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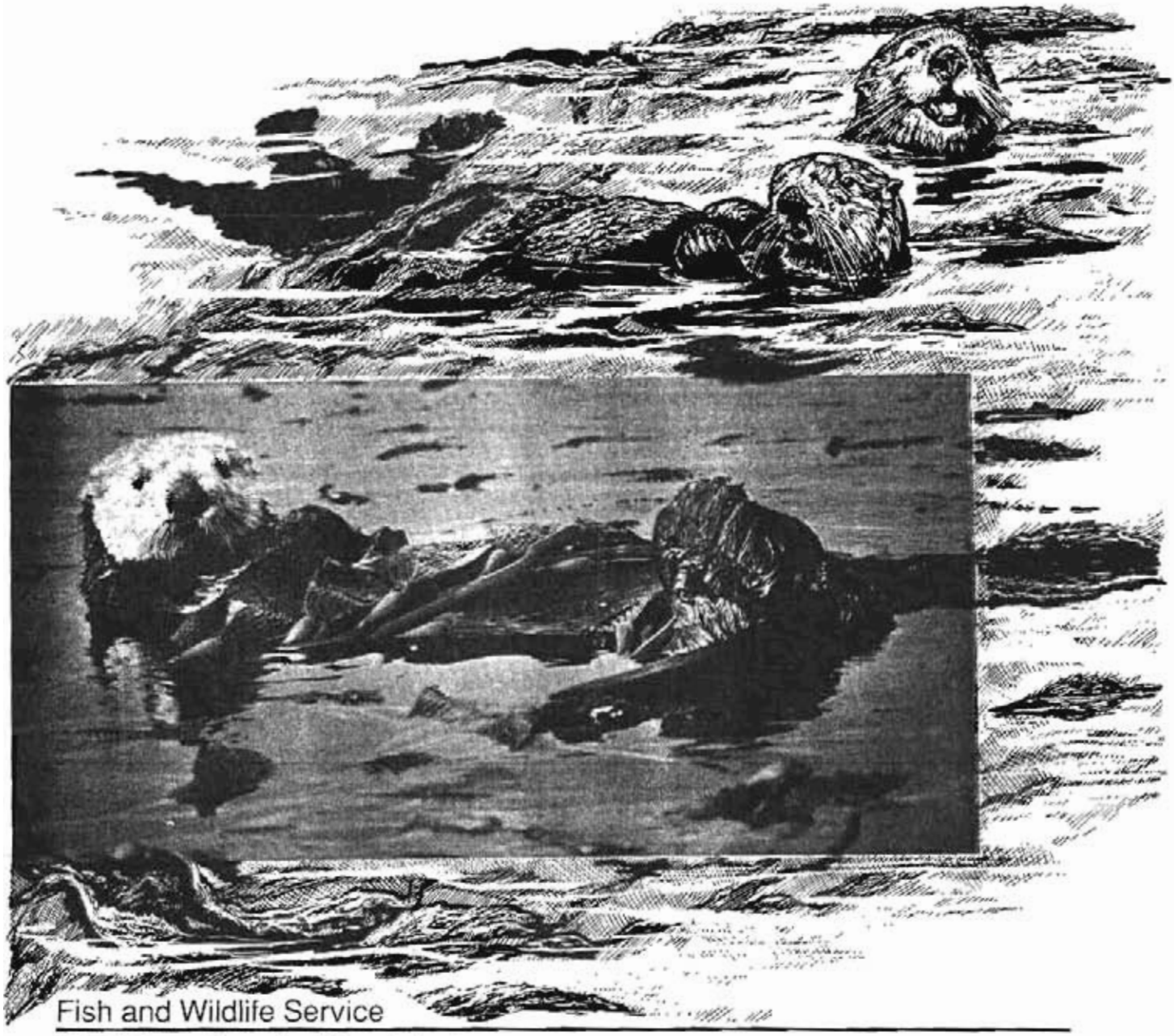
The Sea Otter (*Enhydra lutris*): Behavior, Ecology, and Natural History



Fish and Wildlife Service
U.S. Department of the Interior

Biological Report

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The Sea Otter (*Enhydra lutris*): Behavior, Ecology, and Natural History

By

Marianne L. Riedman and James A. Estes

U.S. Department of the Interior
Fish and Wildlife Service
Washington, D.C. 20240

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The Sea Otter (*Enhydra lutris*): Behavior, Ecology, and Natural History

by

Marianne L. Riedman

Monterey Bay Aquarium
Research Division
886 Cannery Row
Monterey, California 93940

and

James A. Estes

U.S. Fish and Wildlife Service
Institute of Marine Sciences
University of California
Santa Cruz, California 95064

ABSTRACT.—The sea otter (*Enhydra lutris*) represents a clade that separated from the primitive lutrine carnivores by at least the upper Miocene. One extant species and three subspecies are recognized. Many aspects of their morphology and physiology are unique amoug the lutrines but are similar to the pinnipeds, probably reflecting selection and adaptation for marine living. Sea otters feed on a broad range of benthic invertebrates and often limit prey populations. These interactions have broad-ranging ecological and evolutionary consequences.

Sea otters use rocks or other hard objects as tools to break the exoskeletons of their invertebrate prey; except for a number of primate species, this behavior is unique among mammals. There is growing evidence that sea otters have highly individualized diets and patterns of foraging behavior. The species senses and avoids paralytic shellfish toxin. Foraging activity and diurnal patterns seem to vary in relation to population status and food availability. Sea otters are strongly polygynous. Adult males defend contiguous territories from which they exclude other males, perhaps causing males to congregate in suboptimal habitats or at the ends of a population's range. Daily movements usually encompass a few kilometers, although otters occasionally move longer distances, and seasonal movements occur among some age–sex classes in certain areas. Reproduction is weakly seasonal, with most young born during late winter in California and early summer in Alaska. Females become sexually mature at about 3 years and typically give birth to a single pup each year thereafter.

Mortality is poorly known, although entanglement in fishing nets probably has limited the population in central California. Undisturbed populations can increase at about 17–20% yr^{-1}, although the central California population has never increased at >5–7% yr^{-1}. Home range fidelity and postrelcase dispersal are probably the principal barriers to successful reintroductions. Reintroduced populations have been established in southeast Alaska, British Columbia, and Washington. Similar efforts at other locarions were unsuccessful or their status is undetermined.

More than two decades have passed since Kenyon (1969) published his comprehensive monograph on the sea otter in the eastern Pacific Ocean. Since that time, several notable developments have contributed to a large increase in knowledge about this interesting species. Undersea research did not really come into its own until the mid-to-late 1960's. Use of SCUBA diving gear has opened a whole new world to marine ecologists—this includes the shallow sea floor of the North Pacific rim, where sea otters obtain most of their prey. Interactions among sea otters, sea urchins, and kelp beds compose a now well-known story to community ecologists, and

nearly all this information has been assembled during the past 15 years. Similarly, major technical advances in radiotelemetry and other remote sensing methods have been made during recent years. These techniques have permitted researchers to answer questions about the physiology, behavior, and population biology of free-ranging animals that were difficult (if not impossible) to answer before. The use of radiotelemetry has provided important new information (most of which has been assembled during the past 6 or 7 years) concerning the movements, activity patterns, life history, and population dynamics of sea otters.

Effective procedures for field-marking sea otters were unavailable at the time Kenyon's monograph was published; researchers in the field therefore had no means of maintaining longitudinal records of individual sea otters beyond the brief time visual contact with an animal could be kept. By the mid-1970's, State and Federal biologists had begun to develop and use hindflipper tags that allowed individual sea otters to be recognized in the field. In addition, procedures and equipment for capturing sea otters have been greatly improved over the past several years. These improvements have led to a significant shift in behavioral studies, from the population as a whole, to the individual level, in such areas as foraging behavior, movements, social behavior, reproduction, and survival.

Perhaps the most significant development that has helped increase our knowledge of sea otters over the past 20 years was the growth of environmental awareness in the 1960's and 1970's, which gave rise to an elevated public concern for wildlife and, no doubt, passage of two important Federal acts: the Marine Mammal Protection Act of 1972 and the Endangered Species Act of 1973. These, in turn, led to Federal and State agencies hiring additional people and spending more money to learn about sea otters. Most of the large volume of published and unpublished work on sea otters that was generated in the United States during the past 15 years surely would not have been done had it not been for this legislation.

In 1985, the Fish and Wildlife Service began to seriously consider the possibility of reintroducing sea otters to an area currently uninhabited by otters in California to reestablish a second population in order to (1) hasten recovery of the species from its legally threatened status under the Endangered Species Act, and (2) provide scientific information about the sea otter and its habitat that seemed unobtainable by other reasonable means. Because of the highly controversial nature of this proposal, it was decided that an environmental impact statement would be required, which in large part was prepared through a cooperative arrangement between the Fish and Wildlife Service and the University of California at Santa Cruz.

One of us (M.R.) was contracted to write a review of those aspects of sea otter biology deemed relevant to the reintroduction project. That document was a first step in the preparation of this report (Riedman 1987). We subsequently reasoned that much of what had been uncovered and synthesized in preparing the EIS would be of broad and lasting interest, but that this information needed to be made more readily available. Therefore, we decided to expand the review to include several important topics not covered in the original draft.

Our purpose is to provide a current review of the biology, ecology, and behavior of the sea otter. We also offer some of our own thoughts in the form of various syntheses, interpretations, and previously unpublished data. This account is not an even-handed effort to review everything known about sea otters—although we have attempted to cover the results of studies done in Alaska, Canada, and the Soviet Union, we have emphasized the population and its habitat in central California. And although, inevitably, we have touched on several of the management and conservation problems facing sea otters (such as the conflicts with shellfisheries and concerns about oil pollution) in large part we have chosen to omit these controversial and difficult issues.

Evolution

Phylogeny and Fossil Records

Based on the observed dichotomy among species foraging on fish or invertebrates, Pohle (1919) divided living otters into "fish-otters" and "crab-otters." He presumed these groups to be distinct phylogenetic lineages. More recently, based on dentition (van Zyll de Jong 1972) and cerebral morphology (Radinsky 1968), the nominal "crab-otters" were presumed to contain two lineages. By this view the fish-eating forms (represented by the extant *Lutra* and *Pteronura*) are primitive, and crab-eating forms were twice derived from the fish-eating lineage. In one lineage, represented by extant species of *Aonyx*, shearing ability of the carnassials was retained. In the other, represented by the extant sea otter (*Enhydra*) and the extinct *Enhydritherium* and *Enhydriodon*, the carnassial shearing function was lost to progressively improved crushing ability; in addition, body size was much larger.

Cladistic relationships among the sea otters, other lutrine carnivores, and other mustelids have been proposed by Berta and Morgan (1985). In their view, there are two lineages of sea otters: one leads to the extinct *Enhydriodon*, the other to the extinct *Enhydritherium* and the extant *Enhydra*. Extinct lineages are known mainly from dental morphology and tooth fragments. All known fossils of *Enhydriodon* are from Eurasia and Africa, with three well-described species: *E. sivalensis* (Falconer 1868) from the Pliocene of India, *E. falconeri* (Pilgrim 1931) from the late Miocene of India, and *E. africanus*,

from several sites in Africa (Stromer 1931; Hendey 1978). In addition, several specimens with more poorly understood affinities have been provisionally assigned to *Enhydriodon*, including *Enhydriodon latipes* (Pilgrim 1931) from the late Miocene of Greece, *E. reevei* (Newton 1890) from the late Pliocene of England, and as yet unnamed material from east Africa (Howell and Petter 1979).

Enhydritherium is known from the late Miocene of Europe and the late Miocene–middle Pliocene of North America (Berta and Morgan 1985). Two species have been described: *E. lluecai* from the late Miocene of Spain (Villata Comella and Crusafont-Pairo 1945; Crusafont-Pairo and Golpe 1962), and *E. terraenovae* from the late Miocene (6–7 million years ago) to middle Pliocene (3.2–3.7 million years ago) faunas of Florida and California (Berta and Morgan 1985; Fig. 1).

The lineage dichotomies proposed by Berta and Morgan (1985) are distinguished as follows: (1) sea otters from other mustelids: P^1, lost; short, robust jaw; broad M_1, with low, inflated cusps; (2) *Enhydriodon* from *Enhydritherium*: very large size; P^4 with isolated hypocone; (3) *Enhydritherium* and *Enhydra* from *Enhydriodon*: P^4 triangular, lacking parastyll; deep masseteric fossa terminating below M_2; ventral border of ramus sharply upturned and flattened posteriorly; M_1 metaconid larger than proconid; and M_1 with squared off talonid; (4) *Enhydritherium* from *Enhydra*: P^3 protocone in anteromedial position; M_1 metastylid present, lacking talonid; and (5) *Enhydra* is distinguished by having greatly inflated tooth cusps; P^4 with reduced hypoconal crest; and M_1 with metastylid lost and metaconid extending far posteriorly.

Enhydritherium seem to have lived exclusively in or near coastal marine habitats. Berta and Morgan (1985) based this conclusion on the absence of *Enhydritherium* from other Hemphillian faunas in the interior of North America. From this fossil distribution, they surmised an epicontinental route of dispersal between the Atlantic and Pacific oceans, rather than by way of freshwater or terrestrial habitats.

The *Enhydritherium–Enhydra* lineage apparently originated in the Old World. Its specific route of immigration to North America remains unclear, although several possibilities have been suggested. One possibility is that the lineage dispersed from Eurasia to North America by way of the Bering Land Bridge, with a second phase of dispersal from the Pacific Ocean to the Atlantic Ocean through the Central American Seaway between 6 and 8 million years ago. This view has one clade in the North Atlantic represented by *Enhydriodon reevei*, and another in the North Pacific that led to *Enhydra* from a form resembling *E. lluecai*. A second possibility is that *Enhydriodon reevei* dispersed from the North Atlantic to the North Pacific by way of the Arctic Ocean. A specimen similar to *Enhydriodon reevei* from the late Pliocene in Alaska prompted Repenning (1983) to suggest that this route of dispersal and subsequent evolution led to *Enhydra* in the North Pacific. A third possibility, apparently favored by Berta and Morgan (1985), is that *Enhydritherium* dispersed from Europe around the rim of the North Atlantic and into the Pacific by way of the Central American Seaway in the late Miocene.

Repenning (1976a) wrote that "... *Enhydra* appears to be a product of the Pacific and to have never escaped from there." The earliest occurrence of *Enhydra* is still uncertain. There are two records from the early Pleistocene: one from Cape Blanco, Oregon (Leffler 1964), and the other from Moonstone Beach, California (Repenning 1976a). Mitchell (1966) reported *Enhydra* from the Timms Point Silt Member of the San Pedro Formation, California, and dated the specimen (uncertainly) as late Pliocene–early Pleistocene. On the basis of more recent marine microfossils from the area, Repenning (1976a) suggested that an early Pleistocene date for this specimen is more likely.

One extinct species, *Enhydra macrodonta* (Kilmer 1972) has been described from the late Pleistocene of California. The species was separated from the extant *E. lutris* on the basis of greater size of the posterior cheek teeth, a longer tooth row, and a more generalized coronoid process of the mandible.

In sum, the lutrine lineage that led to modern sea otters

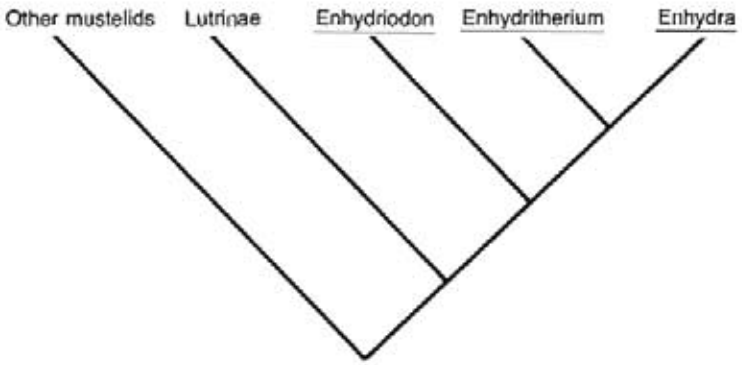


Fig. 1. Cladogram of the Lutrinae (Berta and Morgan 1985).

apparently diverged from the primitive otters late in the Miocene or early in the Pliocene, 7 to 5 million years ago. Current evidence (Berta and Morgan 1985) suggests that this lineage had a Eurasian origin, with various early forms having been widely distributed in Eurasia and North America, and even extending into Africa. The modern sea otter (*Enhydra*) arose in the North Pacific at about the start of the Pleistocene—about 1 to 3 million years ago—and has since been confined to the North Pacific basin.

Environment

Two important events may have led to the evolution of sea otters as invertebrate predators in coastal marine habitats. One was a global cooling trend at high latitudes in the late Cenozoic. The southern distributional limit of sea otters in the eastern Pacific coincided with areas of coastal upwelling, and the associated distribution of kelp forests (Kenyon 1969; Estes 1980). This distribution pattern corresponds with the 20–22° winter minimum isotherm, which occurs at about latitude 23° north (Durham 1950). In the early Miocene, the 20–22° isotherm occurred at about latitude 50° north. Thus, with late Cenozoic cooling, there was a southward expansion of the temperate zones, possibly providing a setting suitable for the evolution of sea otters (Estes and Steinberg 1988). The other event of possible evolutionary significance to sea otters was widespread extinction of the odobenid pinnipeds in the Pliocene (Repenning 1976b). Many species, in particular the dusignathine odobenids, were adapted to shallow-water, benthic foraging (Repenning 1976b). The last of these, *Pliopedia* and *Valenictus*, overlapped spatially and temporally with the earliest records of *Enhydritherium*. Repenning (1976b) suggested that extinction of these odobenids may have opened an environment for radiation of the *Enhydritherium*–*Enhydra* lineage.

The evolutionary consequences of sea otters, their ancestors, and ecologically similar species are poorly known. However, because modern sea otters are important predators in coastal communities, they well may have played important roles in shaping the evolution of many coastal organisms. Estes and Steinberg (1988) suggested that one such effect was a reduced intensity of herbivory, resulting from sea otter predation on herbivorous sea urchins, and speculate that this may have led to a poorly defended marine flora in the North Pacific Ocean.

Spatial and temporal patterns in the evolution and radiation of kelps (Order Laminariales) are consistent with this hypothesis. The extant kelps have a clear geographic affinity for the North Pacific, as do sea otters and the dusignathine odobenids. Of the 27 presently recognized kelp genera, 26 occur in the North Pacific. Only eight kelp genera have been reported elsewhere in the world, and only one of these (*Phyllaria*) is unknown from the North Pacific. Furthermore, kelp radiations appear to be recent, and therefore probably occurred in an environment containing sea otters or their early ancestors. Two kinds of evidence support this contention, one of which is paleoclimatological. The North Pacific was distinctly tropical–subtropical as recently as the middle Miocene (Addicott 1970). Since the Bering Land Bridge was closed at that time, the northernmost extent of the Pacific basin was probably too warm for most kelps—at least, all modern species.

Other evidence for recent kelp radiations comes from kelp-associated faunas, which, unlike the kelps, left a good fossil record. One group of particular interest is the limpets (Patellogastropoda), which are old and broadly distributed, and which left an excellent fossil record. Some limpet species are obligate associates on kelp stipes. These limpets are recognizable by a saddle-shaped shell that enables them to fit tightly against cylindrically shaped kelp stipes. Five species of saddle-shaped limpets are known from four subfamilies. All of these species appeared in the Pleistocene (Carlton 1976; Lindberg 1976), although patellogastropod limpets are known from the Mesozoic. The other faunal group is the dugongid sirenians, which are old (early- to mid-Cenozoic) and primarily tropical in distribution. This group gave rise to coldwater kelp eaters: *Dusisiren dewana* by the middle to upper Miocene (Takahaski et al. 1986) and *Hydrodamalis* by the mid-Pliocene in the North Pacific, culminating with the extinct Steller's sea cow (*H. gigas*), which was widely distributed in the North Pacific through the late Pleistocene–Recent (Domning 1978). Sea cows apparently foraged on shallow sublittoral kelps or surface canopy, and they also may have significantly influenced kelp forest ecosystems before their mid-1700's extinction, which was evidently due to human exploitation.

Certain biogeographical patterns in marine plant–herbivore interactions are consistent with the hypothesis that kelp radiations occurred in a low-herbivory environment. Much of the evidence is based on the idea that chemical defenses (mainly through phenolic compounds) are the principal means whereby fleshy brown algae (Phaeophyta) defend themselves against herbivory (Geiselman 1980; Geiselman and McConnell 1981; Steinberg 1984, 1985; Hay and Fenical 1988). In the North Pacific, many of the common brown algae are poorly defended by phenolics (Steinberg 1985, 1988; Estes and Steinberg 1988). In addition, feeding, growth, and reproductive success of strongylocentrotid echinoids (an important—if not the most important—kelp herbivore in the North Pacific) are strongly inhibited by phenolic compounds (Estes and Steinberg 1988). Conversely, in other temperate seas of the world, the brown algal floras appear to be comparatively depauperate (e.g., South Af-

rica and South America) or well defended by phenolic compounds (e.g., New Zealand and Australia). Steinberg (1989) reported that the diverse brown algal flora of northern New Zealand and southeastern Australia had high phenolic concentrations, and that echinoid herbivores in this area tended to be both less destructive grazers and less affected by phenolic compounds than are the strongylocentrotids in the North Pacific.

On the basis of these observations, Estes and Steinberg (1988) hypothesized the following evolutionary scenario: Kelp species radiated recently in the North Pacific in an environment in which the intensity of herbivory was low due to predation on benthic invertebrate herbivores by sea otters and perhaps the dusignathine odobenids. This resulted in weakly coevolved plant–herbivore interactions—that is, there was little selective pressure for the plants to evolve defenses against herbivores, and consequently, for the herbivores to accommodate to those defenses. Sea otters and dusignathine odobenids never occurred outside the North Pacific, nor is there evidence that predators of comparable influence now inhabit these areas or inhabited them in the past. As a result, populations of herbivorous echinoids may not have been limited by predation in these systems over evolutionary time. Thus, a more tightly coupled plant–herbivore interaction may have coevolved outside the North Pacific. In other words, plants developed extensive chemical defenses in response to abundant herbivores, and herbivores, in turn, developed enhanced capacities to tolerate plant defenses.

Adaptations Associated with a Marine Existence

Marine mammals share several types of adaptations associated with living in a marine environment—adaptions related to vision, hearing, olfaction, feeding, oxygen conservation, thermoregulation, water balance, locomotion, and reproduction. In general, the cetaceans, pinnipeds, and sirenians are substantially more specialized than sea otters for an aquatic existence, having evolved millions of years earlier than the otters. Although sea otters are the most recently evolved and least specialized group of marine mammals, they are the species most highly adapted for aquatic living belonging to the order Carnivora (excluding pinnipeds). Adaptive trends in sea otters are summarized and discussed in greater detail in subsequent sections.

The sea otter's eyes appear to be adapted for both aerial and underwater vision. According to Murphy et al. (1990), sea otters are able to focus clearly both underwater and in air by means of an excellent accommodative ability, which compensates for the loss of their corneal power underwater. Tactile senses appear to be well developed; otters frequently use their sensitive whiskers and paws to locate and capture prey beneath the surface. Hearing in the sea otter is virtually unstudied; however, in contrast to the pinnipeds and cetaceans, there is no evidence of cranial modification for directional sound perception underwater (Repenning 1976b). Olfaction also is virtually unstudied in the sea otter. In contrast to the pinnipeds, which have reduced olfactory sensitivity due to a reduction in nasal turbinates, sea otters have well developed turbinates, and acute olfactory sensitivity, typical of terrestrial carnivores, apparently has been retained. The social behavior of sea otters also suggests that scent production and acute olfactory sensitivity are important in this species. Observations of California sea otters indicates that males may locate estrous females by following waterborne scents across the ocean's surface (M. L. Riedman, Monterey Bay Aquarium, Monterey, Calif., unpublished data; C. Deutsch, University of California, Santa Cruz, Calif., personal communiction; J. E. Vandevere, 93 Via Ventura, Monterey, Calif., personal communication). Sea otters entering a group of otters commonly perform a ritualized greeting with one or more of the group members, probably involving some form of scent recognition.

