in the Monterey Bay National Marine Sanctuary (MBNMS), recent feeding studies observe six diet specializations defined by

prey size and foraging habitats: two large prey specializations in abalone and crab or *Cancer* crabs; three medium prey specializations in varied kelp forest prey, in urchins and/or mussels on rocky hard substrates, and in clams, worms, and other invertebrates on soft-bottom substrates; and a small prey specialization in turban snails (*Tegula* sp.), and some kelp crabs and sea stars (Oftedal et al. 2007:160). Foraging specialization has the effect of dividing finite prey resources, thus reducing intraspecific competition and increasing foraging efficiency. In the case of the modern MBNMS, the diversity of diets is thought to be an adaptation to increasing food limitation, which is currently manifest in the relatively poor body condition of central coast otters compared to populations to the north and south (Oftedal 2007:174–175). Although specialists may increase foraging efficiency, not all observed diet specializations may be viable, with the specialization in turban snails and other small prey appearing to be nutritionally inadequate (Oftedal et al. 2007). Therefore, it may not be expected to persist if resource competition is reduced, either as higher-quality prey becomes more abundant and the suboptimal diet is abandoned, or otter populations decrease due to mortality related to the inadequacy of the small prey diet. Thus, on longer time scales dietary specialization will change in response to changing ecological parameters.

The prey species that compose each of these diets have distinct stable isotopic signatures, so an otter population with a variety of diet specializations will exhibit a greater spread of collagen isotope values than a population of generalists or a population with a single specialization (Bearhop et al. 2004; Oftedal et al. 2007:187–189). Therefore, diachronic change in the scatter of prehistoric otter isotope values can be used as a proxy for foraging specialization. The ultimate driver of specialization may be difficult to identify: for example, food limitation due to declines in basal productivity cannot be distinguished from food limitation as a population reaches carrying capacity. However, rele-

vant archaeological data on human foraging patterns, technological adaptations, and demography can be used to evaluate multiple working hypotheses generated by patterns of isotope variability.

ANALYTICAL METHODS

Analyses of stable C and N isotopes were conducted on bone collagen extracted from 25 of the sea otter bones from CA-SLO-2 that were subjected to DNA analysis, as well as 7 modern samples collected from the central California coast. General procedures follow those of Newsome et al. (2004). Samples ranging from ~250 to 750 mg dry weight were removed with single-use Dremel cut-off wheels, which were changed between each sample. To reduce potential cross-contamination, cutting was done under a hood onto aluminum foil that was disposed of along with the dust after each sample was taken, and the work area was wiped down with 70% ethanol. Samples were physically cleaned of adhering sediment, and the outer surfaces of the bone were scraped away with an X-acto blade. Bone was demineralized over 2 to 5 days in 0.5N HCl at ~5°C in scintillation vials. Lipids were removed by soaking demineralized bone in a methanol-chloroform solution (2:1) and rinsed in multiple baths of deionized water while being sonicated. The resulting collagen was lyophilized and weighed, and % collagen yield was determined. Of an original 43 specimens from CA-SLO-2 that were subject to extraction, 25 produced usable collagen, ranging from ~2.5 to 10% yield by weight. Yields in these ranges reflect good preservation for isotopic analyses (Ambrose 1990; DeNiro and Weiner 1988; van Klinken 1999). Many of the unusable specimens were slightly charred bones that disintegrated during demineralization or lipid extraction. Collagen yield from the modern specimens ranged between ~17 to 24% by weight.

Subsamples of 1.0 ± 0.2 mg of lyophilized, extracted collagen were packed into tin capsules and submitted to the UC Davis Stable Isotope Facility (Dept. of Plant Sciences) where C and