The sea otter has developed distinctive adaptations for feeding on hard-shelled aquatic invertebrates. Shearing function of the cheek teeth, typical of other carnivores (including piscivorous aquatic forms), has been lost in favor of a crushing dentition. Furthermore, the musculature, skeletal anatomy, and neurological function of the strong forelimbs apparently are modified for tactile sensitivity and tool use associated with the detection, handling, and consumption of prey (Radinsky 1968).

The sea otter is also characterized by adaptations for pulmonary function and oxygen conservation associated with diving in the marine environment. Sea otters are capable of deep diving; the record depth is about 100 m (Newby 1975). The large lungs (Fig. 2) maintain surface buoyancy and serve to increase oxygen storage capacity (Kooyman 1973); the blood has a higher buffering capacity than that of nondiving mammals (Lenfant et al. 1970). In addition, Garshelis (1983) presented data that suggest to us that sea otters may use anaerobic metabolism when unusually deep or long dives are required. Cartilagenous airways connect directly with the alveolar sacs, which insure patency until compression collapse. This structure is also found in the pinnipeds and cetaceans but is absent in *Lutra* (Kooyman 1973).

Marine mammals have two modes of insulative heat conservation—blubber and fur. Blubber, which is used by the more highly specialized pinnipeds and cetaceans, is absent in sea otters. However, the sea otter's dense fur, which is probably the most highly adapted and efficient of any aquatic mammal, provides insulation against cold (1–16° C) ocean water. In addition, the sea otter's rapid

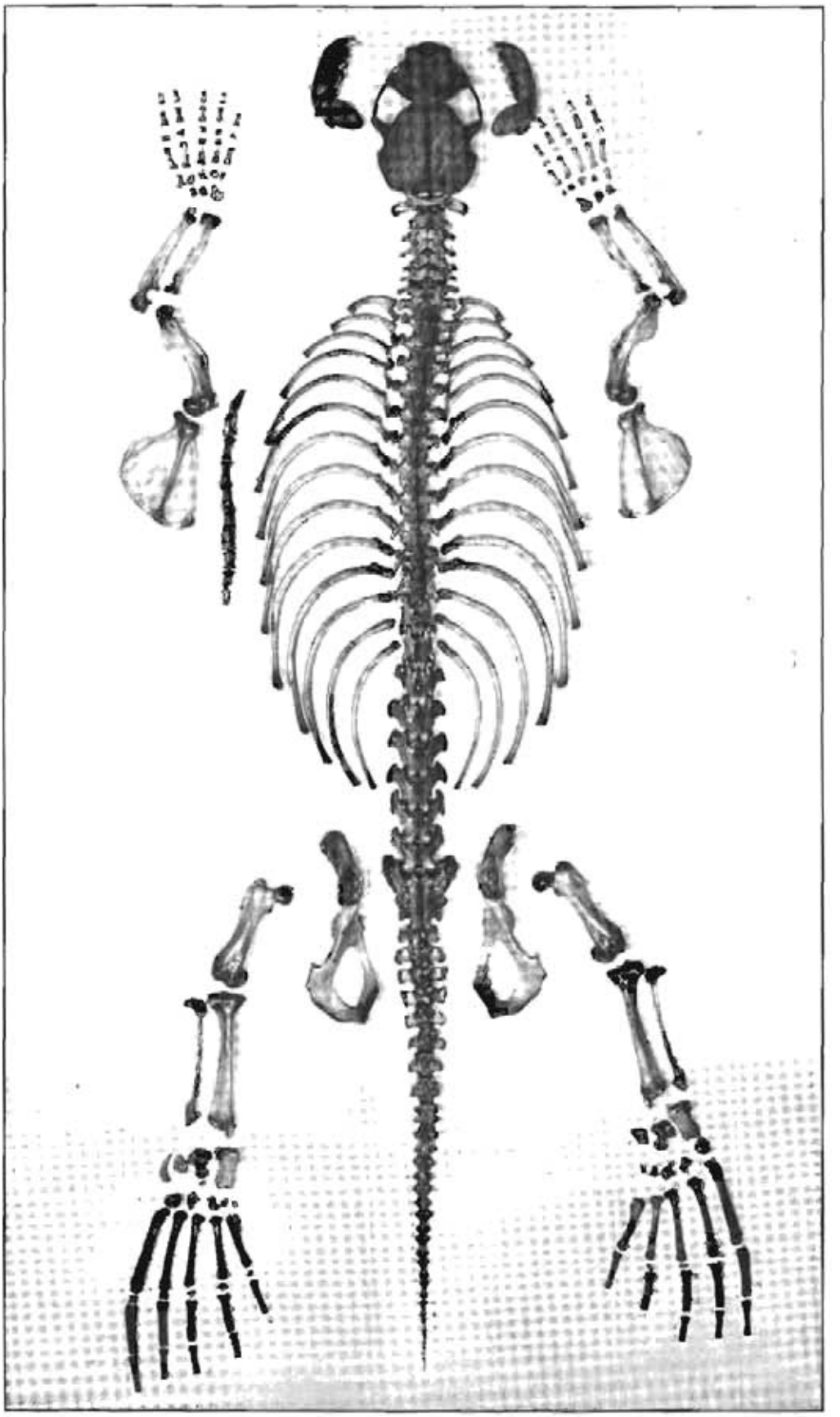


Fig. 2. Adult female sea otter skeleton. The last joint of each digit was removed and is missing (V. B. Scheffer).

metabolism—two to three times higher than a similar-sized land mammal—helps it to generate heat.

To facilitate water conservation and maintain a suitable water balance in the marine environment, sea otters possess large, heavily lobulated kidneys that concentrate urine. The ingestion of seawater by otters may also promote urea elimination (Costa 1982).

The sea otter also has distinctive adaptations for aquatic locomotion. The fifth digit of the hindlimbs (Fig. 3) is extended to provide a flipperlike structure (Kenyon 1969). No other aquatic mammal in the order Carnivora has such highly developed limb structures for aquatic movement. The loosely articulated skeleton and loss of the clavicle help provide the flexibility necessary for grooming and movement in an aquatic environment. Dorsoventral undulations of the entire body are used for rapid aquatic locomotion (Sokolov and Sokolov 1970; Tarasoff et al. 1972). In contrast, aquatic motion in *Lutra* is achieved by movements of the forelimbs and hindlimbs, with little body motion. The aquatic form and movement of sea otters are like those of the pinnipeds and cetaceans rather than other carnivores.

Sea otters share a number of reproductive features with other marine mammal species—adaptations for giving birth and raising young in a marine environment. For example, sea otters nearly always give birth to a single young; twinning occurs but is rare. The absence of multiple-young pregnancies is typical of pinnipeds and cetaceans, but atypical of the other lutrine carnivores (Estes 1979). In addition, the sea otter's 4- to 6-month gestation is relatively long compared with most other lutrines. Sea otters are capable of delayed implantation, a trait which also characterizes pinnipeds and other mustelids. Parturition in the sea otter is apparently more often aquatic, although it can occur on land. Aquatic parturition is unknown for other carnivore species, and even the pinnipeds give birth on land. Like many marine mammals, the period of maternal care in sea otters is relatively long, and milk fat content is high. Such intensive maternal investment helps prepare the young for survival in a harsh environment after weaning.

Socially, sea otters share a tendency with many other marine mammals to form groups (Fig. 4); in contrast, grouping is rare or absent in other lutrine carnivores. The significance of grouping in sea otters is unclear. They commonly rest in groups of widely varying size; however, they usually feed, copulate, and give birth away from other conspecifics. Therefore, grouping does not seem to facilitate foraging or reproduction. However, Garshelis et al. (1984) observed that males in Prince William Sound often forage together, and they speculated that social facilitation of foraging (allowing individuals to locate good feeding areas) promotes gregariousness among males in unfamiliar areas where food resources are patchy. The tendency for sea otters to rest in groups on land or in water may also be related to the environmental constraint of limited suitable or preferred resting sites. Gregariousness may also have evolved as a protective response to predation by species such as humans, white sharks (*Carcharodon carcharias*), bald eagles (*Haliaeetus leucocephalus*), coyotes (*Canis latrans*), and brown bears (*Ursus arctos*). Social exclusion from breeding areas may also promote aggregation of young males.

Classification and Taxonomy

Classification of Sea Otters

The sea otter (*Enhydra lutris*) is the second-largest mustelid, exceeded in size (body length) only by the giant Amazonian otter (*Pteronura brasiliensis*). However, it is the smallest marine mammal in the world, except for the South American marine otter (*Lutra felina*; also known as the sea cat or chungungo). The sea otter represents 1 of about 12 species of otters that are distributed throughout the world.

The only other otter that lives exclusively in the ocean is *Lutra felina*, which weighs only about 4 kg (Harris 1968). Marine otters inhabit kelp beds off the Pacific coast of Peru and Chile, where their declining population is classified as endangered by the International Union for the Conservation of Nature (IUCN) Red Data Book. While marine otters usually forage at sea, they may also swim upstream into rivers in search of freshwater prawns (Hayes 1985*)[1]. Their diet typically consists of molluscs, crustaceans, and fish (Brownell 1978*; Ostfeld et al. 1989). Fish are carried to shore to be eaten, while invertebrates may be consumed either on shore or on the water's surface, with the otter assuming a belly-up position, as sea otters do. Tool use has not been observed among marine otters. While diving, marine otters are able to remain submerged for an average of 30 sec (Ostfeld et al. 1989). Marine otters utilize inaccessible and remote burrows for resting and protection. They tend to be solitary or found in small groups of three to five individuals (Castilla 1981). Ostfeld et al. (1989) suggested that they are monogamous. While little is known of reproduction, litter size is usually two cubs, although four to five cubs per litter have been reported in the Magellan area (Cabello 1985*).

[1]Asterisks(*) throughout text indicate unpublished material; the references are found in the Unpublished References section following the References section.

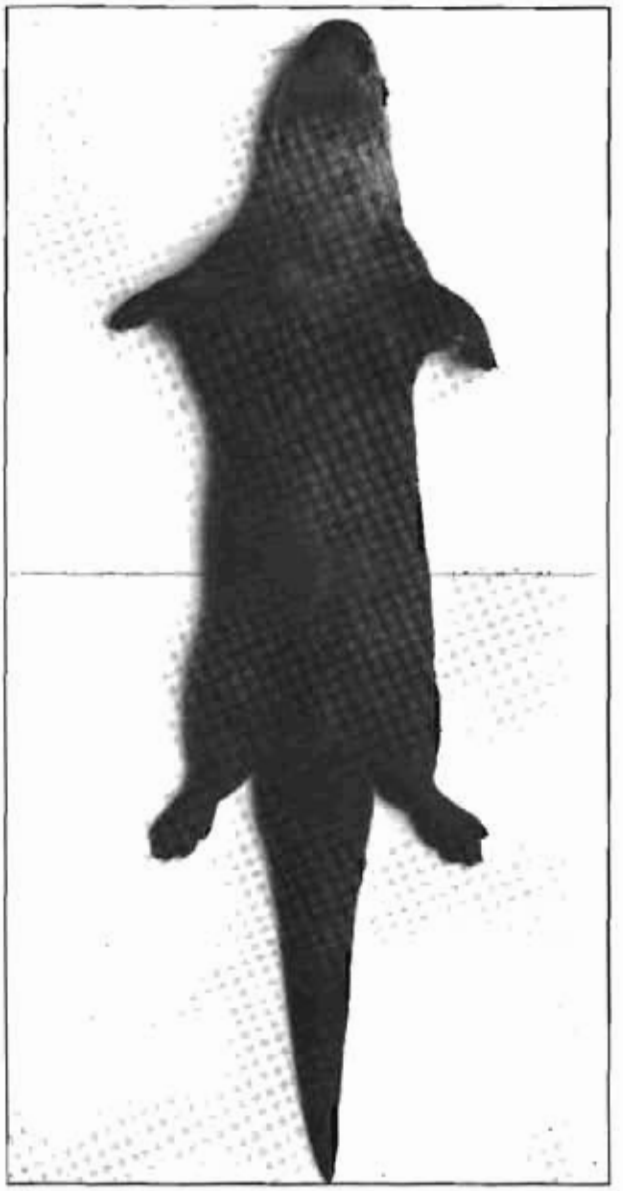
Fig. 3. Left hindflipper (ventral or plantar surface) of adult male sea otter. Note elongated outer or fifth digit, an adaptation which enhances propulsion when the otter swims on its back (K. Kenyon).

Fig. 4. Group of sea otters in California (L. Minden).

Differences in the morphology and life history of sea otters and river otters (*Lutra canadensis*) are listed in Table 1. Sea otters are larger in size, roughly two to four times heavier than river otters. Other obvious characteristics differentiating river otters from sea otters include the sea otter's more elongate body and larger, broadly flattened, webbed hind feet (Fig. 5). In addition, the sea otter's tail is comparatively flat and of uniform width, whereas the

Table 1. *Morphological and life history differences between the sea otter (*Enhydra lutris*) and the river otter (*Lutra canadensis*). (Kenyon 1969; Nowak and Paradiso 1983; Chanin 1985.)*

Sea otter (*Enhydra lutris*)	River otter (*Lutra canadensis*)	Sea otter (*Enhydra lutris*)	River otter (*Lutra canadensis*)
1. Larger sized weight = 20–40 kg length = 120–140 cm	1. Smaller sized weight = 6–10 kg length = 102–118 cm	10. Lives exclusively in the ocean	10. Primarily inhabits freshwater, but also enters the ocean
2. More elongated body	2. Shorter body	11. Usually swims belly up on surface, paddling with hindflippers; floats high in water	11. Usually swims belly down on surface, with much of the back submerged
3. Hindfeet modified to flippers and webbed to tips of toes; fifth or outer digit elongated	3. Hindfeet webbed, but smaller and not flipperlike; fifth digit not elongated	12. Comes ashore less often in most areas; moves awkwardly on land	12. Frequently on land, where movement is agile and swift
4. Tail more flattened, of uniform width, and shorter (< 1/3 of body length)	4. Tail rounder in diameter, thicker at base and tapers to a point, and longer (> 1/2 of body length)	13. Usually rests in kelp beds or open water	13. Usually rests on shore in dens
5. Foreclaws short and partially retractile	5. Foreclaws long and not retractile	14. Diet limited to marine macroinvertebrates and fish	14. More diverse diet, including fish, frogs, crayfish, snails, rodents, and birds
6. Fur longer and softer; underfur denser; guard hair sparse	6. Fur shorter and coarser; underfur not as dense; guard hair covers fur completely	15. Food eaten in water while floating on back	15. Food consumed on shore
7. Longer baculum (6 inches)	7. Shorter baculum (4 inches)	16. Produces single young at one time	16. Produces litter of up to four young
8. Molars broad and flattened for crushing hard-shelled invertebrates; canines rounded and blunt	8. Molars not flattened; carnassial cheek teeth adapted for shearing flesh	17. Young more precocial; eyes open at birth	17. Young less precocial; eyes do not open until ~1 month after birth
9. Two mammae	9. Four mammae	18. Social; usually found in small to extremely large groups	18. Usually found alone or in family groups



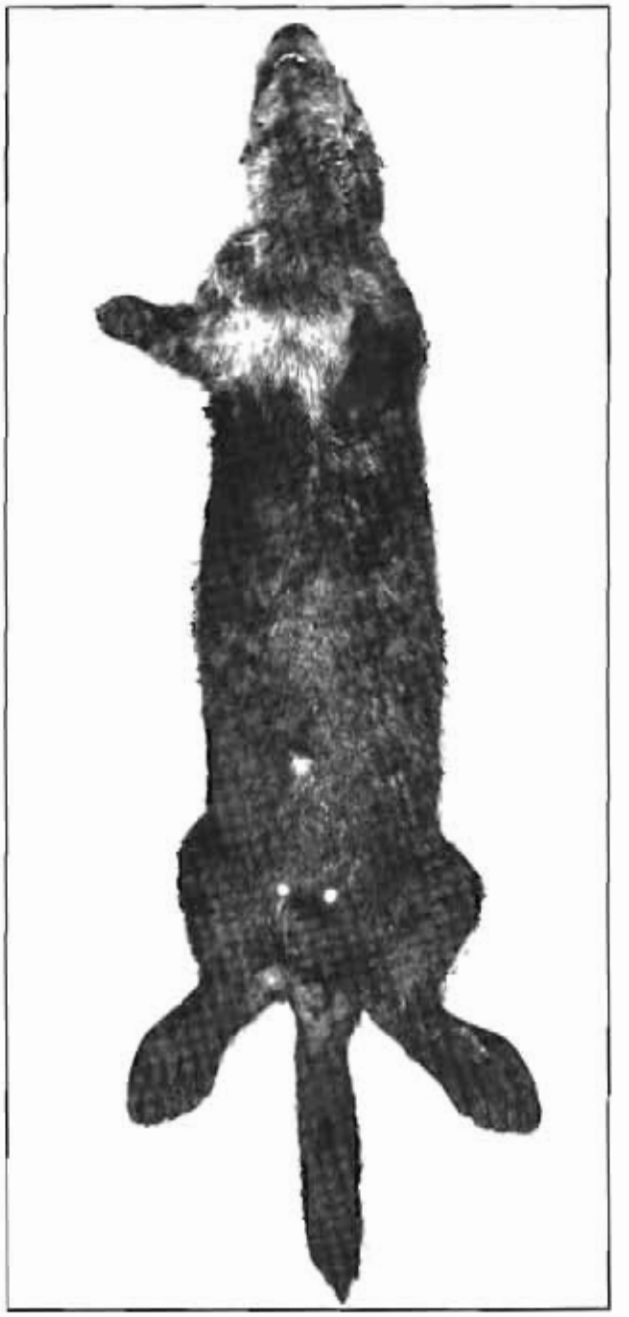


Fig. 5. A) Adult male river otter (*Lutra canadensis*); weight = 10.5 kg; length = 122 cm (V. B. Scheffer). B) Adult female sea otter; weight = 18.1 kg; length = 127 cm. *White dots* indicate mammae and umbilicus (K. Kenyon).

tail of the river otter is considerably longer, thicker at the base, and tapers to a point (Fig. 6).

Subspecies of Sea Otters

The genus *Enhydra* (Fleming 1822:187) has only one species, *E. lutris*. Three subspecies are recognized: *E. lutris lutris* (Linnaeus 1758:45), occupying the Kuril Islands, the east coast of the Kamchatka Peninsula, and the Commander Islands; *E. lutris* [unnamed subspecies] (Wilson et al. 1990), ranging from the Aleutian Islands to Oregon; and *E. l. nereis* (Merriam 1904:159), ranging from northern California to approximately Punta Abreojos, Baja California (Fig. 7). The taxon *E. l. nereis* (southern sea otter) is controversial, and its validity, as well as its northern range limit, was only recently resolved (Table 2).

Several authors concluded that the northern range limit of *E. l. nereis* was the Strait of Juan de Fuca (e.g., Taylor and Shaw 1929; Barabash-Nikiforov 1947; Kenyon 1981), although recently it was suggested that if *E. l.*

Fig. 6. River otters (*Lutra canadensis*) on San Juan Island, Washington (T. Ransom).

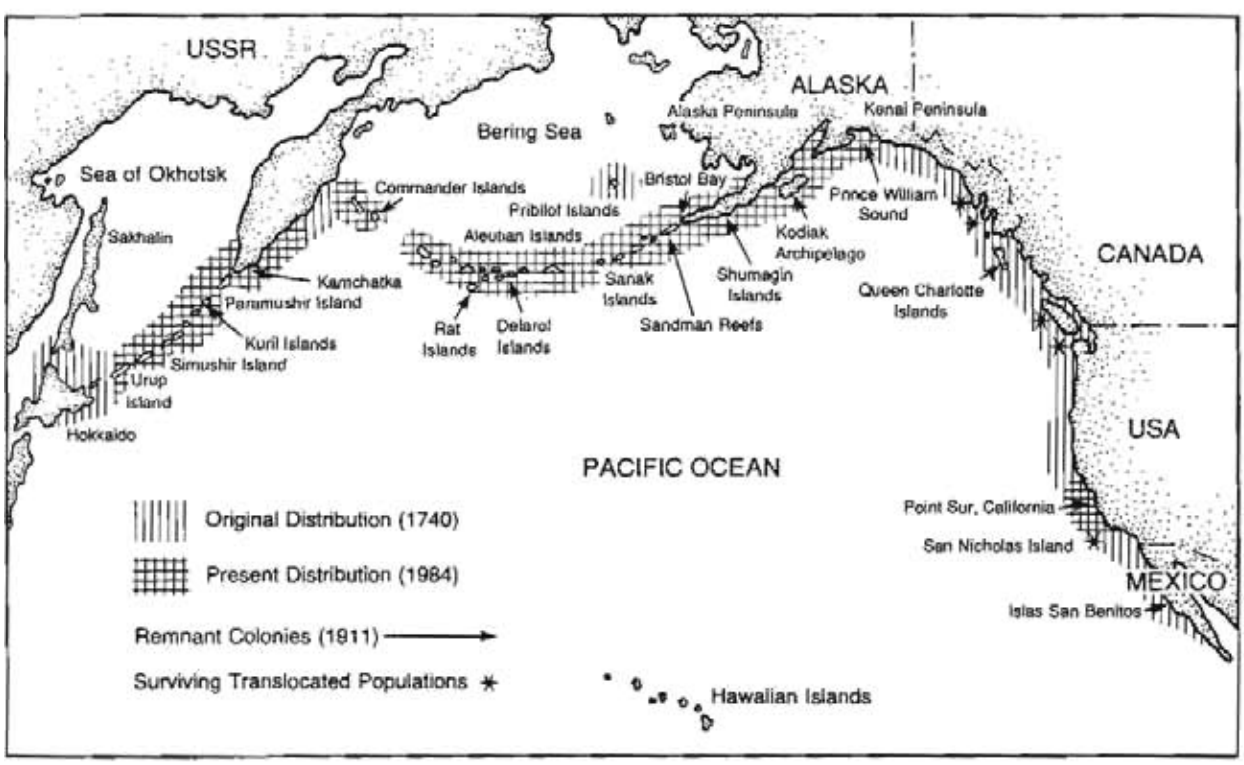


Fig. 7. North Pacific Ocean showing original and current distribution of sea otters and indicating remnant populations existing in 1911.

Table 2. *Taxonomic classification of sea otters. Areas inhabited by subspecies in brackets.*

Class Mammalia	
Order Carnivora	
Family Mustelidae	
Tribe Aonychini	
Enhydra lutris (Fleming 1822: 187)	
Enhydra lutris lutris (Linnaeus 1758: 45)	[Kuril Islands/Kamchatka/ Commander Islands]
Enhydra lutris (unnamed subspecies; Wilson et al. 1990)	[Oregon–Aleutian Islands]
Enhydra lutris nereis (Merriam 1904: 159)	[California]

nereis is a valid subspecies, it probably ranged northward to Prince William Sound (e.g., Roest 1971*; Davis and Lidicker 1975; Rice 1977). However, Wilson et al. (1990) concluded that the northern limit of *E. l. nereis* was northern California or Oregon.

In 1904, Merriam (1904:159) recognized *E. l. nereis* on the basis of a single skull from San Miguel Island, California, which he compared with several skulls from the Bering Sea. Grinnell et al. (1937) confirmed the validity of *E. l. nereis* after comparing the type specimen with a single skull from Alaska. Scheffer and Wilke (1950), however, examined 56 skulls (8 from California, Oregon, and Washington; 48 from Alaska) and found no significant differences in skull features. They concluded that *E. l. nereis* was not a valid subspecies and should therefore be synonymized with *E. l. lutris*. Kenyon (1969) considered sea otters in California and Alaska to be the same subspecies, whereas Miller and Kellog (1955) and Hall (1981) regarded the California population as a distinct subspecies (*E. l. nereis*).

Roest (1971*) examined 50 skulls from California and 214 from Alaska and compiled total length and weight measurements reflecting size differences between the two populations. He concluded that *E. l. nereis* was recognizably different from *E. l. lutris* and constituted a valid subspecies. However, his subsequent, more detailed, analysis of more than 250 skulls from California and Alaska (Amchitka and Adak islands and southwestern Alaska) led Roest (1973, 1976) to conclude that *E. l. nereis* was not a distinct subspecies but rather a variation of a northwest–southeast cline.

Roest (1979*) performed another analysis in which he compared skulls representing nine (rather than four) geographically distinct sea otter groups, including skulls from areas between southwestern Alaska and California. Results supported his earlier interpretation that differences in skull morphology represented a cline, and that all sea otters from the Commander Islands to California should be included within the subspecies *E. l. lutris*.

Davis and Lidicker (1975) disagreed with Roest's conclusions and presented an alternative interpretation of his data. They proposed that a high degree of separability exists between the northern and southern populations, and that otters from southwestern Alaska (the Alaska Peninsula, southern Alaska, and Prince William Sound) represent an area of intergradation between the two subspecies. Davis and Lidicker pointed out that, if the variation is regarded as clinal, there would be a pronounced shift in the slope steepness of the indicated cline between Prince William Sound and the Alaska Peninsula. They concluded that *E. l. nereis* should continue to be recognized as a valid subspecies, based on existing morphological and behavioral differences between the populations and the degree of geographic and genetic isolation characterizing the sea otter population in California. Rice (1977), Hall (1981), and Nowak and Paradiso (1983) subsequently recognized *E. l. nereis* as a distinct subspecies in their respective listings of marine mammals and other mammalian species.

Most recently, Wilson et al. (1990) conducted univariate and multivariate analyses on 20 skull characters of 304 sea otters from throughout the species' geographic range (including 236 specimens from the Soviet Union) from which they concluded that three subspecies should be recognized. The geographical distributions of these subspecies are somewhat different from those previously recognized, resulting in several nomenclatural changes. Wilson et al.'s (1990) analysis indicates that the range of the far western Pacific subspecies—previously designated *E. l. gracilis* (Bechstein 1800:408) and distributed from Kamchatka southwestward through the Kuril Islands to the northern Japanese archipelago—should be expanded to include the Commander Islands. Since the type locality for *E. lutris* is Kamchatka, *E. l. gracilis* becomes a junior synonym of the nominate form, *E. l. lutris*. A second subspecies, previously designated *E. l. lutris* (considered to range from the Commander Islands to about Prince William Sound) was named *E. lutris* (unnamed subspecies). Wilson et al.'s (1990) analysis indicates that *E. lutris* (unnamed subspecies) ranged from the Near Islands (western Aleutian archipelago) eastward across the Pacific rim to Oregon. The third subspecies, which retains the name *E. l. nereis*, ranged from northern California to the central Pacific coast of Baja California, Mexico. Except for occasional extralimital wanderers, the present range of *E. l. nereis* is restricted to central California and San Nicolas Island in the southern California Bight.

Morphology and Physiology

Body Measurements

Sea otters are moderately sexually dimorphic. Adult males are 34% heavier and 8% longer than adult females, and the male's head and neck are heavier and more muscular than those of the female (Kenyon 1969; Estes 1980). However, it is not possible to determine sex in the field solely on the basis of size (Fig. 8). The presence of penial and testicular bulges—most visible when the fur is wet—is the only reliable way of identifying an animal's sex. Measurements taken on dead California sea otters indicated that standard lengths of adult males and adult females average 129.1 cm (N = 58) and 119.8 cm (N = 49; J. A. Ames, California Department of Fish and Game, Monterey, Calif., unpublished data); predicted average weights for healthy sea otters of those sizes are 29.0 kg for males and 19.8 kg for females (Ames et al. 1983). Woodhouse et al. (1977*) reported similar average weights of 29.5 kg for adult males and 19.5 kg for adult females. The largest male found dead in California weighed 41.7 kg and was 134 cm long (Ames, personal communication). At birth, pups weigh 1.4–2.3 kg (Miller 1974; Fig. 9). Monnett and Rotterman (1988b*) found that, in eastern Prince William Sound, male sea otter pups grew at a higher rate (95 g/day) than did females (83 g/day). Based on these patterns, they concluded that more parental resources were required to raise males than females from conception to weaning; more information is needed before this conclusion can be verified.

According to Roest (1971*, 1973, 1979*). Alaskan sea otters are generally somewhat larger than California sea otters. However, size of Alaskan otters varies with geographic location, and some Alaskan otters weigh less than California otters. Kenyon (1969) found that adult sea otters from heavily populated areas (e.g., Amchitka Island) may weigh less than adults from sparse populations. The mean weights and lengths of dead Amchitka adults

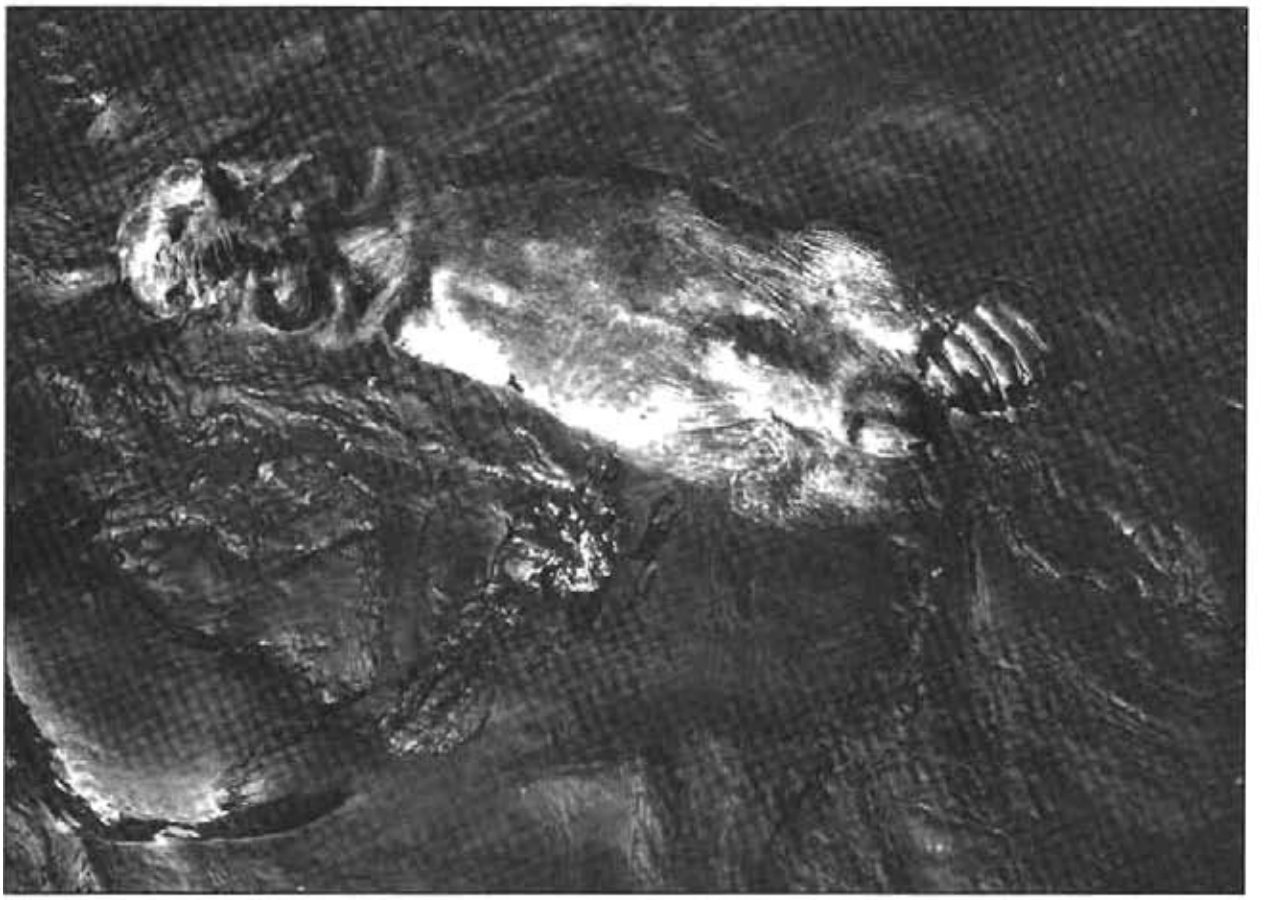


Fig. 8. Adult male sea otter, note penile bulge as field identification for determining sex (K. Kenyon.)

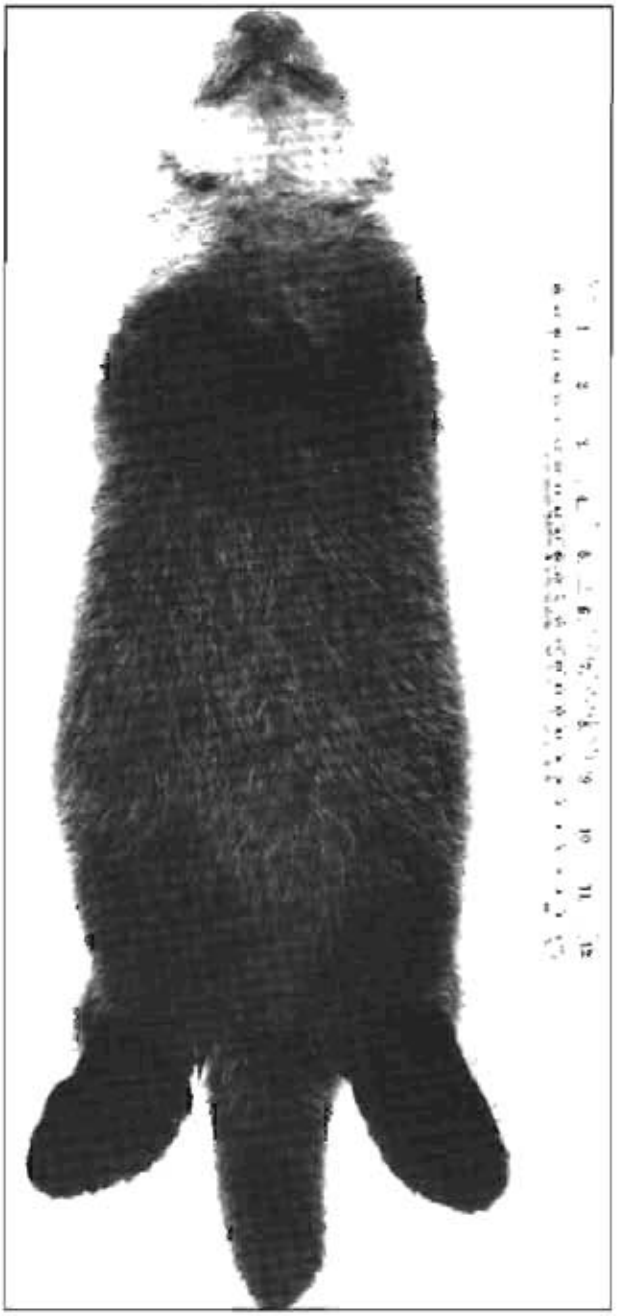


Fig. 9. Dorsal (A) and ventral (B) view of newborn female sea otter pup at Amchitka Island, Alaska: weight = 1.95 kg; length = 56 cm. Note lighter, yellowish natal pelage on head and neck (K. Kenyon).

were 28.3 kg and 135.0 cm for males (N = 79) and 21.1 kg and 125.2 cm for females (N = 254). Sizes of adults killed in sparsely populated areas (Shumagin Islands, Unimak Island, and Adak Island) were 39.5 kg and 140.8 cm for males (N = 5) and 25.2 kg and 129.8 cm for females (N = 4). The largest adult male killed in the Aleutians weighed 45 kg and was 148 cm long, while the largest female weighed 32.6 kg and was 140 cm long. Newborn pups in Alaska measure about 61 cm and weigh 1.9 to 2.3 kg (Kenyon 1969).

Lifespan and Age Determination

Alaskan females live an estimated 15–20 years, while male lifespan appears to be about 10–15 years (Calkins and Schneider 1984*). R. J. Jameson (U.S. Fish and Wildlife Service, San Simeon, Calif., personal communication) estimates a minimum lifespan of 11–12 years for some California males. In the northern part of the range in California, one tagged female was known to have lived for 15–16 years.

and other known-age females 10–11 years old are currently under observation. An adult male was at least 13 years old (probably 2 or more years older) when he disappeared (M. L. Riedman, J. A. Estes, M. L. Staedler, Monterey Bay Aquarium, Monterey, Calif., unpublished data). Garshelis (1984) found that older otters tended to have lighter-colored fur on their necks and related age to pelage color patterns to provide estimates of age categories in field observations of living sea otters. Counts of the incremental lines in tooth cementum have been used to estimate ages of living and salvaged sea otters in Alaska (Schneider 1972c*; Garshelis 1984) and California (Pietz et al. 1988*). Tooth cementum counts typically have been made from the first premolar. In a sample of 580 salvaged carcasses in California, Pietz et al. (1988*) estimated maximum age, based on tooth cementum, to be 16 years for females and 15 years for males. Unfortunately, there are no teeth available from older known-age sea otters to confirm the relation between cementum lines and age; such material will become available, however, as sea otters recently marked as juveniles eventually grow old and die. In captivity, a male sea otter ("John," a yearling captured from Amchitka in 1968) survived to about 20 years at the Vancouver Public Aquarium (M. Butschler, Vancouver Public Aquarium, Vancouver, British Columbia, personal communication) and the Point Defiance Aquarium (T. Otten, Point Defiance Aquarium, Tacoma, Washington, personal communication). He sired a pup born at the Vancouver Aquarium in April 1986 and died on 1 October 1987.

Dentition

Sea otters have bunodont molars, unlike the typically carnassial cheek teeth of most mammalian carnivores. The sea otter's dentition is adapted for crushing hard-shelled macroinvertebrates: molars are broad and flattened, canines are rounded and blunt. The adult dental formula is i 3/2, c 1/1, pc 3/3, m 1/2, total 32 teeth (i = incisor, c = canine, pc = postcanine, m = molar; Kenyon 1969; Fig. 10). Extremely worn teeth indicate old age in sea otters, and serious tooth wear may possibly contribute to mortality in older animals.

Forelimbs and Hindlimbs

The forelegs of the sea otter are used primarily for grooming and foraging, rather than for propulsion. The extremely powerful forelegs and sensitive paws help it to locate, capture, and break open hard-shelled prey (Fig. 11). A loose pouch of skin at the axilla of each forelimb is used to temporarily store and transport food (Kenyon 1969). Unlike the hindclaws, the foreclaws can be extended (Kenyon 1969; Howard 1973). According to Howard (1973), "The claws are closely associated with, and move only with, the terminal phalanx...." This makes them in one sense nonretractable, but they can be extruded to a degree by flexing the terminal digits. In some necropsied California otters the claws are extensively worn and are mere nubbins. The hindfeet are flattened and flipperlike (Murie 1959; Fig. 3). Each of the five hind digits is progressively longer, the outer digit being the longest—an adaptation that enables the otter to more efficiently swim on its back at the surface (Kenyon 1969; Tarasoff 1972, 1974; Tarasoff et al. 1972; Howard 1975). Surface swimming is accomplished by vertical, undulating motions of the tail and hindflippers (Howell 1930; Tarasoff et al. 1972). The tail is horizontally flattened to enhance propulsion. A sea otter floating on its back may move the tail in a sculling action to shift or maintain position (Kenyon 1969, 1981).

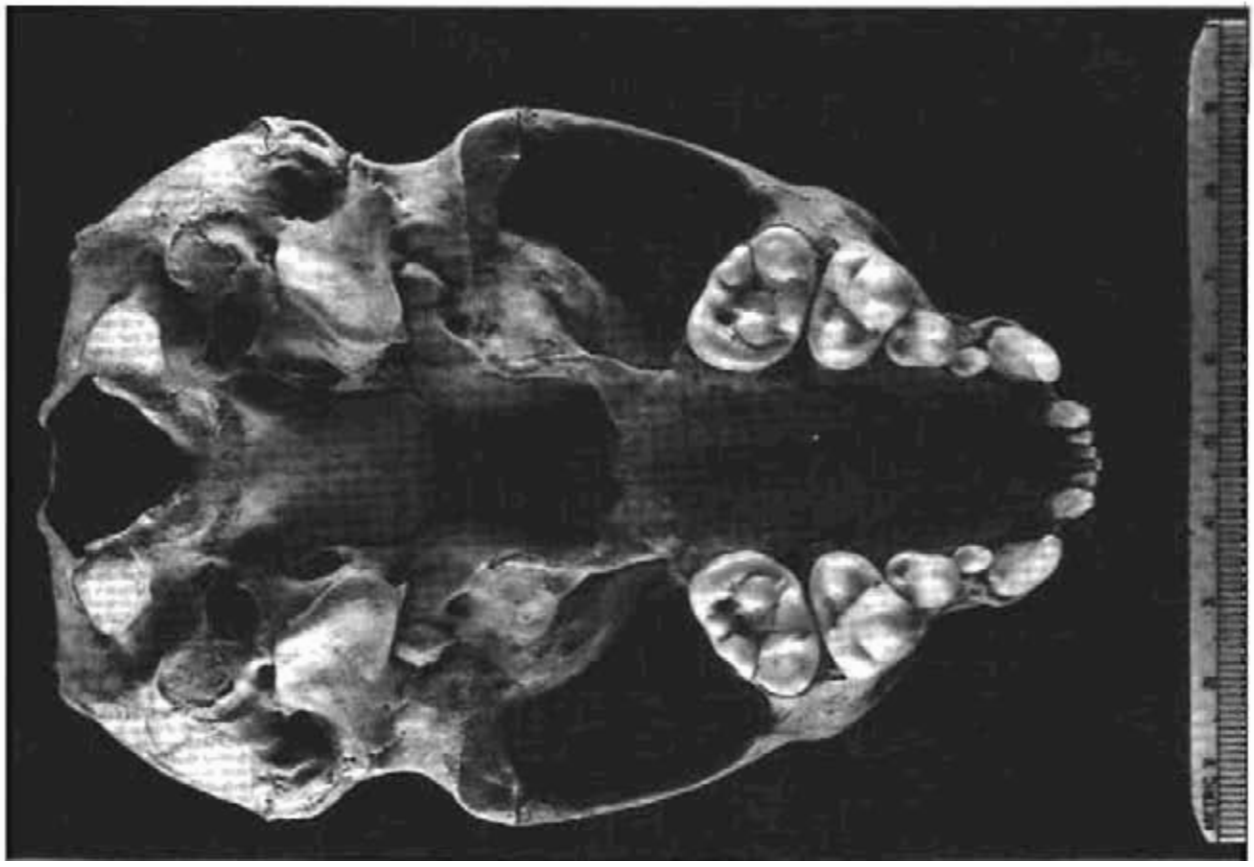
Swimming Speeds

Observations in Alaska indicate that sea otters typically swim at a speed of 1–2.5 km/h on the surface, although speeds of 9 km/h may be attained for short distances underwater (Kenyon 1969). Garshelis (1983) reported that a male Alaskan sea otter traveled 11 km at an average rate of 5.5 km/h. In California, Jameson (personal communication) calculated average speeds ranging from 0.6 km/h (distance of 52 km) to 3.3 km/h (distance of 75 km) for two adult males that moved from male groups to female areas. Observations made on captive female California sea otters indicate that underwater swimming velocities average 3.6 km/h (Williams 1984). Movement on land is comparatively slow and awkward (Barabash-Nikiforov 1947; Tarasoff et al. 1972), partly due to the elongated fifth hindflipper digits, which impede movement. A sea otter walking on land raises one foot at a time and arches its back, moving with a rolling gait or swinging from side to side. When startled, an otter moves quickly by bounding or hopping with forelegs and hind feet together or by sliding across the ground on its belly while pulling with the forelimbs (Kenyon 1969).

Sensory Organs

Little information is available about the sensory organs. Chemoreceptive and tactile senses seem well developed. Although olfaction in the sea otter is poorly known, the existence of extensive nasal turbinates—as well as observations of social interactions among individuals—suggests that olfaction is acute. On numerous occasions, sea otters have been observed actively sniffing the air, the water's surface, or other otters. Adult males may possibly locate and identify estrous females by means of olfactory cues (Deutsch, unpublished data; Riedman, unpublished

Fig. 10. Dentition and skull of older juvenile or young subadult sea otter found dead on Amchitka Island (5 March 1962): Weight = 10.9 kg: length = 100.5 cm. Note broad, flattened molars and blunt, rounded canines (K. Kenyon).



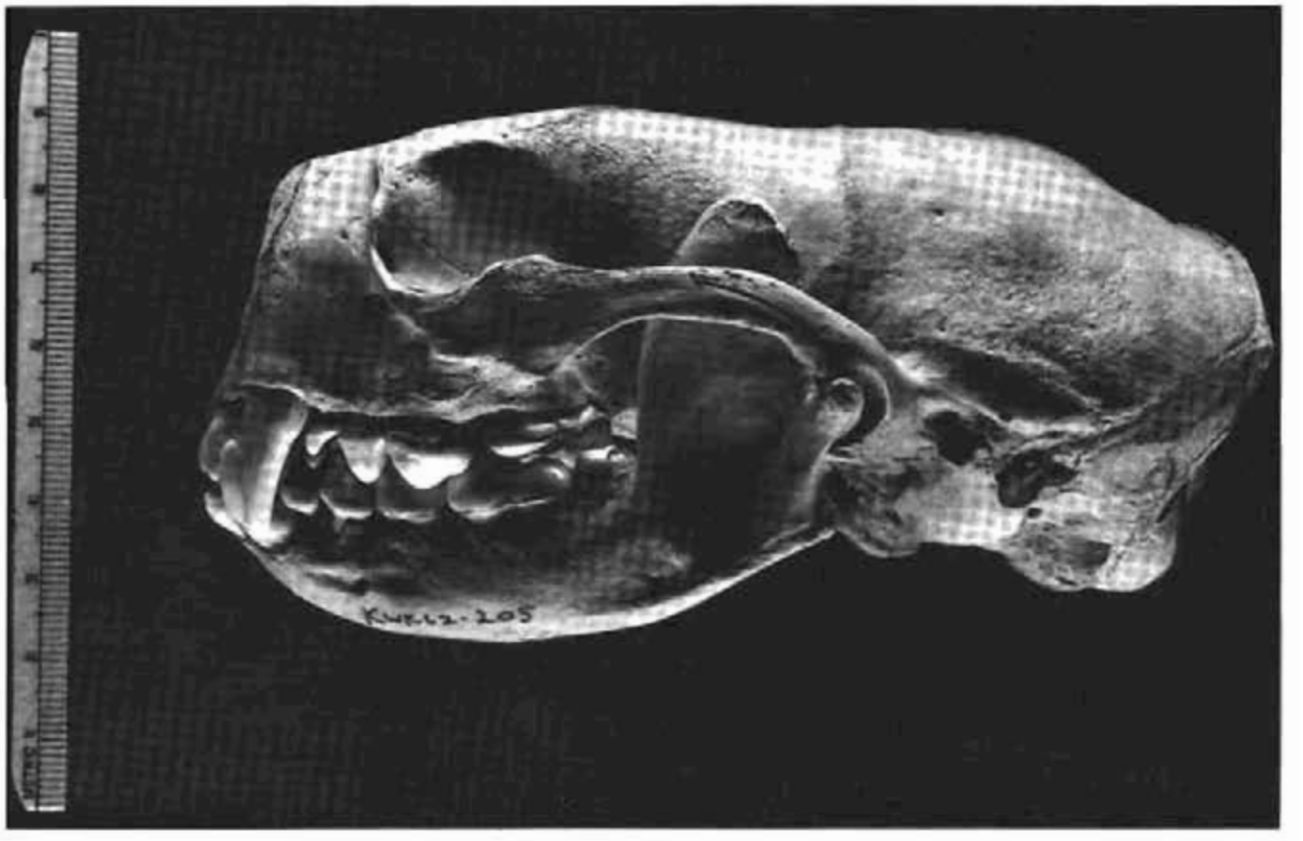


Fig. 11. (A) Sea otter forepaw; note absence of fur on inner ventral surface. (B) Dorsal view of sea otter forepaw (K. Kenyon).