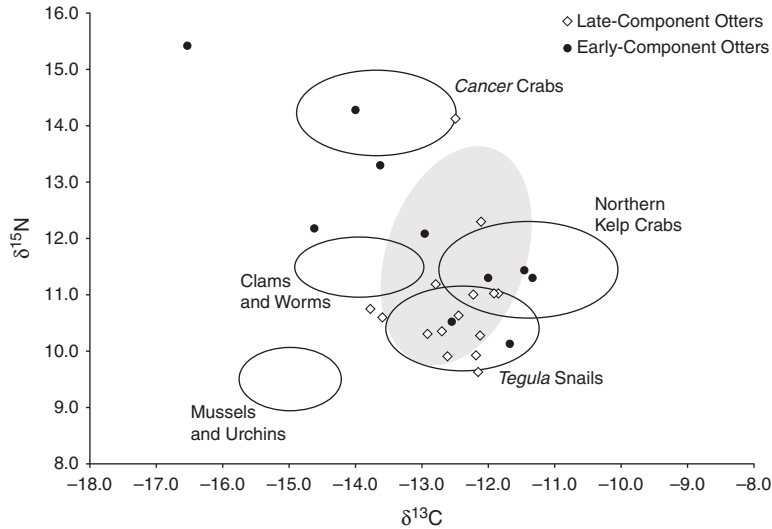


FIGURE 11.8. Stable isotope results for Early component (closed circles) and Late component (open diamonds) sea otter collagen from CA-SLO-2. The range of values for seven modern central coast otters is depicted with a gray ellipse. Typical prey isotope values for the MBNMS (open ellipses) are redrawn from Oftedal et al. (2007:202, figure 6.6). Collagen values are corrected for fractionation to place them in diet space ($\delta^{15}\text{N}_{\text{diet}} = \delta^{15}\text{N}_{\text{collagen}} - 3\text{‰}$; $\delta^{13}\text{C}_{\text{diet}} = \delta^{13}\text{C}_{\text{collagen}} - 2\text{‰}$), and modern otters and prey $\delta^{13}\text{C}$ values are increased 1‰ to correct for modern ^{13}C depletion due to fossil fuel burning (i.e., Suess effect).

N stable isotope concentrations were analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer. Sample isotope ratios are reported as $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values, where $\delta R_{\text{sample}} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, and R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios of measured samples and standards, respectively. Results are reported in ‰ notation (per mil or parts per thousand) with respect to the Pee Dee Belemnite (PDB) scale for $\delta^{13}\text{C}$ and AIR (Ambient Inhalable Reservoir; atmospheric N_2) scale for $\delta^{15}\text{N}$.

RESULTS

Stable isotope results for sea otter bone collagen are presented in Table 11.3 with measured abundances of C and N (in μg) for each sample. The C:N ratio of collagen in terms of elemental abundance [i.e., $(\mu\text{gC} \times \mu\text{mol}/12\mu\text{g}) / (\mu\text{gN} \times \mu\text{mol}/14\mu\text{g})$] gives an indication of collagen preservation, with values between 2.9 and 3.6 being consistent with modern, unaltered colla-

gen (DeNiro 1985). C:N ratios reported in Table 11.3 indicate good collagen preservation in these samples, with the exception of the high value of 4.56 for EL45 that is attributable to a very small sample size (87.5 μgC , 22.4 μgN). The modern otter samples have lower average C:N ratios than archaeological specimens, but all are within the recommended range.

Isotope results for modern and archaeological otters ($n=31$, excluding EL45) are plotted in Figure 11.8 along with isotope ranges for typical otter prey groups recently measured for the Monterey Bay National Marine Sanctuary (Oftedal et al. 2007). All data are presented in “diet space,” i.e., measured collagen values are corrected for trophic fractionation to reflect the isotopic content of the consumer’s diet by reducing $\delta^{13}\text{C}$ by 2‰ and $\delta^{15}\text{N}$ by 3‰ (Kelly 2000; Oftedal et al. 2007). Additionally, $\delta^{13}\text{C}$ values for modern prey groups and otter specimens are increased 1‰ to correct for isotopic depletion of the atmospheric carbon reservoir due to historic fossil fuel burning (i.e., the Se-

TABLE 11.4
Variance in Stable Isotopes by Component at CA-SLO-2

COMPONENT	N	VAR. $\delta^{15}\text{N}$	VAR. $\delta^{13}\text{C}$	TOTAL VARIANCE
Modern	7	1.31	0.60	1.91
Late	15	1.22	0.32	1.54
Early	9	3.02	2.90	5.92
Early (excl. EL44)	8	1.88	1.52	3.40

uss effect). Accounting for these offsets allows for the direct comparison of prehistoric and modern otter diet with a variety of potential prey species.

The number of potential food sources precludes unique solutions for individual diets, because multiple diet combinations could lead to the same mixture (Newsome et al. 2004; Phillips and Koch 2002; Phillips et al. 2005). For example, assuming a linear mixing model, a diet composed of ~50% clams and worms and ~50% kelp crabs would appear similar to a diet of ~25% *Cancer* crabs and ~75% *Tegula* snails. Dietary specialization could therefore be underestimated when considering individuals that fall in the center of the diet space plot. By contrast, any values close to one of the more distinct diet sources must contain a large proportion of that source in the diet.

With the exception of one outlier (EL44), all of the modern and prehistoric otters fall within the diet space defined by the prey species (Figure 11.8), which suggests this is a reasonable first approximation of the prehistoric foraging regime. Comparing the scatter between the otter subsamples, there is clearly a greater spread in the Early component compared to the Late component or the modern samples (their range indicated by the grey ellipse), consistent with decreased dietary specialization within otter populations through time. Reduced scatter can also be expressed by comparing the variance in each stable isotope by component (Table 11.4). Again, modern and Late components show lower variance than the Early component, even

when the sample falling outside of the prey-defined diet space is excluded. The shift in variability is accompanied by a decline in mean $\delta^{15}\text{N}$ values (Early=14.91‰ vs. Late=13.87‰) indicating that the trend towards diet homogeneity in the Late component occurred through the removal of higher trophic-level diet specializations among otters in the CA-SLO-2 assemblage.