Fig. 12. External ear of the sea otter (K. Kenyon).

data). The paws and vibrissae are used to locate and capture prey underwater (Radinsky 1968; Kenyon 1969; Shimek 1977a,1977b; Hines and Loughlin 1980). Unlike other mustelids, however, the sea otter lacks functional anal scent glands (Kenyon 1969).

Although their sense of hearing is not well known, Kenyon (1969) wrote that hearing seems to be "moderately well developed." The ear pinna is moderately curled and resembles that of otariid seals (Fig. 12). An otter's ear is held erect above the surface but folds sharply downward during dives (Pocock 1928; Kenyon 1969). Davis et al. (1988) examined the anatomy of the sea otter cochlea (inner ear) and Organ of Corti (which contains hair cells within the cochlea) and found them to be indistinguishable from that of other placental mammals. In addition, they concluded that sea otter hearing is most sensitive to high frequencies, which is also true of North American river otters (*Lutra canadensis*).

Results of a study conducted near Soberanes Point, California, indicated that sea otters were seemingly undisturbed by experimentally projected waterborne industrial and seismic noise or by recordings of killer whale (*Orcinus orca*) vocalizations (Riedman 1984a*, 1984b*). Davis et al. (1988b*) tested the response of California and Alaska sea otters to a variety of acoustic stimuli and found that while California sea otters exhibited little reaction to killer whale vocalizations, Alaska sea otters showed a stronger response, possibly because killer whales are more common in Alaska and may prey on sea otters there. Other acoustic noise, such as random playback of synthetic sounds (air horn and warble tone), initially startled the otters, but like other marine mammals, they soon habituated to the noise (within 2 h) and did not subsequently avoid the sound source.

Visual acuity in the sea otter seems to be good both above and underwater. Murphy et al. (1990) found that, both above and below water, sea otters are approximately emmetropic: that is, they are able to focus clearly on targets both underwater and in air (although they occasionally exhibit myopic reflexes in both environments). Sea otters depend on accommodation of the eyeball to compensate for the loss of the eye's corneal refractive power when underwater.

Sea otters have an exceptional accommodative range of about 60 diopters (a unit of curvature and of the power of lenses)—at least three times greater than that reported for any other terrestrial mammal (Sivak 1980). In comparison, diving marine birds, such as cormorants (*Phalacrocorax* spp.), have an accommodative ability of <40 diopters (Levy and Sivak 1980). Murphy et al. (1990) found that the sea otter eye is characterized by extensively developed iris musculature, meridional ciliary muscle, and corneoscleral venous plexus surrounding the entire ciliary body region; all these may be associated with a unique and well-developed lenticular accommodative mechanism that is able to change the refractive power of the lens. In addition, they speculate that the well developed anterior epithelium of the cornea may be an adaptation that helps the otter cope with salinity in its environment.

In comparison, Schusterman and Barrett (1973) found that the visual acuity of the Asian small-clawed otter (*Aonyx cinerea*) was the same in air and water when tested during daylight. In relation to pinnipeds, Gentry and Peterson (1967) suggested that sea otters have slightly

poorer underwater vision than California sea lions (*Zalophus californianus*) or harbor seals (*Phoca vitulina*) and speculated that an otter's vision may be better in air than underwater. Although recent studies have shown that sea otters can see clearly in both environments, the orbits of sea otters are not enlarged, as they are in most pinniped species. Orbital enlargement is thought to be an adaptation for increasing visual sensitivity in deep, dimly lit water.

Sea otters appear to have a well-developed tapetum, as do the pinnipeds and most nocturnal carnivores that need to see well at night or in dimly lit waters. The specialized layer behind the retina, the tapetum lucidum (containing many guanine crystals), enables the retina to reflect light. It gives a metallic appearance. By sending light passing once through the retina back through the retina a second time, the tapetum enhances the light-gathering capacity of the eye.

Internal Organs

The lungs are large in relation to body size, nearly 2.5 times that found in other mammals of similar size. Large lungs serve to regulate buoyancy and store oxygen (Lenfant et al. 1970; Kooyman 1973; Leith 1976; Costa and Kooyman 1982). The liver and kidneys are also large relative to body size. An enlarged liver probably helps maintain the high metabolic rate (Kenyon 1969; Morejohn et al. 1975), while the large, lobulated kidneys allow the otter to produce large volumes of moderately concentrated urine (Kenyon 1969; Costa 1982). Costa (1976*, 1978b) demonstrated that sea otters drink sea water. Because California sea otters consume primarily invertebrates (which possess higher electrolyte concentrations than teleost fish), they must process large amounts of electrolytes, nitrogen, and water; ingestion of seawater may therefore promote urea elimination by increasing the urinary osmotic space without increasing the electrolyte concentration in the urine (Costa 1982). Interestingly, captive sea otters at the Monterey Bay Aquarium sometimes drink fresh water from a hose and from water sprinklers cleaning the exhibit windows; in addition, the juvenile male and females in the exhibit ingest their own urine at times (J. Hymer and B. Grey, Monterey Bay Aquarium, Monterey, Calif., personal communication).

Pelage and Grooming Behavior

Unlike most other marine mammals, sea otters have little subcutaneous fat, depending instead on their dense, water-resistant fur to provide insulation against cold. Underneath the outer flattened and protective guard hairs is an extremely fine and dense underfur. In fact, the sea otter's fur is more dense than that of any other mammal. Williams et al. (in press) found that sea otter fur density varied between body regions, with hair amounts ranging from 26,413/cm^2 (170,364/in.^{2}) on the foot to 164,662/cm^2 (1,062,070/in.^{2}) on the foreleg. Previous estimates of average underfur hair density have been reported at 100,800/cm^2 (650,160/in.^{2}; Kenyon 1969) and 131,000/cm^2 (844,950/in.^{2}; Tarasoff 1974). In comparison, domestic cats (*Felis silvestris*) have 16,000–32,000 hairs/cm^2, dogs (*Canis familiaris*) have 200–9,000 hairs/cm^2, and humans average only about 100,000 hairs on the entire head. The northern fur seal (*Callorhinus ursinus*) has an estimated 40,000–60,000 hairs/cm^2 (Scheffer 1962). The sea otter has specialized glands that secrete oil and enhance the water-repellent quality of the fur. In addition, the sea otter's lack of arrector pili muscles in the epidermis allows the hairs to lie close to the animal's skin when immersed (Kenyon 1969).

Molting takes place gradually throughout the year (Ognev 1931; Kenyon 1969), although a peak period of molting seems to take place in spring among captive Alaska otters (Kenyon 1969). The number of fur fibers in each bundle may increase as an otter ages, indicating that some of the fibers are not shed later in the molt, but instead remain attached within the bundle. Throughout the year, individual fibers are probably in molt while others are at rest (Kenyon 1969).

An air layer is trapped within the fur fibers, providing insulation and buoyancy and enabling the skin to remain dry when immersed (Kenyon 1969; Morrison et al. 1974; Tarasoff 1974, Costa and Kooyman 1982). When contaminated with pollutants (such as oil), the fur loses its insulative properties, and the otter subsequently dies of hypothermia or pneumonia (Stulken and Kirkpatrick 1955; Kenyon 1969; Kooyman et al. 1977*; Williams 1978; Kooyman and Costa 1979*; Costa and Kooyman 1979*, 1980*, 1982; Siniff et al. 1982).

Frequent grooming of the fur is essential to maintaining its insulative properties. In addition to trapping air within the pelage, grooming essentially serves four purposes: (1) to clean the fur, (2) to straighten and align the hair shafts so that the loft is maintained, (3) to stimulate the production of natural oil and distribute the oil over the skin and hair, and (4) to enhance blood circulation (Williams et al. 1990). Vigorous grooming bouts generally occur before and after feeding episodes and rest periods. Intermittent grooming takes place at other times (often during and at the end of rest periods), but this type of grooming is brief and languid (Kenyon 1969; Loughlin 1977).

Loughlin (1977) found that the intensive grooming bouts of longest duration (which generally occurred after feeding) involved a highly stereotyped sequence of four stages. Stage 1 is characterized by energetic somersaulting and lateral rolling, with vigorous rubbing of the entire body, especially the back, base of tail, and nape. Air is blown or rubbed into the fur of the abdomen and chest. In

Fig. 13. California sea otter in "stage 4" grooming, slowly rubbing face with forepaws (D. Buchich).

stage 2, vigorous grooming continues, but no rolling or somersaulting occurs, as though the otter is trying to keep its ventral surface dry. The chest, face, and nape are rubbed with the paws, while the hindflippers are rubbed together rapidly. An otter might roll laterally and entwine itself in kelp. Stage 3 is characterized by slow licking and rubbing of the tail and hindflippers. In stage 4, the animal is nearly fully groomed, but slowly continues to lick its paws and chest, rub its face and nape, and rub the hindflippers together. The limbs are held high above the water while the otter wraps itself in kelp (Fig. 13).

Pelage color in adults varies in shades of brown. The fur of some individuals may become progressively grizzled and lighter in color on the head, neck, chest, and forelimbs due to loss of pigmentation in the guard hairs (Barabash-Nikiforov 1947; Jones 1951; Kenyon 1969; Miller 1974; Estes 1980; Fig. 14). Garshelis (1984) suggested that "light-headedness" develops with age in both sexes but is most pronounced in old males whose heads may appear to be nearly white. He found that in Prince William Sound, males appeared to become "white-headed" at 6 years, which is younger than the age most females became white-headed (8–9 years). While it may generally be true that the fur gradually lightens with age as the hairs lose pigment, this is not always the case; dark-headed older otters, as well as light-headed young, are observed. Newborn pups are characterized by a light brown or yellowish, woolly, natal pelage (Fisher 1940), which is completely replaced by the adult pelage by 13 weeks (Payne and Jameson 1984; Fig. 15).

Metabolism and Energetics

Because of their small body size and lack of blubber, which in other marine mammals provides insulation as well as a reserve of energy, sea otters compensate for the problem of thermal stress not only by means of their insulative fur but also by maintaining a high level of internal heat production (Iverson and Krog 1973; Morrison et al. 1974; Costa and Kooyman 1982). A sea otter's rate of heat production is 2.4–3.2 times that expected for a terrestrial mammal of similar size (Costa 1978a; Costa and Kooyman 1982, 1984). Sea otters are characterized by an elevated standard metabolic rate (SMR) of about 2.5 met, or 0.67–0.72 cm^3 per gram of body weight per hour, which enables the maintenance of an average body temperature of $38.1 \pm 0.34^{\circ}$ C under typical environmental

Fig. 14. California sea otter with heavily grizzled head and chest (J. Mattison).

conditions (Morrison et al. 1974).

Energetic requirements are high and critical for maintenance of the elevated SMR. Captive adults require 189–253 kcal/kg body weight per day, equivalent to 20–25% of their total body weight (Kenyon 1969; Costa 1976*). A 20-kg adult otter would therefore need between 4,295 and 5,750 kcal/24 h. Costa (1978a, 1982, 1985*) estimated that free-ranging adults daily consume an amount of food equivalent to 23–33% of their body weight. The sea otter's assimilation efficiency of 80–85% is low compared to other mammals (Fausett 1976; Costa 1982) and may result from the rapid rate of food passage (typically about 3 h) through the gastrointestinal tract (Stulken and Kirkpatrick 1955; Costa 1982).

Ecology

Habitat Characteristics

Sea otters inhabit shallow coastal waters and seldom range more than 1–2 km from shore. In areas with rocky substrates, they usually occur between the shoreline and the outer limit of the kelp canopy, which generally corresponds to the 18-m depth contour. Occasionally, California sea otters are seen further offshore to the 36-m depth curve (Odemar and Wilson 1969a; Wild and Ames 1974; Loughlin 1977; Ribic 1982a; Ralls et al. 1988a*, 1988b*; D. Croll, Moss Landing Marine Laboratories, Moss Landing, Calif., personal communication), but they are rarely found many miles out to sea. In some areas, especially portions of Alaska, water shallow enough for sea otter foraging may extend many miles offshore, and in such areas large numbers of otters may be distributed accordingly. Foraging activity in California is generally restricted to water depths 25 m or less (Wild and Ames 1974; California Department of Fish and Game 1976*; Estes 1980; U.S. Fish and Wildlife Service 1980*), although California otters have been reported foraging in waters up to 36 m deep (R. A. Hardy, California Department of Fish and Game, Morro Bay, Calif., unpublished data). The record dive depth occurred in the Aleutian Islands, where a sea otter drowned in a king crab (*Lithodes* and *Paralithodes*) pot that was set in about 100 m of water (Newby 1975). In the deep fjords of northeastern Prince William Sound, Garshelis (1983) reported that sea otters typically dive to depths of 28 m when

Fig. 15. Small California sea otter pup showing natal pelage, which is replaced by adult fur by 3 months of age (S. Webster).

feeding on Dungeness crab (*Cancer magister*).

Sea otters occur in areas with widely ranging exposure, substrate types, and community composition. In California, they are usually found in rocky-bottom areas, although they also occur in soft-bottom habitats. Rocky-bottom habitats typically support diverse and productive communities, including prey frequently consumed by sea otters (e.g., sea urchin, abalone, crab). Sea otter density in California is probably related to substrate type. On average, rocky-bottom habitats in California support sea otter densities around 5 individuals/km, whereas sandy-bottom areas support average densities of 0.8 individuals/km (California Department of Fish and Game 1976*). The type and structure of rocky bottom also seems to affect sea otter density. Areas with extensively fractured or topographically heterogeneous substrates seem capable of supporting higher densities of sea otters than areas with flat and unbroken substrates.

Sea otters seem to prefer areas with surface kelp canopies, although this is not an essential habitat requirement. Large numbers of sea otters are found in areas of Prince William Sound and southwestern Bristol Bay, where the bottom is composed exclusively of soft sediments. In other areas, such as the western Aleutian Islands, the surface kelp canopy in rocky-bottom habitats is formed entirely by the annual species *Alaria fistulosa*. Although sea otters in such areas typically associate with this surface canopy in summer, the canopy is absent during much of the rest of the year. In California, sea otters may also inhabit areas devoid of canopy-forming kelps and rest in open water. However, the kelp canopy, used for foraging and resting, is an important habitat component, and the density, areal extent, and species composition of kelp canopies are known to influence the distribution patterns as well as territorial and home range boundaries (Benech 1981*; Jameson 1989; G. R. VanBlaricom and R. J. Jameson, U.S. Fish and Wildlife Service, University of California, Santa Cruz, Calif., unpublished data). California sea otters preferentially associate with giant kelp (*Macrocystis pyrifera*) as opposed to bull kelp (*Nereocystis leutkeana*). Specific kelp beds are used as habitual rafting sites for groups of otters as well as for individuals (Loughlin 1977; Jameson 1989; Vandevere, personal communication; Riedman unpublished data). Territorial males may rest in the same kelp beds, at nearly the same specific location, for many years (Jameson 1989; Deutsch, personal communication; M. L. Riedman, J. A. Estes, and M. Staedler, unpublished data).

Fig. 16. Adult male sea otter hauled out on beach in Monterey, California (D. Buchich).

Haul-out Behavior

Sea otters in California have been observed hauled out on the shore at numerous sites throughout their range (Vandevere 1971*, 1973b*; Vandevere and Baldridge 1973*; Miller 1974; Faurot et al. 1985; Riedman et al. 1988; Jameson, personal communication). Preferred haul-out sites are characterized by low-relief, algal-covered rocks that are exposed at low tide (Faurot 1985), although sand or cobble beaches are occasionally used as haul-out sites (Fig. 16). Sea otters and harbor seals (*Phoca vitulina*) often haul out close to one another. While harbor seals and otters usually ignore one another, a seal may occasionally behave aggressively towards an otter that attempts to haul out too close to the seal (Riedman, unpublished data). The number of otters hauled out at a particular site usually ranges from 1 to 6 (sometimes including mother–pup pairs); however, up to 18 adults and 4 pups were observed hauled out at Cypress Point on one occasion (Faurot et al. 1985), and 14 adults and 4 pups were seen hauled out near Bird Rock at Point Lobos State Reserve in May 1986 (Riedman and Vandevere, unpublished data). In the northern part of the range, certain individuals haul out more frequently than other otters in the same area (Riedman et al. 1988*; K. Lyons and E. Faurot, personal communication). In addition, females often tend to haul out during their estrus period (Riedman et al. 1988*).

Although the frequency of haul-out behavior in California is unknown, California otters do not come ashore as often or in groups as large as do sea otters in parts of Alaska (Kenyon 1969; Estes, personal observation; Fig. 17). For instance, up to several hundred otters were observed hauled out in groups at Amchitka Island, particularly in male areas, during winter (Estes, personal observation). In one instance, a group of males had hauled out inland several hundred meters from shore. This behavior is rarely seen elsewhere and probably relates to the absence of terrestrial predators and human disturbance. Sea otters in the Aleutian Islands tend to haul out less often after they have been disturbed by people (Estes, personal observation).

Fig. 17. Group of 39 male sea otters resting on shore at St. Makarius Point East, Amchitka Island, Alaska (K. Kenyon).

Role in Marine Communities

Pronounced and complex relations between sea otters, a "keystone" (sensu Paine and Vadas 1969) or "foundation" (sensu Dayton 1972) species, and the nearshore community have been documented in Alaska (Estes and Palmisano 1974; Dayton 1975; Palmisano and Estes 1977; Estes et al. 1978; Simenstad et al. 1978; Duggins 1980; VanBlaricom and Estes 1988; Duggins et al. 1989; Kvitek and Oliver, University of Washington, Seattle, Wash., in preparation), British Columbia (Farr and Bunnell 1980; Breen et al. 1982), Washington State (Jameson et al. 1986; Kvitek et al. 1989), and California (McLean 1962; North 1965*, 1974*; Ebert 1968a, 1968b; Lowry and Pearse 1973; Wild and Ames 1974; Haaker and Wilson 1975; VanBlaricom 1984a, 1984b; Estes and VanBlaricom 1985; VanBlaricom and Estes 1988).

Direct Effects of Sea Otter Predation

The direct reduction of benthic invertebrate populations by sea otter predation is the most general and well documented part of these complex relations. Several factors lead to the strong limiting influence sea otters have on populations of many species of benthic invertebrates. One is that sea otters are abundant (especially in Alaska and the Soviet Union) and, on an individual basis, have a high rate of food consumption. For example, an estimated 5,000–8,000 sea otters inhabit the roughly 150 km of shoreline surrounding Amchitka Island in the western Aleutian archipelago (Estes 1977, 1990), and each daily consumes an estimated 25–30% of its 23-kg average body weight. In addition, their extreme mobility, highly developed forelimb sensory and motor functions (Radinsky 1968), crushing dentition, and proficient use of tools for breaking open the exoskeletons of invertebrate prey render sea otters easily capable of locating, capturing, and consuming invertebrates of nearly any size and shape. Indeed, the only apparent refuges or defense mechanisms from sea otters available to most invertebrates are very deep water (Estes, unpublished data), deep holes and crevices in rocky substrates (Lowry and Pearse 1973), being small in size (Estes et al. 1989, Estes and VanBlaricom 1988), or sequestering of PSP toxins as a chemical defense (Kvitek et al., in review*). Burrowing deep into soft sediments (Kvitek and Oliver 1988; Kvitek, personal communication) is also thought to be effective,

although Kvitek commented that he recently observed sea otters eating geoducks (*Panopea generosa*) in southeastern Alaska and found huge pits they had excavated to obtain them.

Evidence that sea otters have such profound limiting influences on many of their invertebrate prey populations comes mainly from comparisons of areas with and without otters, through either space or time. For example, in central California large sea urchins (*Strongylocentrotus purpuratus*) are almost never found outside of protective substrate cracks and crevices within the sea otter's range (Lowry and Pearse 1973; Foster and VanBlaricom 1986*). Yet sea urchins are among the most abundant, conspicuous, and important invertebrates on rocky reefs that occur beyond the sea otter's range in central California (Foster and Schiel 1985, 1988; Harrold and Pearse 1987). We are aware of only a single case in which abundant sea urchins have been reported within the sea otter's range in central California, and that is the report of Watanabe and Harrold (Monterey Bay Aquarium, Monterey, Calif., unpublished manuscript) from an area known as "the pinnacles," located about 1 km off the shore of Carmel Bay. These urchin populations seem to have developed following a heavy settlement event around 1985. Although this observation poses an apparent paradox with our previously stated contentions, the urchin population at the pinnacles developed in rather deep water (20–30 m), and the previously well-developed kelp canopy in the area has also been lost. It is still unknown whether the urchins occur below a depth at which sea otters can profitably forage (as occurs in the Aleutian Islands), or whether otters have foraged at all in that area in recent years. It could be that loss of the kelp canopy has made the urchin populations at the pinnacles difficult for sea otters to locate, although this is unlikely.

Most sea urchin population reductions that have occurred through time following the reestablishment of sea otters have been documented anecdotally (McLean 1962; Ebert 1968a, 1986b; Benech 1977, 1981*), and in all cases the reported patterns were similar. Laur et al. (1988) conducted one of the few studies in California designed to document the community level effects of the expanding sea otter population: within a year of the arrival of sea otters on their two study reefs, red urchin (*S. franciscanus*) and purple urchin (*S. purpuratus*) densities declined to zero.

There is similar evidence that sea otters limit sea urchin populations in other geographical areas. For example, Breen et al. (1982) reported that sea urchins were rarely found within the range of the sea otter in British Columbia, whereas outside the otter's range, urchins were perhaps the most conspicuous and important herbivore. A more recent survey by J. Watson (University of California, Santa Cruz, Calif., personal communication) has confirmed these patterns. She also was unable to find more than an occasional sea urchin within the sea otter's range in British Columbia. Furthermore, she found that several sites surveyed by Breen et al. (1982)—which at the time of their studies were outside the otter's range and supported abundant sea urchin populations—had been reinhabited by otters and lacked sea urchins at the time of her surveys in summer 1987. One of her sites, which lacked otters and supported an abundant urchin population when she first surveyed it, was reinhabited by otters when she revisited it about a month later, at which time she found little more than broken urchin tests covering the sea floor. Similar results have been obtained by Duggins (1980) for an area near Glacier Bay in southeastern Alaska. Sea urchins were abundant in Torch Bay, a site lacking sea otters; however, he was unable to find more than an occasional urchin in nearby Surge Bay, where otters were abundant. Sea otters reinhabited Torch Bay around 1986, and in an extensive survey of this area done in May 1988 (including all five of Duggins' study sites) only an occasional small urchin could be found (Estes et al. 1989; Estes and Duggins, unpublished data).

Estes et al. (1978) reported similar differences between islands with and without sea otters in the western Aleutian archipelago, with one rather striking exception. At Amchitka Island, where sea otters not only were abundant but also apparently at or near equilibrium density, high densities of small sea urchins (<35 mm and most <25 mm test diameter) were found, especially at depths greater than about 10–15 m. At Shemya and Attu islands, where sea otters were absent, sea urchins typically reached 65–85 mm test diameter. We subsequently surveyed a large number of sites in the western and central Aleutian Islands and found that these urchin population structures were predictably associated with the presence or absence of sea otters. Our preliminary analyses (Estes et al. 1989; Estes and Duggins, in preparation) indicated that high densities of small sea urchins persist amidst abundant sea otters for two reasons: (1) sea urchins recruit heavily each year throughout the central and western Aleutian Islands, and (2) there is a lower size limit below which urchins gain refuge from otter predation.

Sea otters are known to effectively limit populations of various other benthic invertebrates, such as Pismo clams (*Tivela stultorum*), abalone (*Haliotis* spp.), Dungeness crabs, and mussels (*Mytilus californianus* and *M. edulis*; Ebert 1968a, 1968b; Lowry and Pearse 1973; Wild and Ames 1974; Miller et al. 1974, 1975; Gotshall et al. 1976*; Stephenson 1977; Estes and VanBlaricom 1985; Wendell et al. 1986; Garshelis et al. 1986; Kvitek and Oliver 1988; VanBlaricom 1988). The behavior and distribution of certain prey, such as sea urchins and abalone, are also affected by sea otter predation. For instance, in central California, abalone are found almost entirely in crevice refuges that, among other things, provide shelter from foraging sea otters and perhaps other predators

(Ebert 1968a; Faro 1970; Lowry and Pearse 1973; Cooper et al. 1977; Hines and Pearse 1982). Hines and Pearse (1982) presented evidence showing that the abundance, size, and species composition of abalone remained stable from 1972 to 1981 at the Hopkins Marine Life Refuge in Monterey—an area that had been occupied by sea otters for nearly 20 years—although the overall density and average size of abalones were substantially reduced from that found in areas not occupied by otters. Garshelis et al. (1986) similarly concluded that sea otter predation was responsible for the collapse of the Dungeness crab fishery in eastern Prince William Sound—shortly after foraging sea otters moved into the area, crab populations declined, and the fishery had to be closed. It was known that the otters fed extensively on crabs and very likely reduced crab populations; however, this case was confounded somewhat by the fact that bivalve populations, which are prey for Dungeness crabs, had declined substantially due to coastal uplifting from the great Alaska earthquake of 1964. This perhaps, in turn, caused an observed long-term decline in the crab population (Estes and VanBlaricom 1985).

Sea otters also feed at high tide in intertidal communities. Intertidal mussels have been reported in dietary studies of sea otters from the Kuril Islands to central California. VanBlaricom (1987, 1988) has studied the interaction between sea otters and intertidal mussel populations in central California and Prince William Sound. In Prince William Sound, mussels (*Mytilis edulis*) are one of the main sea otter foods (Estes et al. 1981). Sea otter predation was found to reduce the size and density of mussels, although this effect varied among areas, depending on age and sex composition of the local sea otter population. Through translocation and caging experiments, VanBlaricom (1987) was able to demonstrate that growth rate and maximum attainable size of mussels were comparable or greater in populations depredated by sea otters than in unexploited populations.

In Prince William Sound, VanBlaricom (1987) found that mussels were consumed primarily by recently weaned juveniles and females with dependent pups, whereas they were rarely eaten by adult males or single females. Since sea otters segregate spatially by age and sex, the composition of the local sea otter population influences the extent to which mussels are consumed in a particular area. Because of the high mussel abundance and calm sea conditions throughout most of Prince William Sound, it is likely that mussels are more easily captured than other prey, such as decapods and burrowing bivalves, perhaps explaining why they are so commonly eaten by juveniles and females with large pups. However, Garshelis (1983) suggested that whereas mussels were easily obtained, their nutritional value was relatively low, possibly explaining why they were less frequently eaten by the more experienced adults. In addition, VanBlaricom (1987) suggested that mussels were sporadically consumed in areas supporting large aggregations of males. When this occurred, the foraging sea otters caused the virtual local elimination of the mussel populations.

The foraging pattern of sea otters in mussel (*M. californianus*) beds along the exposed coast of central California is considerably different from that observed in Prince William Sound. VanBlaricom (1988) found that sea otters only feed sporadically in these mussel beds, creating gaps remarkably similar in size to those caused by wave shear on the outer coast of Washington (Paine and Levin 1981). However, gaps formed by sea otter foraging are created in calm seas when the otters can effectively forage over the intertidal zone at high tide, whereas gaps generated by wave shear are created during rough, stormy conditions.

VanBlaricom (1988) also reported that whereas sea otters were nonselective in the removal of patches of mussels from the intertidal zones, they consumed only those individuals longer than about 40 mm. In Prince William Sound, mussel populations subjected to intense sea otter predation mainly contained individuals <40 mm in shell length, seemingly because of such size-selective predation. It is interesting to note that this size preference, and the resulting influence of sea otter predation on the size distribution of prey, is similar to that reported by Estes et al. (1978, 1989) for green sea urchins (*Strongylocentrotus polyacanthus*) in the western Aleutian Islands.

The recent findings of Kvitek and Oliver (1988) and Kvitek et al. (1988) are in contrast with the view that sea otter predation is the major controlling influence on some of their prey populations. Their study of a soft-bottom habitat in lower Elkhorn Slough demonstrated that sea otters had little effect on either the density or size distribution of infaunal bivalves. Kvitek et al. (1988) argued that sea otters incurred large time and energy costs in digging the deep-burrowing bivalves (*Tresus nuttallii* and *Saxidomus nuttallii*) that inhabited their study site, thus preventing the otters from substantially reducing their prey populations. Although this pattern may be at least partially a result of seasonal and recent sea otter occupancy, it contrasts with the well-documented interaction between sea otters and Pismo clams (Miller et al. 1975; Stephenson 1977; Wendell et al. 1986), which are comparatively shallow burrowers, and which decline quickly and substantially following the arrival of sea otters in areas supporting dense clam populations. Compelling evidence for this interaction is provided by Wendell et al. (1986), who reported that recreational landings of Pismo clams at Pismo Beach, California, declined to near zero shortly after sea otters dispersed into the area. The large male group of otters that caused the clam decline has since moved on; there has been a heavy recruitment of clams, and it is possible that a recreational fishery may again be

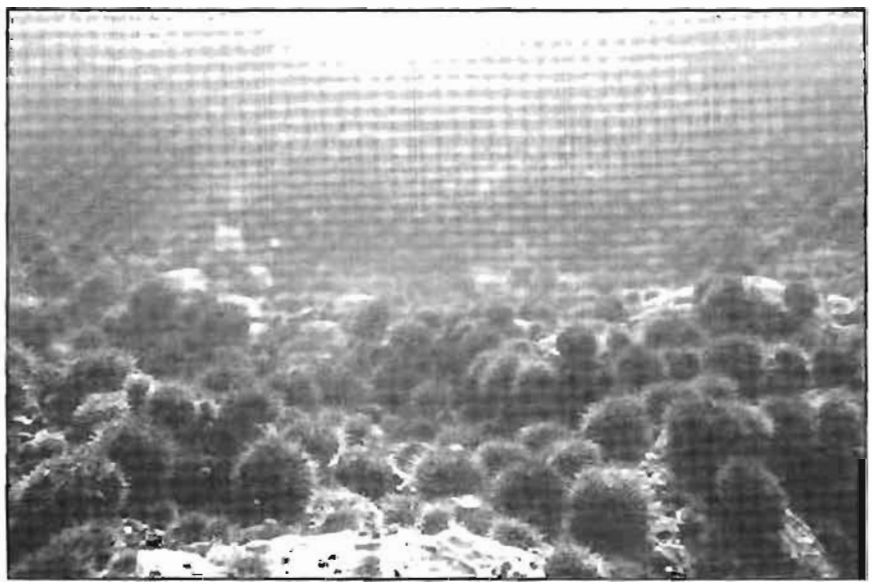


Fig. 18. (A) Kelp forest at Amchitka Island, Alaska (the kelp understory near the diver was cleared). (B) Sea urchin barrens at Shemya Island, Alaska (J. Estes).

possible, at least for smaller-sized Pismo clams. Estes and VanBlaricom (1985) reviewed the evidence for the effect of sea otter predation on benthic invertebrate populations and speculated on the potential for sea otter depredations on a wide range of marine invertebrates, which are of commercial and recreational value throughout the historical range of the sea otter in the northeastern Pacific Ocean.

Indirect Effects of Sea Otter Predation

Sea otters limit herbivorous sea urchins in many areas of the North Pacific Ocean, which in turn promotes the growth of kelp and other macroalgae. This scenario predicts that rocky reef communities are dominated by kelps and other macroalgae when sea otters are present, but that these communities become deforested by sea urchin graz-

ing when sea otters are absent (Fig. 18). Evidence for this effect, summarized by Estes and Harrold (1988), is of three general kinds: (1) comparative observations, either between nearby areas with and without sea otters or through time with the reestablishment and growth of sea otters at specific locations (Estes and Palmisano 1974; Estes et al. 1978; Duggins 1980; Breen et al. 1982; Laur et al. 1988); (2) historical information on kelp beds with sea otter population changes (VanBlaricom 1984a); and (3) small-scale experimental manipulations that mimic the influence of sea otter predation (Duggins 1980).

Comparative studies provide the most well-known, and probably the most compelling, evidence of the influence of sea otter predation on kelp forest communities. Estes and Palmisano (1974) reported that rocky reef habitats at islands with abundant sea otter populations in the western Aleutian archipelago were characterized by dense stands of kelps and other fleshy macroalgae, whereas comparable habitats at nearby islands lacking sea otters were largely deforested. Similar reports were subsequently published by Duggins (1980) for southeast Alaska, Breen et al. (1982) for British Columbia, Jameson et al. (1986) for Washington State, and Laur et al. (1988) for central California. VanBlaricom (1984a) used maps, prepared by the U.S. Department of Agriculture in 1911 and 1912, to demonstrate that the areal extent of the surface kelp canopy had expanded considerably and that species composition shifted from bull kelp (*Nereocystis leutkeana*) to giant kelp (*Macrocystis pyrifera*) following expansion of the sea otter's range into these areas (Fig. 19). Duggins (1980) removed sea urchins from subtidal plots in southeastern Alaska and found significant increases in kelp settlement and growth compared with unmanipulated control plots. Similar results have been obtained from numerous other areas of the North Pacific Ocean, as well as elsewhere in the world (Harrold and Pearse 1987).

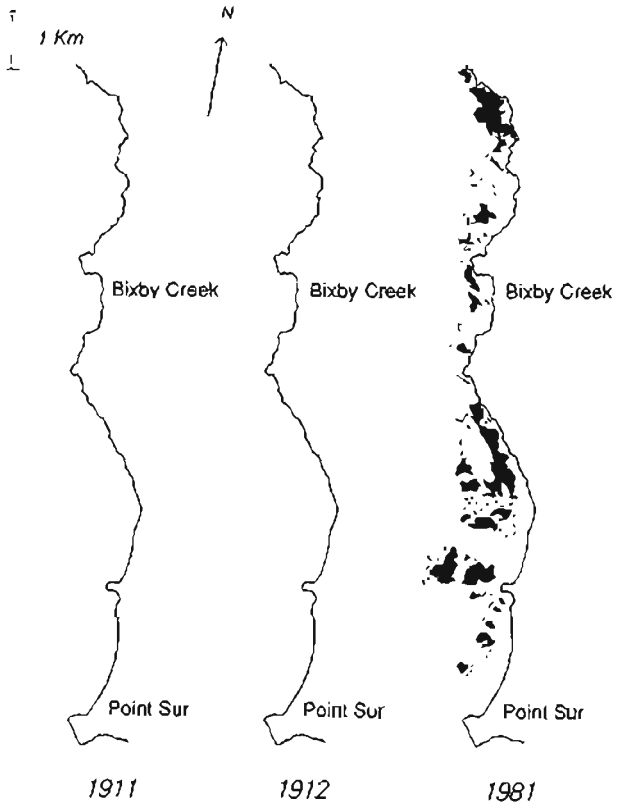


Fig. 19. Density and distribution of kelp beds in central California before and after the recolonization of sea otters (from VanBlaricom 1984b).

There are various problems with all the evidence of indirect effects of sea otter predation. Comparative observations suffer from possible confounding influences of spatial or temporal variation unrelated to the influence of sea otter predation. Because kelp forest communities are known to vary substantially in space and through time (Foster and Schiel 1985; Estes and Harrold 1988), this problem could be notable. Historical reconstructions suffer from problems of interpretation, which is to say that changes correlated with the sea otter's recovery, but causally unrelated to the influence of sea otter predation, cannot be discounted when attempting to interpret the otter's role in observed changes. Furthermore, the quality of historical information is often suspect and always poorer than that obtained from contemporary studies. When properly done, experimental studies are not confounded by community effects unrelated to sea otter predation, although such studies probably experience other problems. For example, while experimental treatment effects usually are absolute (i.e., sea urchins are undisturbed or they are removed entirely), the effects of sea otter predation may not be. Additionally, small-scale manipulations may produce effects different from those that occur when the same factors change on a larger scale, particularly if larval or spore dispersal is narrowly confined. Nonetheless, these studies collectively provide strong evidence that kelp beds are enhanced by sea otter predation, and that this effect occurs widely in the North Pacific Ocean. The important questions now are: (1) How general is this scenario? (2) How broad is the influence of sea otter predation on other kelp forest species? and (3) What is the time course of community changes with the reestablishment and growth of sea otters? These difficult questions are being investigated.

Estes and Duggins (unpublished data) addressed the question of generality by sampling a large number of randomly selected sites from islands in the western Aleutian archipelago with and without sea otters. Depending on which community characteristics were measured, these data showed that the extent to which benthic communities between such areas differed was predictable. In general, sites at islands without sea otters were deforested.

whereas those at islands where otters were abundant were not.

The most predictable character of these communities was sea urchin size distribution. Urchins with test diameters >30–35 mm were seldom found at the islands with otters, whereas all of the samples from otter-free islands contained sea urchins with test diameters of 60–80 mm. Sea urchin biomass per unit area was predictably low at islands with otters, whereas it was high but variable at otter-free islands. Similarly, kelp densities were predictably near zero at otter-free islands, whereas they were high but variable at islands with sea otters. Watson's (personal communication) Vancouver Island data, which were obtained similarly to those of Estes and Duggins, show similar patterns, except that sea urchins were virtually absent from Watson's sites occupied by sea otters. Ongoing research throughout the Kodiak archipelago and southeastern Alaska (Kvitek and Oliver, unpublished data), on the outer coast of southeastern Alaska near Glacier Bay (Estes and Duggins, unpublished data), and in Sitka Sound (J. Estes, G. VanBlaricom, and D. Carney, unpublished data) indicate patterns resembling those observed in British Columbia.

Comparable data from randomly selected sites in areas with and without sea otters are lacking for California. Foster and Schiel (1988) sent questionnaires to workers familiar with different regions of the California coast, and based on the responses, they argued that sea otters play a relatively minor role in California kelp forests, contending instead that both sea urchin populations and macroalgal assemblages are limited by a range of physical and biological factors. Consistent with this view, Laur et al. (1988) concluded that substrate relief influences the extent to which, in the absence of sea otter predation, rocky-bottom habitats in California have become deforested by sea urchin grazing. However, Foster and VanBlaricom (1986*) surveyed 9 sites within the sea otter's central California range from Villa Creek to Granite Canyon. Whereas site selection was not random (sampling was done only under *Macrocystis* canopies), no evidence of grazing disturbance by sea urchins or other invertebrates was noted. These sites were generally characterized by understories that graded from *Laminaria setchellii* (a kelp) and articulated coralline algae in shallow water (6 m) to *Pterygophora californica* and encrusting coralline algae in deeper water (≤15 m). Foster and VanBlaricom (1986*) reported that among the sites, plant densities and the cover of sessile invertebrates and algal turf varied considerably.

Temporal and spatial patterns of community change following reestablishment of sea otters are even less well known. In several sites at Attu Island, Alaska, Estes and Harrold (1988) reported that the only remarkable change in benthic community structure with reestablishment of sea otters was a reduction in the maximum size of sea urchins; otherwise, these areas remained as deforested sea urchin barrens with high densities of small individuals preventing settlement and growth of macroalgae. However, at one site where sea urchins apparently recruited unpredictably, a kelp forest became reestablished soon after otters reinhabited (J. A. Estes, unpublished data). Laur et al. (1988) documented the structure of two reef communities near Point San Luis in central California before and after sea otters became established in that area. One was a shallow-water, high-relief site, which supported a kelp bed before the arrival of sea otters. The other was a deeper-water, low-relief site, which was extensively deforested (by sea urchin grazing) before the arrival of sea otters. Sea urchin densities declined to near zero at both sites within several months following the arrival of otters. A kelp bed developed within a year in the area that previously had been deforested, and the abundance of several fish species also increased. Although similar data are lacking from other geographic locations in the northeastern Pacific Ocean, anecdotal evidence suggests that where deforested habitats occur, these are transformed rather quickly into kelp beds following the arrival of sea otters.

There has been further speculation that the interaction between sea otters, sea urchins, and macroalgae can have far-reaching influences on coastal communities (Estes et al. 1978). For example, reduction in the intensity of herbivory by sea otter predation may promote strong competitive interactions within algal assemblages (Dayton 1975; Duggins 1980; Reed and Foster 1984). The presence of kelp may act on coastal ecosystems in many important ways, such as by providing food and habitat for other organisms or by altering water flow (Gerard 1976; Mann 1982; Jackson 1984; Ebeling et al. 1985; Duggins 1988). Evidence for these influences is mainly suppositional, coming from studies in which sea otters were not a factor in the design, and usually not even a point of concern. For example, several studies have shown important relations between kelp and a number of fish species (Quast 1968a; Ebeling and Laur 1985, 1988; Ebeling et al. 1985, Bodkin 1986, 1988; Simenstad, Estes, and Cowen, unpublished data). Kelp may create or improve fish habitat, for instance, by providing shelter from predators (especially to juvenile fishes); by increasing overall substrate area; and by expanding the food base and habitat for kelp forest organisms that in turn provide food for fishes (Davies 1968; Quast 1968a, 1968b; Haaker and Wilson 1975; Leamon 1976, 1980; Wilson et al. 1977; Bodkin 1986). In the Aleutian Islands, populations of certain fish species, most notably the rock greenling (*Hexagrammos lagocephalus*), occur at higher densities in kelp habitats than in sea urchin barrens (Simenstad et al. 1978; C. A. Simenstad, J. A. Estes, and R. K. Cowen, unpublished data). That sea otters themselves may be influenced by algal–fish interactions is indicated by the

fact that in parts of Alaska and the Soviet Union, fish constitute an important element of the otter's diet (Estes et al. 1981, 1982). Similarly, Trapp (1979) and Irons et al. (1986) found that where sea otters were absent, glaucous-winged gulls (*Larus glaucescens*) in the western Aleutian Islands fed extensively on sea urchins and other intertidal invertebrates but consumed mainly fish where sea otters were abundant.

In the western Aleutian Islands, the importance of kelp as a source of organic carbon between communities with and without sea otters was studied by Duggins et al. (1989). Their study was based on the fact that sessile macroalgae and water column-borne phytoplankton fix the two stable isotopes of carbon (^{12}C and ^{13}C) in different relative amounts. The study demonstrated that, although stable carbon isotope ratios within species vary considerably among sites at any given island, highly significant differences existed between islands with and without sea otters.

Other Influences on Kelp Forest Communities

Kelp forest communities are influenced by many physical and biological processes, such as unstable substrata, chronic surge or wave action, climatic and hydrographic conditions (such as those accompanying the El Niño Southern Oscillation [ENSO or "El Niño"] of 1982–83), intensity and quality of available light, water temperature, nutrient conditions, severe storms, and predation by other kelp herbivores (see Dayton 1985; Foster and Schiel 1985; Schiel and Foster 1986 for reviews). However, discussion of these variables is beyond the scope of this review.

The diets of several other species or groups of consumers in California and Alaska overlap with the diet of the sea otter, including several asteroid species, octopus (*Octopus* spp.), crabs, birds (gulls and eiders), harbor seals, and fishes such as cabezon (*Scorpaenichthys marmoratus*) and wolf-eels (*Anarrhichthys ocellatus*). However, the extent to which competition for food occurs among these species is unknown.

Other sea urchin predators in central and southern California include invertebrates (e.g., asteroids; Landenberger 1967; Rosenthal and Chess 1972; Dayton et al. 1980*), spiny lobsters (*Panulirus interruptus*; Tegner and Levin 1983; Robles 1987), and octopus, as well as fishes such as cabezon, wolf-eels, and California sheephead (*Semicossyphus pulcher*; Hobson and Chess 1976; Cowen 1983). Sheephead are found primarily in southern California, beyond the present range of the sea otter, although sea otters recently were relocated to San Nicolas Island where sheephead occur. In particular, sheephead predation seems to limit sea urchins (Nelson and Vance 1979; Cowen 1983). Cowen (1983) speculated that because sheepbead limit red and purple urchin populations in some areas at San Nicolas Island, they may prevent urchin grazing on attached macroalgae. In southern California, commercial harvest of urchins may also limit red urchin populations within established kelp forests. The sunflower star (*Pycnopodia helianthoides*) preys on urchins and may impose an important structuring influence on some urchin populations, with consequent effects on macroalgae (Duggins 1983). Locally abundant populations of sunflower stars occur from the eastern Aleutian Islands to central California. In addition, severe storms, sediment scour, changing climatic conditions, disease, and recruitment failure may limit sea urchin populations along the California coast in areas not subject to heavy sea otter predation (Pearse et al. 1970*; Miller and Geibel 1973; Pearse et al. 1977; Yellin et al. 1977; Pearse and Hines 1979; Cowen et al. 1982; Ebeling et al. 1985; Ebert and Russell 1988).

Foraging Behavior and Diet

Feeding and Diving Behavior

Sea otters forage in rocky substrate and soft bottom communities, along the bottom as well as within the kelp understory and canopy. Foraging activity takes place most frequently in subtidal zones, although otters also forage intertidally to some extent (Vandevere 1969*; Estes 1980; Kovnat 1982; VanBlaricom 1988; Harrold and Hardin 1986; Jameson, unpublished data; Riedman, Staedler, and Estes, unpublished data). In California, otters usually forage at depths of < 25 m (Wild and Ames 1974; California Department of Fish and Game 1976*; Estes 1980; U.S. Fish and Wildlife Service 1980*), beyond which the canopy-forming kelps and certain prey items become scarce (Abbott and Hollenberg 1976). However, along the northern Monterey peninsula, certain territorial males sometimes forage offshore in depths of 30–40 m (Riedman, unpublished data; Deutsch, personal communication), and in the center of the range, juvenile males tend to forage deeper and further offshore (1–2 km) than other age or sex classes of otters (Ralls et al. 1988a*, 1988b*). In the Aleutian Islands, in contrast, sea otters commonly feed at depths of 40 m or more (Estes 1980).