DISCUSSION

Assuming that intraspecific variation in stable isotope values is a proxy for the variety of diet specializations within a population, the data indicate that individual otter diets became less differentiated in the vicinity of CA-SLO-2 over the course of the Holocene. That is, there are fewer distinct foraging strategies evident in the Late component versus the Early component. For otters, the effect of adopting different foraging strategies is to reduce intraspecific competition by dividing available resources, and thereby increasing foraging efficiency (Oftedal et al. 2007). In the modern context, the degree of observed specialization in central coast otter populations is interpreted as a response to food limitation. The behavioral response of foraging specialization could be predicted to occur as a population approaches the effective carrying capacity of its habitat, which could be caused by several processes working singly or in combination: increased otter population; decreased prey abundance due to external environmental change; or increased interspecific competition for resources. Conversely, a population exhibiting fewer foraging specializations would

be predicted to be below its effective carrying capacity because of suppressed numbers, increased abundance of high-quality prey, or less direct competition from other predators for resources.

SUMMARY AND CONCLUSIONS

The archaeological data on otter hunting by Native Californians summarized in this chapter provides evidence for growing predatory pressure on otter populations through the Holocene, while at the same time, the historic record indicates that a robust population of otters (ca. 20,000 animals as opposed to only 3000 today) was present along California shores at the end of the prehistoric era. It is fairly apparent that growth in human populations over the Holocene led to increased exploitation of otters for food and their pelts as trade goods. While the available sample is small and results must be considered preliminary, DNA analysis of sea otter bones shows that Native exploitation focused heavily on females rather than males. Females spend more time on land, dive to shallower depths, and occupy territories closer to shore than males, so a focus on females would be consistent with attempts to maximize hunting yields relative to pursuit costs. A modest increase in males during the Late Holocene suggests a slight decrease in foraging efficiency over time as lower-ranked males were eventually targeted in addition to females although the sample available for the Early to Middle Holocene is very small. Since otters often occupy single-sex areas, it is possible that the overabundance of females at CA-SLO-2 reflects the site's proximity to a female-dominated territory. Nonetheless, heavy focus on females at any location would be antithetical to stewardship or conservation of otter populations. In this seemingly paradoxical case, nonconservative hunting over a 9000-year period culminated at the end of prehistory in an extremely large population of sea otters along the California coast. Findings from Diablo Canyon also show no evidence for major alterations in the structure or distri-

bution of kelp forests as a consequence of otter exploitation; there is no evidence for any significant increase in sea urchin remains akin to that associated with otter overexploitation in the Aleutians (Simensted et al. 1978), and no evidence for any collapse of kelp forest habitats.

Preliminary results from isotope studies suggest, however, that increasingly intensive otter exploitation over the course of the Holocene was not without its effects. Molluscan remains from CA-SLO-2 show increased abalone harvesting concomitant with increased exploitation of otters, suggesting a greater human presence in nearshore habitats. Both direct competition between humans and otters for the same food sources (e.g., abalone and sea urchins), and the increased human presence in the otter's offshore habitat (as a result of increased hunting) would have reduced the foraging options for otters. From the otters' perspective, habitat occupied by human hunter-gatherers would have become less accessible. Isotopically, this could lead to increased variability because greater diet specialization would be required. However, if certain isotopically distinct foraging specializations are excluded by human competition (e.g., nearshore foraging), the range of values within a component could be seen to decrease. The observed pattern of decreased diet specialization from the Early to Late components at CA-SLO-2 argues that human predation of otters both suppressed local otter populations and decreased the available foraging habitats through competitive exclusion.

Overall, the combined archaeological, historic, genetic, and stable isotopic records show unequivocally that humans, otters, and abalone coexisted for 9000 years along the central California coast and that robust populations of one species did not preclude the existence of the other. Paradoxically, otters were harvested regularly along the entire central coast in a nonconservation-oriented manner, yet this increasingly intensive harvest was sustainable, as a robust population of otters was available for commercial hunters at the beginning of the 19th century and there is no archaeological evidence for

the collapse of local kelp forests. This seems to speak to a level of productivity in California's pre-contact nearshore environments that is almost inconceivable in comparison with that of recent times. During the prehistoric era, conservation seems to have been an epiphenomenon that resulted from this richness and human populations that were still below the carrying capacity of these remarkably productive habitats.

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