From direct observations of foraging sea otters, Estes et al. (1981) reported that average dives lasted from about 50 to 60 s and that dives exceeding 125 s were extremely rare. However, Ralls et al. (1988b*), using radiotelemetry, found that 5 of 31 otters in central California had mean dive times exceeding 125 s, 12 individuals had maximum dives exceeding 200 s, and the maximum dive time recorded was 246 s. These findings indicate that visual studies are biased against animals feeding in deep

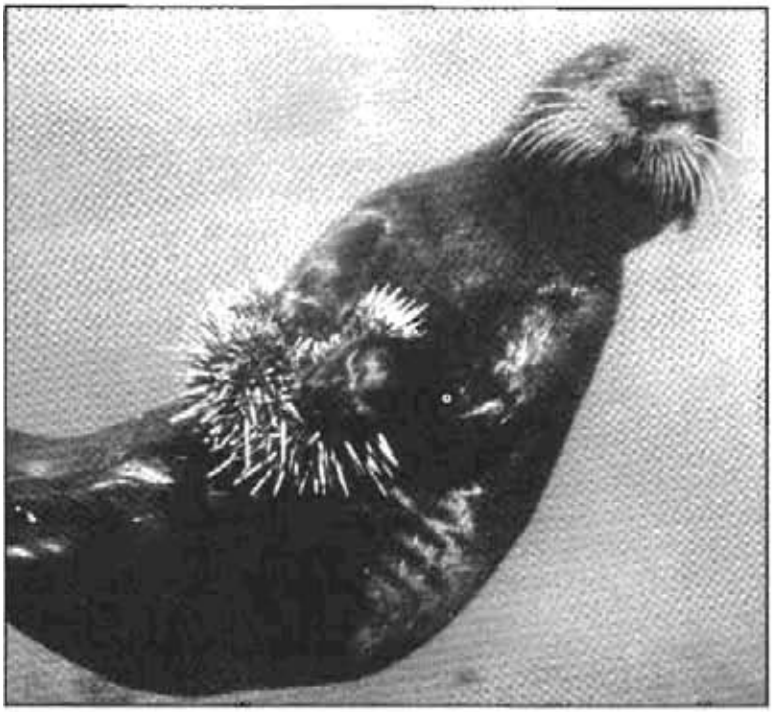


Fig. 20. California sea otter holding red sea urchin (*Stongylocentrotus franciscanus*) underwater (R. Mattison).

water far from shore. Maximum dive times in all age or sex classes studied by Ralls et al. (1988b*) ranged to about 4 min; however, average dive time was longest for juvenile males and shortest for females with pups. This pattern reflects their finding that juvenile males tend to feed far from shore in deep water, whereas adult females with pups tend to feed close to shore in shallow water. Ralls et al. (1988b*) found that the mean dive time and surface interval between dives for all instrumented otters was 74 s and 65 s. Most individuals differed significantly between day and night in length of dives, but the direction of this difference varied among individuals. The average foraging bout duration of radio-instrumented otters studied by Ralls et al. (1988b*) in central California was between 77 and 373 min. Juvenile females tended to have longer feeding bouts than other age or sex classes. The fact that juvenile females have long feeding bouts may be related to their tendency to forage on small-sized prey (Riedman, Staedler, and Estes, unpublished data). The average interval between feeding bouts was 188 min, from the range of 81–300 min for individuals.

An average of 70–73% of all diurnal feeding dives in California result in the successful capture of prey (Loughlin 1977; Estes et al. 1981), although a complex array of variables may affect the proportion of successful dives, type of prey obtained, dive times, and foraging strategies (Estes et al. 1981). Adult otters make unsuccessful dives more often than juveniles, although adults also obtain more rewarding but less easily captured prey. Longer dives—and often several dives—are required to capture large prey items that are less accessible but more rewarding in terms of energetic value (such as abalone and *Cancer* crabs) than are necessary to obtain less valuable prey (such as turban snails; Loughlin 1977; Costa 1978a, 1978b; Estes et al. 1981; Ralls et al. 1988b*). As might be expected, surface times were highly correlated with prey size and type, and lasted longest for large prey such as abalone, large crabs, and octopus, which frequently took an otter several minutes to consume (Ralls et al. 1988b*).

Sea otters capture prey with their forepaws, often storing food items within loose flaps of skin beneath the axilla of each foreleg until the prey can be consumed at the surface (Barabash-Nikiforov 1947; Kirkpatrick et al. 1955; Fig. 20). A sea otter may capture two or more prey items of the same or different species in a single dive. Prey such as clams are captured by rapid and repetitive digging in soft substrates with the forepaws, and the otter often dives several times before it can excavate the clam (Shimek 1977a; Hines and Loughlin 1980).

Food Stealing

Sometimes one otter steals another otter's food at the surface (Fisher 1939; Miller 1980). It is possible that food stealing also takes place underwater, since a feeding otter may occasionally surface while interacting with another otter after a foraging dive. Incidents of food stealing are common among mother–pup pairs, with older dependent pups regularly taking food from their mothers during a

foraging bout. The majority of other food-stealing incidents involve territorial males, who often take prey from females and mother–pup pairs foraging in their territory (Riedman et al. 1988*). Territorial males do not seem to be selective when stealing prey; they usually take whatever food the female has obtained. Such males steal prey in which they do not specialize, as well as prey they obtain on their own (Riedman, Staedler, and Estes, unpublished data). Generally, a female's food is stolen by a territorial male at least once or at most several times during a complete foraging bout. Females usually relinquish prey to males with little resistance. A territorial male who is pair-bonded to a female may also frequently steal her prey. In fact, pair-bonded males sometimes solicit or steal prey from their mates in the same manner as dependent pups: the female occasionally even offers prey to the male as she would to her pup. Particular territorial males may steal food from females more often than others. An interesting male strategy, termed hostage behavior, has also been observed along the Monterey peninsula. This occurs when a male approaches and grabs a dependent pup while its mother is foraging underwater. The pup is relinquished to the mother only when she gives the male her prey in apparent exchange for her offspring (Riedman, Staedler, and Estes, unpublished data).

Stealing of food occurs occasionally between adult females, one or both of which may be accompanied by a pup. Observations of such incidents suggest that prey may be selectively stolen by females. For example, in one case only abalone was taken. Whether such food stealing incidents among adult females are based on age or social status is currently under investigation (Riedman et al. 1988*). Juvenile females have also been observed attempting to steal food from each other as well as from adults (Riedman, Staedler, and Estes, unpublished data). However, Ralls and Siniff (1988*) found that juvenile females often had food stolen from them and speculate that their tendency to feed at different times (throughout a 24-h period) than other otters may reduce the chances that food is stolen from them. Only large and valuable prey was stolen from the juvenile females, indicating that such stealing was selective. Victims of food stealing may either temporarily stop foraging, move to another location, or simply continue foraging in the same area.

Tool Use

The use of tools such as rocks to break open or dislodge hard-shelled macroinvertebrates is common among sea otters (Fisher 1939; Limbaugh 1961; Hall and Schaller 1964; Kenyon 1969; Houk and Geibel 1974; Miller 1974; Fig. 21). Tool use is uncommon among mammals and has only been reported in humans, chimpanzees, dolphins, and (occasionally) polar bears (*Ursus maritimus*) as well as sea otters (Alcock 1972; Beck 1980). Tool use appears to be more frequent among sea otters in California than in the Aleutian Islands (Estes, unpublished observation). The reason for this may be the increased occurrence of more heavily shelled forms at latitudes closer to the tropics (Vermeij 1978). In addition, Aleutian Island sea otters feed heavily on fish in areas such as Amchitka Island, in which case tool use is unnecessary. In Prince William Sound, however, otters frequently use tools to open bivalves (Calkins 1978; Garshelis 1983).

Sea otters may use rocks or other objects underwater to pry loose or break apart prey such as urchins or abalone that adhere tightly to rocks or are wedged in crevices. About 80% of the abalone shells examined by Ebert (1968a) in California had breakage patterns suggesting that they had been struck by tool-using otters. Sea otters along the northern Monterey peninsula often carry a rock or other tool with them while diving underwater, yet do not always use it to break open captured prey only at the surface. When brought to the surface, mollusks (e.g., abalone or rock oysters [*Pododesmus cepio*]) often bear a large hole near the center of the shell, which it seems the otter created underwater with its tool (Riedman, unpublished observation).

Recent research has shown that California sea otters are quite versatile in tool use techniques and foraging tactics, indicating well-developed learning and cognitive abilities. The most common form of tool use occurs when an otter places a rock on its chest while floating on its back and pounds hard-shelled prey (e.g., snails, mussels, clams) against the rock as an anvil to crack open the outer shell. Numerous variations of this method may be employed, and sea otters are capable of learning new and innovative tool use techniques and capture strategies to enhance foraging ability (Riedman, Staedler, and Estes, unpublished data). Sometimes an otter may use the rock tool as a hammer, or it may use two rocks as hammer and anvil. At other times, pieces of the shell or crab carapace may be broken off and pounded against the prey itself. In addition to rocks, which are the most frequently used tool, otters may use empty shells, driftwood, empty glass or plastic bottles, aluminum beverage cans, and other man-made objects discarded by humans (Riedman et al. 1988*). Live clams may also be pounded against each other to break the shells in Alaska (Kvitek, personal communication) and California (Riedman, Staedler, and Estes, unpublished data).

Many otters vary their tool use behavior appropriately with the particular prey species obtained. For instance, a female who captures both turban snails and purple urchins may eat the urchins using her teeth, then dive specifically for the purpose of obtaining a tool to crack the hard-shelled snails. Other feeding methods include rolling

Fig. 21. California sea otter using rock tool to break open prey (D. Buchich).

urchins between the paws to break off the spines and using the hindflippers to hold crabs on the abdomen while eating another food. An otter may even immobilize a crab by wrapping it in kelp fronds draped over the otter's abdomen while it eats another food item (Riedman et al. 1988*).

Observations on tagged sea otters along the Monterey peninsula have shown that individual variation exists in tool use methods, as it does in choice of prey, with certain otters consistently using the same type of tool and tool use technique. An otter may also keep a tool to use throughout a particular forage bout (Riedman et al. 1988*; K. Lyons, Institute of Marine Sciences, University of California, Santa Cruz, unpublished data). For instance, one tagged female in Monterey consistently used an extremely large flat rock or slab of concrete underwater, seemingly to dislodge abalone. Another female in Monterey Harbor used a glass bottle to pry rock oysters from rocks beneath the surface. Studies on the cognitive aspects of tool use abilities in captive sea otters are currently under way at the Monterey Bay Aquarium (J. Curland, R. Gisiner and R. Schusterman, Moss Landing Marine Laboratories, Moss Landing, Calif., personal communication).

Individual Variation in Diet and Foraging Tactics

There is substantial variation among individual California sea otters with respect to diet and the amount of time allocated to diving and foraging on the surface (Estes et al. 1981; Lyons and Estes 1985*; Riedman et al. 1988*; Lyons 1989). Among animals foraging within an area, individual variation in diet has also been documented in tropical marine snails (*Thais emarginata*; *T. melones*; West 1986a, 1986b), Cocos Island finches (*Pinaroloxia inornata*; Werner and Sherry 1987), possibly among chimpanzees (*Pan troglodytes*; Goodall 1986), and in some pinnipeds (Riedman 1990). In all of these cases, individuals specialize in particular foods or foraging strategies regardless of age, sex, or body morphology. For sea otters, these individual dietary patterns seem to vary greatly in their energetic profitability. For example, from estimates of caloric content of prey (Costa 1978a) and prey-specific search, pursuit, and handling times (Estes et al. 1981), Estes et al. (1989) calculated that foraging times required to meet daily energy intake ranged from <4 to >21 h for the individual sea otters studied by Lyons (1989).

Fig. 22. California sea otter consuming kelp crab, *Pugettia*. (D. Buchich).

Although diet of the sea otter population in a given area may be extremely diverse, individual otters tend to specialize on selected prey (usually 1–3 species). In the Monterey area, for instance, one female fed on mussels, kelp crabs, and turban snails (Fig. 22); another female specialized in clams and fat innkeeper worms (*Urechis caupo*); and a territorial male ate turban snails (*Tegula*) almost exclusively (Riedman, Staedler and Estes, unpublished data). These individual patterns seem to persist for at least 2.5 years (Lyons 1989) to 5 years (Riedman et al. 1988*). However, Lyons (unpublished data) found that the diet of tagged females changed predictably with birth and again with weaning of their pups. According to Riedman et al. (1988*), the diet and foraging strategies of some (but not all) tagged females vary with their reproductive status (the presence of a pup, age of pup, and period in which a female is in estrus). In Prince William Sound, the diet of females with pups was often of poor quality because the mothers frequently foraged on prey items of low nutritive value that were easily captured by pups (Garshelis 1983; VanBlaricom 1988).

Currently in progress in Monterey are investigations that focus on the acquisition of individual foraging strategies in otters, development of foraging skills in pups, and changes in dietary composition and foraging tactics as an animal matures. Observations of tagged weaned pups and juvenile offspring of tagged females indicate that juvenile females may in fact forage on the same types of prey, and employ the same tool use method and use similar foraging strategies as their mothers (Riedman et al. 1988*; Riedman et al. 1989*).

Sea otters exhibit individual differences not only in choice of prey, but also in choice of tool, method of tool use, area in which they tend to forage, water depth (e.g., some otters consistently forage in the intertidal or shallow water areas), and other foraging strategies. A few otters solicit food from humans, and one otter learned to reach into a bucket on the stern of a boat in Monterey Harbor to obtain squid (*Loligo opalescens*). Another otter, a juvenile female raised in Monterey Harbor, regularly waits for hand-outs of bait fish such as anchovies (*Engraulis mordax*) from tourists, occasionally threatening adult male California sea lions for their anchovies. In another instance, a male otter learned to bite into aluminum beverage cans and extract small octopuses that had taken refuge inside (McCleneghan and Ames 1976). Another male otter (presumably one individual) learned to capture, kill, and eat large seabirds, as have other otters in the

northern part of the California range (Riedman and Estes 1988a). Using radio-instrumented sea otters, Ralls et al. (1988b*) reported individual differences in length of dive, surface interval between dives, feeding bout length, interval between feeding bouts, and nocturnal versus diurnal feeding patterns.

Diet in Alaska and the Soviet Union

Whereas the diet of California sea otters consists primarily of macroinvertebrates, sea otters in Alaska and Russia feed on epibenthic fish as well as invertebrates in many areas where the otter populations are near equilibrium density (Simenstad et al. 1977; Estes et al. 1978, 1982). Prey availability varies with location and the time an area has been occupied by sea otters; it also influences diet (Table 3).

In areas of Alaska where otter populations have been established for long periods (e.g., Amchitka Island), fish constitute an important part of the diet (Fig. 23). The high proportion of fish in the diet of Amchitka Island sea otters is apparently associated with an increased availability of nearshore fish and a corresponding scarcity of benthic invertebrates, such as sea urchins. As populations of herbivorous invertebrates at Amchitka were reduced by sea otter predation, the abundance of kelp beds and nearshore fishes inhabiting kelp forest communities has increased. In contrast, sea otters feed primarily on sea urchins (*Strongylocentrotus polyacanthus*), as well as various crustaceans and molluscs, in recently reoccupied areas of the Aleutians (such as Attu Island), where otter populations exist below equilibrium densities. Fish are rarely consumed in such areas (Estes et al. 1982).

These ecological relations may have profound influences on the behavior and population biology of sea otters. For example, Estes et al. (1982) showed that fish were captured by sea otters at Amchitka Island only near

Table 3. *Prey reported to be consumed by sea otters (*Enhydra lutris*) throughout the range. (Principal sources: California—U.S. Fish and Wildlife Service 1982 [and references therein], Lyons 1989, R. Kvitek, University of Washington, personal communication, J. Vandevere, Pacific Grove, Calif., personal communication, G. VanBlaricom, Fish and Wildlife Service, Santa Cruz, Calif., personal communication; Oregon—Jameson 1975; Washington—Bowlby 1988*; Southeast Alaska—Rosenthal and Barilotti 1973*, Pitcher 1987*, R. Kvitek, personal communication; Aleutian Islands—Kenyon 1969, Estes et al. 1981, J. Estes, unpublished data; Commander Islands—Barabash-Nikiforov 1947, A. Zorin, Soviet Ministry of Fisheries, Moscow, personal communication; Prince William Sound—Calkins 1978, Estes et al. 1981, R. Kvitek, personal communication, G. VanBlaricom, personal communication; Kodiak archipelago—R. Kvitek, personal communication; Shumagin Islands—R. Kvitek, personal communication.)*

Prey	California	Oregon	Southeast Alaska	Aleutian Islands	Commander Islands	Prince William Sound	Kodiak archipelago	Washington	Shumagin Islands
Echiura									
Echiurus echiurus	.	.	.	.	.	X	.	.	.
Urechis caupo	X	.	.	.	.	.	.	.	.
Nemertea									
Emplectonema sp.	.	.	.	X	.	.	.	.	.
Annelida									
Polychaeta									
Arenicola sp.	.	.	.	X	.	.	.	.	.
Eudistylia polymorpha	X	.	.	.	.	.	.	.	.
Eudistylia sp.	.	.	.	.	.	X	X	.	.
Nereis sp.	.	.	.	X	.	.	.	.	.
Nereis vexillosa	X	.	.	.	.	.	.	.	.
Arthropoda									
Crustacea									
Cirripedia									
Thoracica									
Balanus cariosus	.	.	.	.	X	.	.	.	.
Balanus nubilus	X	.	X	.	.	.	.	.	.

Table 3. *Continued.*

Prey	California	Oregon	Southeast Alaska	Aleutian Islands	Commander Islands	Prince William Sound	Kodiak archipelago	Washington	Shumagin Islands
Lepas anatifera	.	.	.	.	X	.	.	.	.
Malacostraca									
Isopoda									
Idotea sp.	.	.	.	X	.	.	.	.	.
Isopod (unidentified)	.	.	.	X	.	.	.	.	.
Amphipoda									
Amphipod (unidentified)	.	.	.	X	.	.	.	.	.
Gammarus sp.	.	.	.	.	X	.	.	.	.
Decapoda									
Blepharipoda occidentalis	X	.	.	.	.	.	.	.	.
Cancer antennarius	X	X	.	.	.	.	.	.	.
Cancer magister	X	X	.	.	.	X	X	.	X
Cancer oregonensis	.	.	.	X	.	.	.	.	.
Cancer productus	X	X	.	.	.	.	.	.	.
Cancer sp.	.	.	.	X	.	.	.	X	.
Chionecetes bairdi	.	.	.	X	.	.	.	.	.
Chionecetes opillio	.	.	.	.	X	.	.	.	.
Cryptolithodes sitchensis	X	.	.	.	.	.	.	.	.
Dermaturus mandtii	.	.	.	X	.	.	.	.	.
Emerita analoga	X	.	.	.	.	.	.	.	.
Hapalogaster cavicauda	X	.	.	.	.	.	.	.	.
Hapalogaster grebnitzkii	.	.	.	.	X	.	.	.	.
Hemigrapsus sp.	X	.	.	.	.	.	.	.	.
Hyas coarctatus	.	.	.	.	X	.	.	.	.
Lopholithodes foraminatus	X	.	.	.	.	.	.	.	.
Loxorhynchus crispatus	X	.	.	.	.	.	.	.	.
Pachygrapsus crassipes	X	.	.	.	.	.	.	.	.
Paguristes sp.	X	.	.	.	.	.	.	.	.
Pagurus gilli	.	.	.	X	.	.	.	.	.
Pagurus hirsutiusculus	.	.	.	X	X	.	.	.	.
Pagurus sp.	.	.	.	X	.	.	.	.	.
Panulirus interruptus	X	.	.	.	.	.	.	.	.
Placetron wosnessenski	.	.	.	X	.	.	.	.	.
Pleuroncodes planipes	X	.	.	.	.	.	.	.	.
Pugettia producta	X	X	.	.	.	.	.	.	.
Pugettia richii	X	.	.	.	.	.	.	.	.
Pugettia sp.	.	.	.	.	.	.	.	X	.
Sclerocrangon boreas	.	.	.	X	.	.	.	.	.
Telmessus cheiragonus	.	.	.	X	.	X	X	.	.
Mollusca									
Gastropoda									
Astraea gibberosa	X	.	.	.	.	.	.	.	.
Astraea undosa	X	.	.	.	.	.	.	.	.
Argobuccinium oregonensis	.	.	.	X	.	.	.	.	.
Buccinium sp.	.	.	.	X	.	.	.	.	.
Calliastoma sp.	X	.	.	.	.	.	.	.	.
Crepidula adunca	X	.	.	.	.	.	.	.	.
Haliotis cracherodii	X	.	.	.	.	.	.	.	.
Haliotis kamtschatkana	.	.	X	.	.	.	.	.	.
Haliotis rufescens	X	.	.	.	.	.	.	.	.
Haliotis walallensis[a]	X	.	.	.	.	.	.	.	.
Haliotis sp.	.	X	.	.	.	.	.	.	.
Lottia gigantea	X	.	.	.	.	.	.	.	.
Lottia ochracea	.	.	.	.	X	.	.	.	.
Megathura crenulata	X	.	.	.	.	.	.	.	.

Table 3. *Continued.*

Prey	California	Oregon	Southeast Alaska	Aleutian Islands	Commander Islands	Prince William Sound	Kodiak archipelago	Washington	Shumagin Islands
Natica clausa	.	.	.	X	X	.	.	.	.
Notoacmaea persona	.	.	.	.	.	X	.	.	.
Polinices lewisii	X	.	.	.	.	.	.	.	.
Tectura spp.	.	.	.	X	.	.	.	.	.
Tegula brunnea	X	.	.	.	.	.	.	.	.
Tegula funebralis	X	.	.	.	.	.	.	.	.
Tegula montereyi	X	.	.	.	.	.	.	.	.
Tegula pulligo	X	.	.	.	.	.	.	.	.
Tegula sp.	.	X	.	.	.	.	.	.	.
Thais sp.	.	.	.	X	.	.	.	.	.
Bivalvia									
Clinocardium ciliatum	.	.	.	X	.	.	.	.	.
Clinocardium facanum	X	.	.	.	.	.	.	.	.
Clinocardium nuttallii	X	.	.	.	.	X	.	.	.
Gari californica	X	.	.	.	.	.	.	.	.
Hiatella arctica	.	.	.	.	.	X	.	.	.
Hinnites giganteus	X	.	.	.	.	.	.	.	.
Hinnites multirugosus	.	X	.	.	.	.	.	.	.
Humilaria kennerlia	.	.	X	.	.	X	X	.	X
Liocyma viridis	.	.	.	X	.	.	.	.	.
Macoma incongrua	.	.	.	.	.	X	.	.	.
Macoma inquinata	.	.	.	.	.	X	X	.	.
Macoma sp.	.	.	.	X	.	.	X	.	.
Modiolus modiolus	X	.	.	X	X	.	X	.	.
Musculus niger	.	.	.	.	X	.	.	.	.
Musculus vernicosa	.	.	.	.	X	.	.	.	.
Musculus sp.	.	.	.	.	.	.	.	.	X
Mytilus californianus	X	X	X	.	.	.	.	.	.
Mytilus edulis	X	.	.	X	X	X	X	.	.
Mya arenaria	.	.	.	.	.	X	.	.	.
Mya truncata	.	.	X	.	X	X	X	.	.
Panopea generosa	.	.	X	.	.	.	.	.	X
Pecten beringianus	.	.	.	X	.	.	.	.	.
Pecten islandica	.	.	.	X	.	.	.	.	.
Pododesmus cepio	X	.	.	.	.	.	.	.	.
Pododesmus macroschisma	.	.	.	X	X	.	.	.	.
Protothaca staminea	.	.	.	.	.	X	X	.	X
Protothaca sp.	X	X	.	.	.	.	.	X	.
Saxidomus giganteus	.	.	X	.	.	X	X	.	X
Saxidomus nuttalli	X	X	.	.	.	.	.	.	.
Saxidomus sp.	.	X	.	.	.	.	.	.	.
Serripes groenlandicus	.	.	.	X	.	X	.	.	.
Siliqua patula	X	.	.	.	X	.	.	.	.
Solen sicarius	X	.	.	.	.	.	.	.	.
Spisula alascana	.	.	.	.	X	.	.	.	.
Spisula hempelli[a]	X	.	.	.	.	.	.	.	.
Tagelus californianus	X	.	.	.	.	.	.	.	.
Tivela stultorum	X	.	.	.	.	.	.	.	.
Tresus capax	.	.	.	.	.	X	X	.	.
Tresus nuttallii	X	.	.	X	.	.	.	.	.
Venericardia paucicostatus	.	.	.	X	.	.	.	.	.
Voluplopsius beringi	.	.	.	.	X	.	.	.	.
Polyplacophora									
Callistochiton crassicostatus	X	.	.	.	.	.	.	.	.
Cryptochiton stelleri	X	X	X	X	X	.	.	X	.
Ischnochiton sp.	X	.	.	.	.	.	.	.	.

Table 3. *Continued*

Prey	California	Oregon	Southeast Alaska	Aleutian Islands	Commander Islands	Prince William Sound	Kodiak archipelago	Washington	Shumagin Islands
Mopalia sp.	.	.	.	X	.	.	.	.	.
Schizoplax brandtii	.	.	.	X	.	.	.	.	.
Tonicella marmorea	.	.	.	X	.	.	.	.	.
Tonicella ruber	.	.	.	X	.	.	.	.	.
Cephalopoda									
Loligo opalescens	X	.	.	.	.	.	.	.	.
Octopus sp.	X	X	.	X	.	X	.	X	.
Polypus sp.	.	.	.	.	X	.	.	.	.
Echinodermata									
Echinoidea									
Dendraster excentricus	X	.	.	X	.	.	.	.	.
Strongylocentrotus drobachiensis	.	.	X	X	X	.	.	.	.
Strongylocentrotus franciscanus	X	X	X	.	.	.	.	X	.
Strongylocentrotus polyacanthus	.	.	.	.	X	.	.	.	.
Strongylocentrotus purpuratus	X	X	.	.	.	.	.	X	.
Asteroidea									
Asterina miniata	X	.	.	X	.	.	.	.	.
Ceramaster sp.	.	.	.	X	.	.	.	.	.
Evasterias troschelii	.	.	.	.	.	X	.	.	.
Henricia sp.	.	.	.	X	.	.	.	.	.
Leptasterias sp.	.	.	.	X	.	.	.	.	.
Pisaster brevispinus	X	.	.	.	.	.	.	.	.
Pisaster giganteus	X	.	.	.	.	.	.	.	.
Pisaster ochraceus	X	X	.	.	.	.	.	.	.
Pycnopodia helianthoides	X	.	.	.	.	.	X	.	.
Ophiuroidea									
Brittle star	.	.	.	X	.	.	.	.	.
Gorgonocephalus eucnemis	X	.	.	.	.	.	.	.	.
Holothurioidea									
Cucumaria miniata	.	X	.	.	.	.	.	X	.
Cucumaria piperata	X	.	.	.	.	.	.	.	.
Cucumaria sp.	.	.	X	X	.	X	.	.	.
Parastichopus sp.	X	.	.	.	.	.	.	.	.
Chordata									
Ascidiacea									
Styela montereyensis	X	.	.	.	.	.	.	.	.
Tunicata	.	.	.	X	.	.	.	.	.
Pisces									
Ammodytes hexapterus	.	.	.	X	X	.	.	.	.
Anoplopoma fimbria	.	.	.	X	X	.	.	.	.
Aptocyclus ventricosus	.	.	.	.	X	.	.	.	.
Cottidae	X	.	.	X	.	.	.	.	.
Cyclopterichthys glaber	.	.	.	X	.	.	.	.	.
Embiotocidae	X	.	.	.	.	.	.	.	.
Gadus morhua	.	.	.	X	X	.	.	.	.
Gymnocanthus pistilleger	.	.	.	X	.	.	.	.	.
Hexagrammos superciliosus	.	.	.	X	.	.	.	.	.
Hexagrammos sp.	X	.	.	.	X	.	.	.	.
Hemilepidotus hemilepidotus	.	.	.	X	.	.	.	.	.

Table 3. *Continued*

Prey	California	Oregon	Southeast Alaska	Aleutian Islands	Commander Islands	Prince William Sound	Kodiak archipelago	Washington	Shumagin Islands
Hemilepidotus jordani	.	.	.	.	X	.	.	.	.
Lepidopsetta bilineata	.	.	.	.	X	.	.	.	.
Mallotus villosus	.	.	.	.	X	.	.	.	.
Oncorhynchus nerka	.	.	.	.	X	.	.	.	.
Pleurogrammus monoterygius	.	.	.	X	.	.	.	.	.
Theragra chalcograma	.	.	.	.	X	.	.	.	.
Aves									
Anatidae									
Anas crecca	.	.	.	X	.	.	.	.	.
Melanitta perspicillata	X	.	.	.	.	.	.	.	.
Gavidae									
Gavia immer	X	.	.	.	.	.	.	.	.
Laridae									
Larus sp.	X	.	.	.	.	.	.	.	.
Phalacrocoracidae									
Phalacrocorax sp.	X	.	.	.	.	.	.	.	.
Podicipedidae									
Aechmophorus occidentalis	X	.	.	.	.	.	.	.	.

[a] Indirect evidence of foraging noted; actual feeding not observed.

Fig. 23. Sea otter eating fish at Adak Island, Alaska (J. Watson).

dawn and dusk, and they speculated that diel variation in the availability or vulnerability of fishes caused the distinct crepuscular peaks in foraging activity observed there. Estes (1990a) speculated that the inclusion of fish in the sea otter's diet resets the equilibrium population size of otters well above that which is attainable on a diet of invertebrates alone, thus perhaps explaining the 3- to 5-fold differences in population size reported for Amchitka Island by Kenyon (1969; about 1,500 in 1965) and Estes (1977, 1990a; 5,000 individuals in 1972 and 1986). Estes et al. (1989) suggested that, for the sea otter, foraging on fish is a dietary innovation that may have been lost when the species was reduced to a few remnant colonies at the end of the fur hunting era. We hypothesize that benthic invertebrates were more common and nearshore fishes more rare when otters were near extinction, and that the economics of prey choice may have excluded fish from the otter's diet under those circumstances. Our studies of prey selection in California have shown highly individualized diets (Lyons and Estes 1985*; Riedman et al. 1988*), which may possibly be inherited matrilineally (from mother to pup; Riedman et al. 1989*). If similarly individualized diets occur in Alaska—and if foraging on fish requires search and capture skills substantially different from those required for feeding on benthic invertebrates—then the innovation of foraging on fish by individuals in a population that had lost this behavior may occur only rarely. However, under the ecological conditions where this behavior is cost-effective (i.e., when otter populations are food-limited, benthic invertebrates are rare, and fish are common), once the innovation occurred it would be expected to grant an advantage to the individuals who adopted it, and might thus be expected to spread rapidly through the population by way of learning. Although largely speculative, these processes would explain the timing of the population change seen at Amchitka Island (Estes 1981), as well as the comparatively small sea otter population at Medny Island in the Commander Islands (i.e., about 1,000 at an island similar in size to Amchitka), which appears to be food-limited but where individuals nonetheless do not feed on fish (A. Zorin, Soviet Ministry of Fisheries, Moscow, U.S.S.R., personal communication).

In the Kuril Islands of the Soviet Union, a similar relation exists among diet, long-term and seasonal changes in prey availability, and the length of time a given area has been occupied by sea otters (Fig. 24). At Simushir Island, where the sea otter population was below equilibrium density in the late 1960's, sea urchins were large and abundant, and otters consumed them almost exclusively (Shitikov 1973). However, at Urup and Paramushir islands, where sea otter populations had been established for many years, sea otters consumed a substantial amount of fish, in addition to various bivalve molluscs (*Modiolus difficilis*, *Mytilus edulis*, and *Tellina* spp.) and sea urchins, which were small and relatively scarce (Maminov and Shitikov 1970; Shitikov et al. 1973).

Dietary composition also changed seasonally among sea otters in the Kuril Islands. In winter, sea otters consumed mainly sea urchins and mollusks, while in summer, the diet broadened to include fish, fish eggs, octopus, and crab (Barabash-Nikifovov 1947; Shitikov 1971). In the Aleutian Islands, rock greenling may be most vulnerable to otter predation in summer, when they spawn and must defend their eggs. Sea urchins attain maximum gonadal development in winter, which is probably when they are of highest nutritional value to otters. A similar situation may exist at the Kuril Islands.

Diet in California

In recently reoccupied habitats of central California, the diet consists principally of abalones (*Haliotis* spp.), rock crabs (*Cancer* spp.), and large red sea urchins (*S. franciscanus*; Ebert 1968a; Vandevere 1969*; Wild and Ames 1974; Wade 1975; Stephenson 1977; Benech 1981*; Estes et al. 1981). These food items are higher in caloric value and therefore more rewarding than other prey species (Costa 1978a, 1978b). In time, populations of preferred prey are reduced by sea otter predation, and diet at the population level diversifies to include large numbers of food items: kelp crabs (*Pugettia* spp.), clams (various spp.), turban snails, mussels (*Mytilus* spp.), octopus (*Octopus* spp.), barnacles (*Balanus* spp.), scallops (*Hinnites* spp.), fat innkeeper worms, sea stars (*Pisaster* spp.), and chitons (*Cryptochiton* spp.; Boolootian 1961; Limbaugh 1961; Ebert 1968a; Hennessey 1972; Wild and Ames 1974; Estes 1980; Benech 1981*; Estes et al. 1981; Ostfeld 1982; U.S. Fish and Wildlife Service 1982; Jameson, unpublished data). Predation on fish in California is extremely rare (Hall and Schaller 1964; Miller 1974; Estes et al. 1981; U.S. Fish and Wildlife Service 1982). Surprisingly, while wild otters are rarely observed eating kelp, the captive sea otters at the Monterey Bay Aquarium frequently consume giant kelp. The four exhibit otters share one large piece of kelp once or twice each week, when available. They appear to prefer the stipes and bulbous gas floats; they eat these parts first when given an unlimited supply of kelp. However, the exhibit otters seem to eat kelp so readily because of its novelty, rather than using it as a food source (Hymer, personal communication). Table 4 provides a complete list of prey items consumed by otters in California. Some of these species are consumed frequently, while others are eaten only rarely.

Dietary composition in California is also influenced by habitat type and time of year. Bivalve molluscs are heavily consumed in soft-sediment communities. For example, Pismo clams make up a significant proportion of the diet of sea otters foraging along the sandy shores of

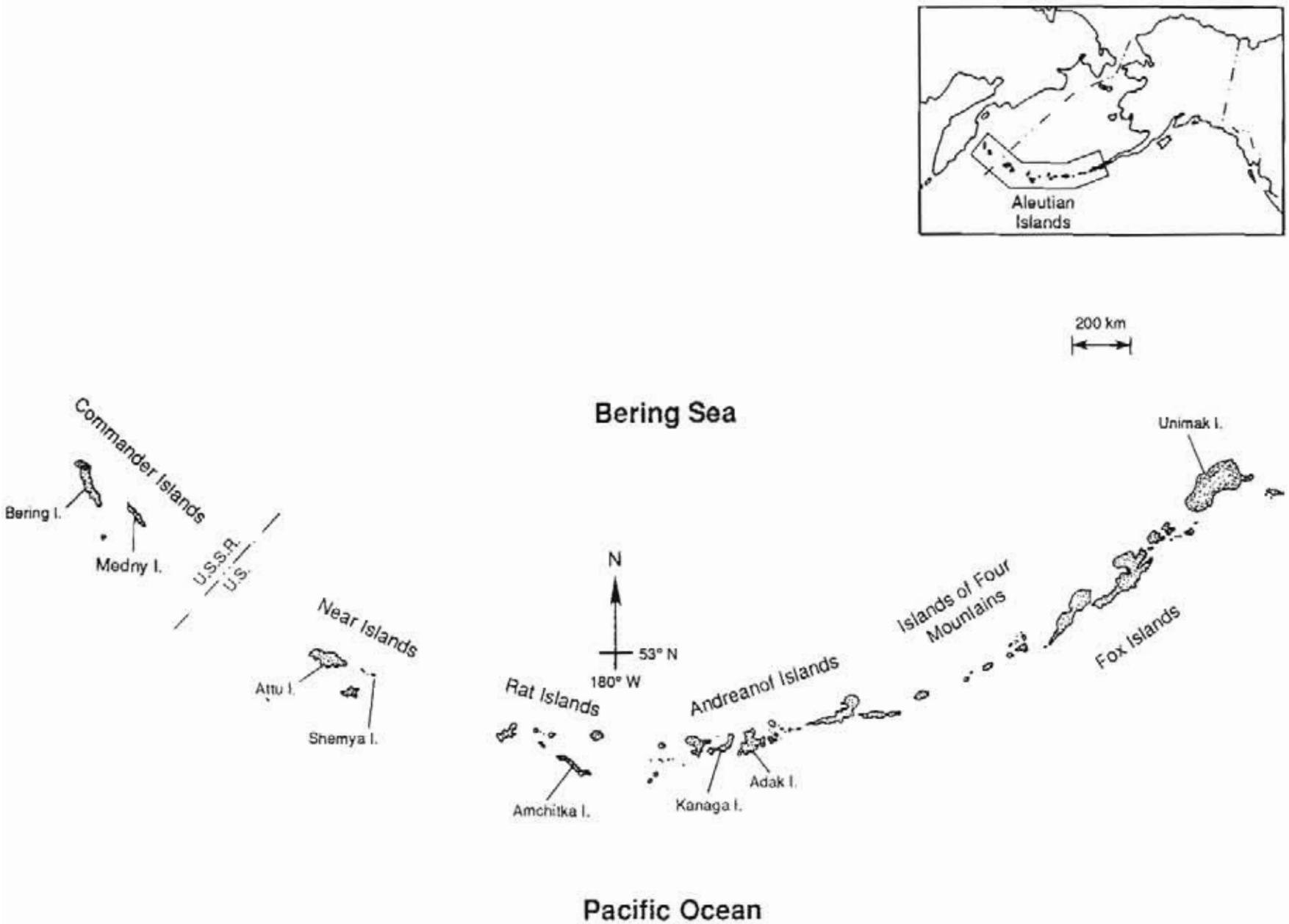


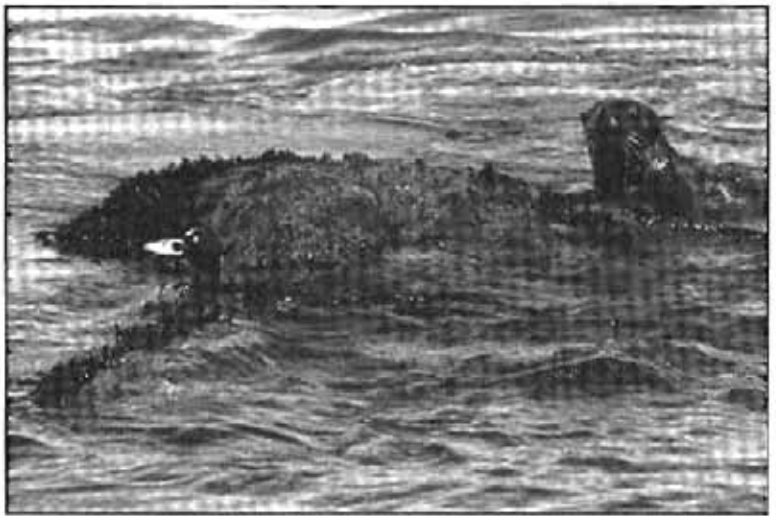
Fig. 24. Aleutian and Commander islands, indicating areas referred to in text.

Table 4. *Scientific and comon names of prey items of the California sea otter* (Enhydra lutris). *Some of these species are commonly eaten, while others are rarely consumed.* [a]

- Phaeophyta
  - Kelp (*Macrocystis pyrifera*)
  - Echiurida
    - *Urechis caupo* (fat innkeeper)
  - Annelida
    - Polychaeta
      - *Eudistyla polymorpha* (sabellid worm)
      - *Nereis vexillosa* (clam worm)
  - Arthropoda
    - Crustacea
      - Cirripedia
      - Thoracica
        - *Balanus nubilis* (barnacle)
    - Malacostraca
      - Decapoda
        - *Blepharipoda occidentalis* (spiny sand crab)
        - *Cancer antennarius* (rock crab)
        - *Cancer magister* (Dungeness crab)
        - *Cancer productus* (red crab)
        - *Cryptolithoides sitchensis* (umbrella crab)
        - *Emerita analoga* (sand crab)
        - *Hapalogaster cavicauda* (furry crab)
        - *Hemigrapsus* spp. (purple shore crab)
        - *Lopholithodes foraminatus* (stone crab)
        - *Loxorhynchus crispatus* (decorator crab)
        - *Pachygrapsus crassipes* (green shore crab)
        - *Pagurisles* sp. (hermit crab)
        - *Panulirus interruptus* (California spiny lobster)
        - *Pleuroncodes planipes* (pelagic red crab)
        - *Pugettia producta* (kelp crab)
        - *Pugettia richii* (kelp crab)
  - Mollusca
    - Gastropoda
      - *Astrea gibberosa* (brick-red top snail)
      - *Astrea undosa* (wavy turban snail)
      - *Calliostoma* sp. (top snail)
      - *Crepidula adunca* (hooked slipper shell)
      - *Haliotis cracherodii* (black abalone)
      - *Haliotis rufescens* (red abalone)
      - *Haliotis walallensis* (flat abalone)[b]
      - *Lottia gigantia* (owl limpet)
      - *Megathura crenulata* (giant keyhold limpet)
      - *Polinices lewisii* (giant *or* Lewis' moon snail)
      - *Tegula brunnea* (brown turban snail)
      - *Tegula funebralis* (turban snail)
      - *Tegula montereyi* (turban snail)
      - *Tegula pulligo* (turban snail)
    - Bivalvia
      - *Clinocardium facanum* (cockle)
      - *Clinocardium nuttallii* (basket cockle)
      - *Gari californica* (sunset clam)
      - *Hinnites giganteus* (rock scallop)
      - *Modiolus* (= *Volsella*) *modiolus* (giant horse mussel)
      - *Mytilus californianus* (California sea mussel)
      - *Mytilus edulis* (bay mussel)
      - *Pododesmus cepio* (rock oyster *or* abalone jingle)
      - *Protothaca staminea* (littleneck clam)
      - *Saxidomus nuttallii* (Washington clam)
      - *Siliqua patula* (northern razor clam)
      - *Solen sicarius* (razor clam)
      - *Spisula hempelli*[a]
      - *Tagelus californianus* (jacknife clam)
      - *Tivela stultorum* (Pismo clam)
      - *Tresus nuttallii* (gaper clam)
    - Amphineura
    - Polyplacophora
      - *Cryptochiton stelleri* (gumboot chiton)
      - *Ischnochiton* sp. (chiton)
      - *Callistochiton crassicostatus* (chiton)
    - Cephalopoda
      - *Loligo opalescens* (market squid)
        - (also squid egg case)
      - *Octopus* spp. (octopus)
- Echinodermata
  - Echinoidea
    - *Dendraster excentricus*
    - *Strongylocentrotus franciscanus* (red sea urchin)
    - *Strongylocentrotus purpuratus* (purple sea urchin)
  - Asteroida
    - *Asterina miniata* (bat star)
    - *Pisaster brevispinus* (short-spined sea star)
    - *Pisaster giganteus* (sea star)
    - *Pisaster ochraceus* (common sea star)
    - *Pycnopodia helianthoides* (sunflower star)
  - Ophiuroidea
    - *Gorgonocephalus eucnemis* (basket star)
  - Holothurioidea
    - *Cucumaria miniata* (orange sea cucumber)
    - *Cucumaria piperata* (black-speckled white sea cucumber)
    - *Parastichopus* (sea cucumber)
- Chordata
  - Ascidiacea *Styela montereyensis* (stalked tunicate)
  - Pisces
    - Scorpaeniformes
    - Cottidae (sculpins)
    - Hexagrammidae
      - *Hexagrammos* sp. (greenling)
    - Perciformes
      - Embiotocidae (surfperches)
- Aves
  - Anatidae
    - *Melanitta perspicillata* (surf scoter)
  - Gavidae
    - *Gavia immer* (common loon)
  - Laridae
    - *Larus* sp. (gull)
  - Phalacrocoracidae
    - *Phalacrocorax* sp. (cormorant)
  - Podicipedidae
    - *Aechmophorus occidentalis* (western grebe)

[a] Sources: U.S. Fish and Wildlife Service 1982; Reidman and Estes 1988b*; Riedman, Staedler, and Estes, unpublished data; R. Kvitek, personal communication; G. VanBlaricom, personal communication.

[b] Indirect evidence of foraging noted; actual feeding not observed.



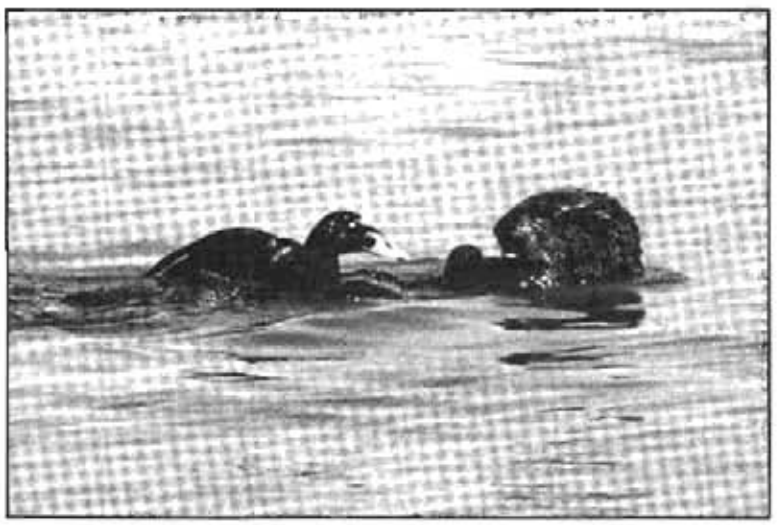


Fig. 25. (A) California sea otter stalking male surf scoter in Monterey. (B) Same otter as in (A) holding surf scoter on abdomen (G. Cathers).

Monterey Bay and Atascadero State Beach near Morro Bay (Miller et al. 1975; Wade 1975; Shimek 1977b; Stephenson 1977; Hines and Loughlin 1980). In the Elk horn Slough estuary of Monterey Bay, sea otters primarily consume the deep-burrowing bivalves *Tresus nuttallii* and *Saxidomus nuttallii* (Kvitek et al. 1985, 1988; Kvitek and Oliver 1988). In Prince William Sound, the diet of otters feeding in soft-sediment areas of Montague Strait consists principally of clams (particularly *Saxidomus giganteus*), which represent the most abundant food resource (Calkins 1978). At Green Island and Sheep Bay in Prince William Sound, otters consume primarily mussels and clams (Estes et al. 1981).

Squid spawning takes place during fall and spring in Monterey Bay. At this time, squid constitute a substantial portion of the diet of some individuals, as foraging tactics shift to take advantage of this seasonally abundant food source (California Department of Fish and Game 1976*; Ames, unpublished data; Riedman, Staedler, and Estes, unpublished data). Large-scale, unusual oceanographic conditions, such as the "El Niño" event of the early 1980's, can supply additional food resources such as the pelagic red crab (*Pleuroncodes planipes*; K. J. Lyons, unpublished data; Riedman, Staedler, and Estes, unpublished data), which otherwise occurs farther south.

Predation on Seabirds

Sea otter predation on seabirds occasionally occurs in California (VanWagenen et al. 1981; Riedman and Estes 1988a), as well as in Alaska (Kenyon 1969; Fig. 25). Riedman and Estes (1988a) described recent incidents of predation on seabirds and reviewed previous observations of such predation in California and Alaska. Their findings are summarized in the next paragraph. At Amchitka Island, three cases have been reported, involving either a shearwater (*Puffinus* sp.) or fulmar (*Fulmarus*

glacialis) in one case, a pelagic cormorant (*Phalacrocorax pelagicus*; Kenyon 1969), and a green-winged teal (*Anas crecca*; P. Holden, Utah State University, Logan, unpublished data). In 20 cases in California, seabirds consumed included western grebes (*Aechmophorous occidentalis*), surf scoters (*Melanitta perspicillata*), cormorants (*Phalacrocorax* spp.), common loons (*Gavia immer*), and gulls (*Larus* spp.). Western grebes were most frequently captured. The amount of nourishment derived from seabirds is unknown, although Kirkpatrick et al. (1955) and Kenyon (1969) presented evidence that the flesh of cormorants and emperor geese (*Chen canagica*; fed to a captive otter) passed largely undigested through the gastrointestinal tract.

Most recorded incidents of sea otter predation on seabirds in California have taken place in the northern part of the range in three areas: Point Lobos, Stillwater Cove, and Monterey Harbor. (Several additional incidents of predation on birds between Santa Cruz and Granite Canyon near Soberanes Point have been reported since the Riedman and Estes [1988a] review; Riedman, unpublished data). Sea otters often initially capture the bird by diving and grabbing it from underwater while the bird floats on the surface, similar to the capture methods used by coastal river otters to obtain seabirds. If one compares mink, river otters, and sea otters, a graded reduction in the tendency to consume birds seems to have taken place in the more aquatic mustelids, so that the relative importance of birds is greatest in mink (*Mustela vison*) and least in sea otters.

Riedman and Estes (1988a) also point out some possible trends with respect to the incidents of sea otters foraging on seabirds: (1) Particular individuals may repeatedly prey on seabirds, with six birds at Point Lobos killed by what appeared to be the same otter; (2) otters in a particular area may learn new foraging strategies by observing other feeders; and (3) male sea otters seem to be involved in the majority of seabird-eating cases (although the otter's sex was not determined in all incidents). This tendency for males to feed on warm-blooded prey coincides with a similar trend among other mammals that sometimes feed on birds and mammals, such as chimpanzees (Goodall 1986) and some pinnipeds (Riedman 1990).

Effects of Paralytic Shellfish Poisoning (PSP)

Sea otters prey on numerous bivalve species that accumulate paralytic shellfish poisoning toxins (PSPT) during blooms of toxic dinoflagellates (*Protogonyaulax* spp.; Quayle 1969; Kvitek and Oliver 1988). Specifically, Alaskan sea otters prey heavily on the butter clam, which sequesters the most-lethal PSPT, saxitoxin (STX), and which may retain the toxin for a year or more after being exposed to a toxic bloom (Chambers et al. 1955*; Boyer et al. 1986). Mortalities of sea otters in the Commander Islands (Sidorov 1987) and at Kodiak Island, Alaska, may have been caused by PSPT, because butter clams constitute a major food resource there (DeGange and Vacca 1989).

Kvitek et al. (in review*) investigated the little known but potentially significant effects of PSPT on sea otters by observing the behavior of five captive Alaskan sea otters that were fed butter clams containing various levels of STX. They found that the otters either significantly reduced their feeding rates when given only high toxicity prey or discarded clam siphons and kidneys, which contain most of the toxins. Most of the otters changed their feeding behavior rapidly after being given toxic clams. One female, who consumed the highest amount of STX, cracked the toxic clams and held them to her mouth, but then emitted screams and discarded them. She was the only otter to exhibit any obvious PSPT symptoms, such as lack of coordination, sluggishness, and paralysis (Quayle 1969; Kvitek and Beitler 1988, 1989).

These results suggest that sea otters, while not immune to PSPT, are able to detect and avoid consumption of lethal levels of this toxic prey, and so are probably not at mortal risk from PSPT. Kvitek et al. (in review*) suggested that sea otters may have not dispersed into otherwise suitable food-rich habitat because they are avoiding PSPT-contaminated prey, especially in areas of southeast Alaska known for the occurrence of PSPT and where butter clams are the primary prey of sea otters (Kvitek and Oliver, unpublished data). The lack of overlap between the present (and historic) range of sea otters and the broad geographic areas in southeastern Alaska known to contain highly toxic prey further supports this contention. Such potential exclusion of the sea otter from otherwise suitable habitat has significant influences on the nearshore marine communities and shellfisheries in these areas.

Activity Patterns and Time Budgets

Many complex variables influence activity patterns and the amount of time allocated to various activities in sea otters, and they seem to be related to factors in the environment and in the individual. Diurnal activity cycles of sea otters tend to be characterized by crepuscular peaks in foraging activity and a midday (late morning to late afternoon) period of rest in California (Fisher 1939; Hall and Schaller 1964; Sandegren et al. 1973; Miller et al. 1975; Loughlin 1977; Shimek and Monk 1977; Benech 1981*; Ribic 1982b; Estes et al. 1986; Ralls and Siniff 1988*), in the Aleutian Islands (Lensink 1962; Kenyon 1969; Estes 1977; Estes et al. 1982), and in some areas of Prince William Sound (Garshelis 1983; Fig. 27).

In California, Loughlin (1977, 1979) made observations using radiotelemetry over a 24-h period and found that nocturnal activities were similar in nature to diurnal ac-

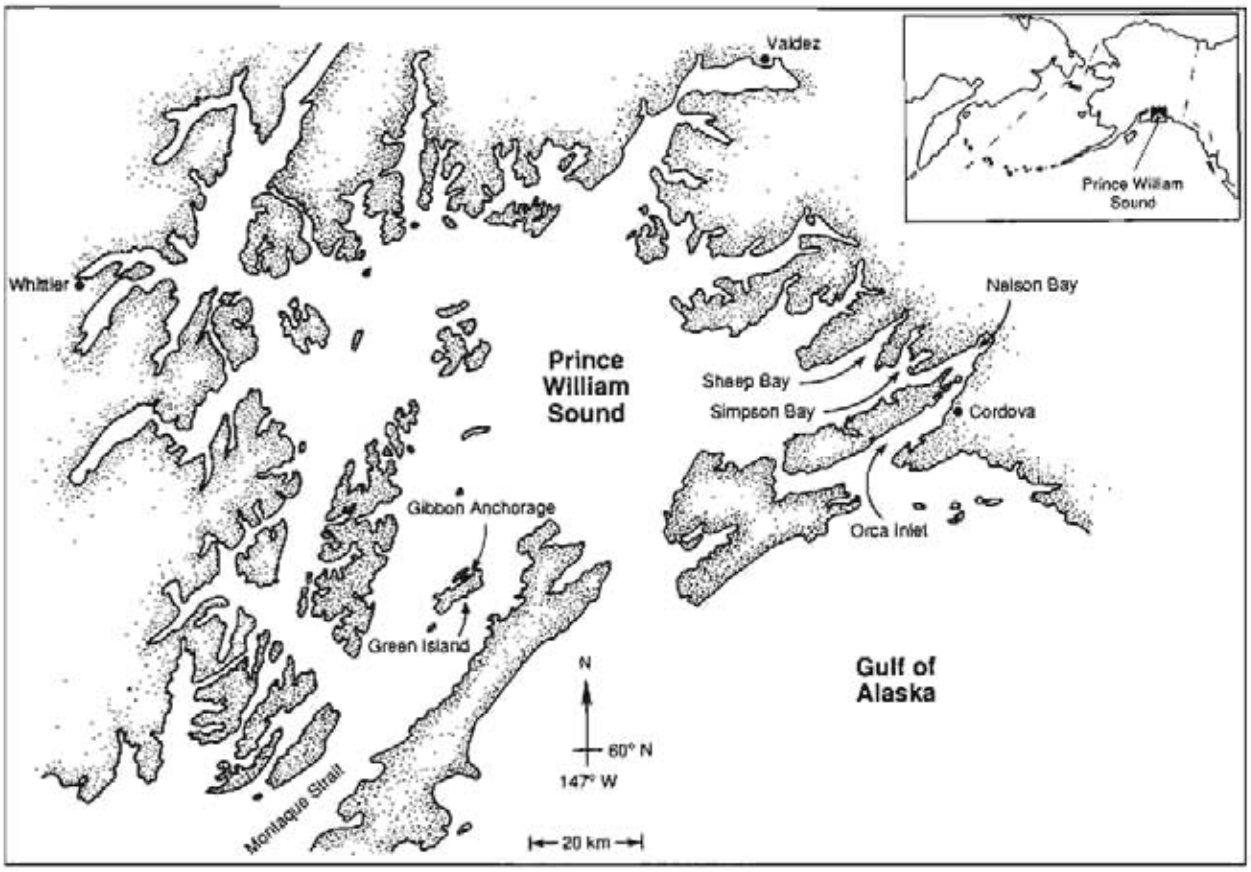


Fig. 26. Prince William Sound, Alaska, indicating areas referred to in text.

tivities and that foraging occurred throughout the night. Subsequent information collected by Ribic (1982b) and Ralls and Siniff (1988*)—also using radiotelemetry—confirmed that nocturnal feeding occurred. Observations made by Shimek and Monk (1977), Benech (1981*), Ribic (1982b), and Payne and Jameson (1984) suggested that a third peak in foraging activity may take place between 2300 and 0200 h. In the central and southern portions of the range, information on radio-instrumented otters collected by Ralls and Siniff (1988*) indicates that another peak in foraging activity occurs between midnight and dawn among all age or sex classes except juvenile females.

Observations of sea otters (using visual scan samples) along the California coast from Point Piedras Blancas to Santa Cruz show that the average amount of time allocated to various activities during daylight hours falls within the following ranges: foraging, 21–28%; resting, 51–63%; grooming, 5–16%; swimming, 2–9%; and interacting, 0–8% (King 1976; Harris 1977; Shimek and Monk 1977; Yellin et al. 1977*; Estes et al. 1986). Telemetry data obtained by Ralls and Siniff (1988*), however, strongly suggest that scan sampling underestimates time spent foraging by as much as 15–20%. Most of this difference is accounted for when the activity-specific probabilities of sighting (Estes and Jameson 1988) are used to correct scan sampling estimates of the percentage of time spent foraging.

Throughout a 24-h period, California sea otters seem to be active about half of the time. Loughlin (1977) found that individual telemetered otters in the Monterey area spent an average of 34% of their time foraging, 54% resting, and 12% engaged in other activities. These estimates were generally similar to those obtained from a larger sample and more extensive study in the central and southern part of the sea otter's range (Ralls and Siniff 1988*). Loughlin found that about 45% of feeding activity took place at night, although there was substantial individual variation in the proportion of nocturnal foraging (22–73%). Juvenile otters tended to engage in more nonfeeding activities (e.g., playful interaction) than adults (Loughlin 1977, 1979).

An extensive study of activity in telemetered sea otters was completed recently by Ralls and Siniff (1988*). They found that, except for juvenile females, there is a general increase in feeding activity early and late in the day, as

reported by Shimek and Monk (1977) and Estes et al. (1986) on the basis of scan sampling. Ralls and Siniff (1988*) also reported a third peak in foraging between midnight and dawn. Juvenile females, in contrast, tended to feed more during midday and to rest more at night.

Ralls and Siniff (1988*) found that all age or sex classes except juvenile females spent 36–37% of the time feeding; juvenile females spent 48% of the time feeding. Although these results indicate that juvenile females spend more time feeding than the others, individual variation within all age and sex classes was large, and analyses have not been done to determine if there are statistically significant differences among age or sex classes.

Each major activity (foraging, resting, grooming) takes place over a relatively long time. According to Loughlin (1977), the average duration of a foraging bout was 2.5 h, and at least three foraging bouts occurred within a 24-h period on the Monterey peninsula. In the San Simeon area, Ribic (1982b) showed that, on average, an otter was active three or four times a day (each activity period lasting about 3 h), followed by an inactive period of about 4 h.

A considerable amount of individual variation in 24-h activity rhythms and the amount of time allocated to foraging and resting appears to exist. Activity patterns may vary with the sex, age, and reproductive status (whether or not a female has a pup) of an otter, as well as its location in both California (Loughlin 1977, 1979; Ribic 1982b; Ralls and Siniff 1988*) and Alaska (Garshelis 1983). In the central and southern parts of the range in California, a greater degree of synchrony exists among resting otters, while individuals seem to vary the times and lengths of their foraging bouts from day to day. In the northern part of the range, females with older pups seem to spend as many or more daylight hours feeding than other animals, while females with very young pups may spend less time feeding during the day than other otters (Sandegren et al. 1973; K. J. Lyons personal communication; Riedman, Staedler, and Estes, unpublished data). In Prince William Sound, females with pups spend more time feeding than independent adults, probably because they must obtain additional food for their pups (differences in a mother's activity patterns in relation to the age of her pup were not discussed). Recently weaned pups in Prince William Sound also spend more time feeding than solitary adults or older juveniles, apparently because they are less adept at obtaining prey (Garshelis 1983).

Several aspects of activity cycles and time budgets may be influenced by such environmental variables as daily fluctuations in prey availability, geographical location, time of year, weather, and sea conditions in California and Alaska. Within a given stretch of coastline in California, specific segments (of perhaps 1–2 km) are characterized by variation in the amount of utilization by otters for different activities. Foraging is most common in some areas, for instance, while other areas are used primarily for resting (Miller 1974; Shimek and Monk 1977; Riedman 1984a*, 1984b*; Estes et al. 1986). Preliminary observations in California suggest that inclement weather and sea conditions (in the form of high winds, choppy seas, and heavy rain) may promote an increase in activity, inhibit the formation of resting groups in habitual rafting spots, and disrupt resting otters (Sandegren et al. 1973; Estes et al. 1986; Riedman, unpublished data). During windy or rainy conditions in Alaska, otters are more active, and raft size diminishes significantly (Garshelis 1983).

Diurnal peaks in foraging and resting activity have been attributed to several factors, including food availability, energy conservation, and the disruptive influence of wind or inclement weather. Estes et al. (1982) argued that crepuscular peaks in foraging by sea otters at Amchitka Island were related to their piscivorous behavior and the likely situation that fish are more available or vulnerable to predation near dawn and dusk. This conclusion was based on (1) the finding that in 584 foraging dives observed by Estes et al. (1982), all 60 fish that were seen to be eaten were captured during the crepuscular foraging peaks, and (2) the conclusion by Munz and McFarland (1973) that fishes are highly vulnerable to their predators near dawn and dusk because of visual impairment associated with shifts between photopic and scotopic vision. This conclusion was further supported by the fact that crepuscular foraging peaks were not observed at Attu Island or in Oregon waters, where fish were not eaten by otters. Garshelis et al. (1986) also reported that activity peaks varied among different parts of Prince William Sound in relation to differences in prey availability. At Green Island, where the otters fed mainly on mussels and infaunal bivalves, foraging activity peaked in day-light, whereas in northeastern Prince William Sound, where the otters fed extensively on the nocturnally active Dungeness crabs, foraging activity peaked at night.

Estes et al. (1986) suggested that the typically elevated afternoon peak in foraging that occurred in central California was related to diurnal patterns in wind intensity that occurred there; they also suggested that foraging peaks in California might be related to changes in food availability. Garshelis (1983) also reported that wind and inclement weather disrupted resting otters, which became more active and tended to spend more time foraging. Ralls and Siniff (1988*) suggested that the tendency of sea otters to rest at midday, when the intensity of solar radiation is greatest, should minimize heat production needed for thermoregulation and thus represents an energy conservation strategy. Ralls and Siniff (1988*) contended that the tendency for juvenile females to rest at night and feed during the day was consistent with this explanation. They believed that juvenile females were at a competitive disadvantage with adults for food, making it necessary to feed when the adults were resting.

The activity patterns of groups of otters in Alaska and

the individual activity patterns of California otters may also vary with respect to location of the otters. In Morro Bay, the 24-h activity pattern of males (N = 4) was bimodal, with one main feeding time in early morning and one in late afternoon (Ralls and Siniff 1988*). San Simeon females (N = 7) seemed to feed primarily in the morning, with no distinct peaks throughout the day and night (Ribic 1982b). Females in the Big Sur area (N = 12) had foraging peaks in midmorning, evening, and after midnight (Ralls et al. 1985*). In Alaska, Garshelis (1983) found that general activity patterns differed in two locations: Nelson Bay, an area recently occupied by male sea otters, and Green Island, an area otters had inhabited for over 25 years, which was occupied primarily by females and seasonally breeding males. Sea otters in one area of Nelson Bay rested during the day and foraged at night, while Green Island otters rested at night and fed during the day. At Green Island, males and females had similar average activity patterns, although females with older pups spent significantly more time feeding. The extensive nocturnal foraging in one area of Nelson Bay seemed to be related to the fact that Nelson Bay otters fed heavily on Dungeness crabs, which are nocturnal. In another area of Nelson Bay where otters fed primarily on clams, the activity cycle was crepuscular. The activity pattern of males that traveled between each area shifted to correspond to the general activity cycle characteristic of a particular area (e.g., diurnal versus nocturnal feeding).

Male otters in Nelson Bay allocated 23% less of their time to foraging but obtained an estimated 38% more calories per day than otters at Green Island, where food resources were apparently less abundant. In one male area in Nelson Bay, large Dungeness crabs provided 70% of the caloric intake of some otters, yet were captured on only 9% of the foraging dives.

In Prince William Sound, seasonal changes in activity were most pronounced in the female area at Green Island and seem to be related to changes in weather and length of daylight. The spring crepuscular activity peaks were displaced towards midday during the fall period of diminishing daylight, and eventually merged into an extended diurnal activity period during winter. Stormy weather conditions in fall and winter—besides causing an increase in activity—often caused otters to haul out and rest on land. Rest periods in autumn and winter occurred nocturnally in female areas, since solitary females generally hauled out when it was dark. In some male areas, the diurnal rest period was maintained throughout winter, which seemed to be related to the tendency of males to haul out together in large numbers during daylight. In one area, periods of rest and hauling out were synchronized with winter tidal conditions, since otters usually hauled out on mudbars exposed by low tide (Garshelis 1983).

Estes et al. (1986) reported that diurnal activity time budgets throughout much of the California range (from Point Piedras Blancas to Santa Cruz) were characterized by a high degree of similarity with respect to general geographic region and time of year. Data presented by Estes et al. (1986) indicate no relation between the percent of time allocated to foraging and the length of time a particular area had been occupied by sea otters. However, variation in the amount of food resources between male areas (in the newly occupied range peripheries) and female areas (in the center of the range) may not be as pronounced as the variation in food resources between newly occupied male areas and long-established female areas in Alaska.

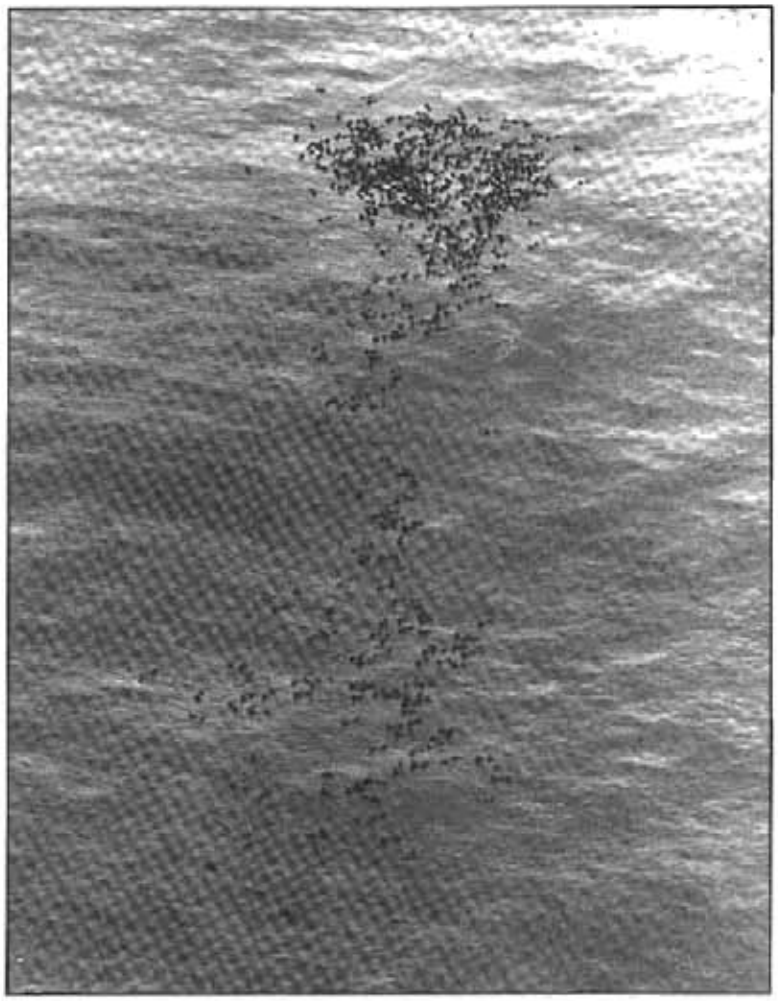
Social Organization and Behavior

Social Structure and Behavior

California sea otters generally rest singly or in small groups (called rafts) of two or more individuals, although larger rafts of twenty or more animals are not uncommon, especially among males (Miller 1974, 1980; Jameson, unpublished data). For instance, large groups of 40–50 otters were observed off Soberanes Point and offshore of Point Joe in the northern part of the range in the mid-1980's (Riedman, unpublished data). In a survey of six sites within the sea otter's range in California (excluding male groups at the range ends), groups of up to 12 were sighted (Estes and Jameson 1988). The frequency distributions of group size varied substantially among activity categories. Ninety-eight percent of foraging otters were alone (or with only their pups); the few other feeders were in groups of two. About 20% of those resting were alone; others were nearly evenly distributed among groups numbering 2 to 12. About 70% of all "other" otters (i.e., those classified as swimming, interacting, or grooming) were alone, with the rest occurring in twos or threes.

In Alaska, females also generally rest in small rafts, although males frequently rest in very large groups (Fig. 26). In Prince William Sound, the average maximum group size for females was about five animals in spring and two animals in fall (Garshelis et al. 1984). In contrast, Kenyon (1969) and Garshelis et al. (1984) observed male groups of up to 440 and 330 otters, respectively. Estes (1980) reported that K. B. Schneider observed a resting congregation of about 2,000 animals in an area devoid of kelp beds in Bristol Bay. At times, females with pups seem to form "nursery groups," in which most of the otters consist of resting mothers and pups in California (Riedman, Staedler, and Estes, unpublished data) and in Alaska (Ralls et al. 1985*). In Prince William Sound, Ralls et al. (1985*) observed one large group of 150 females in May, of which nearly two-thirds had pups.

Although otters commonly rest in tightly to loosely structured groups, foraging activity generally takes place



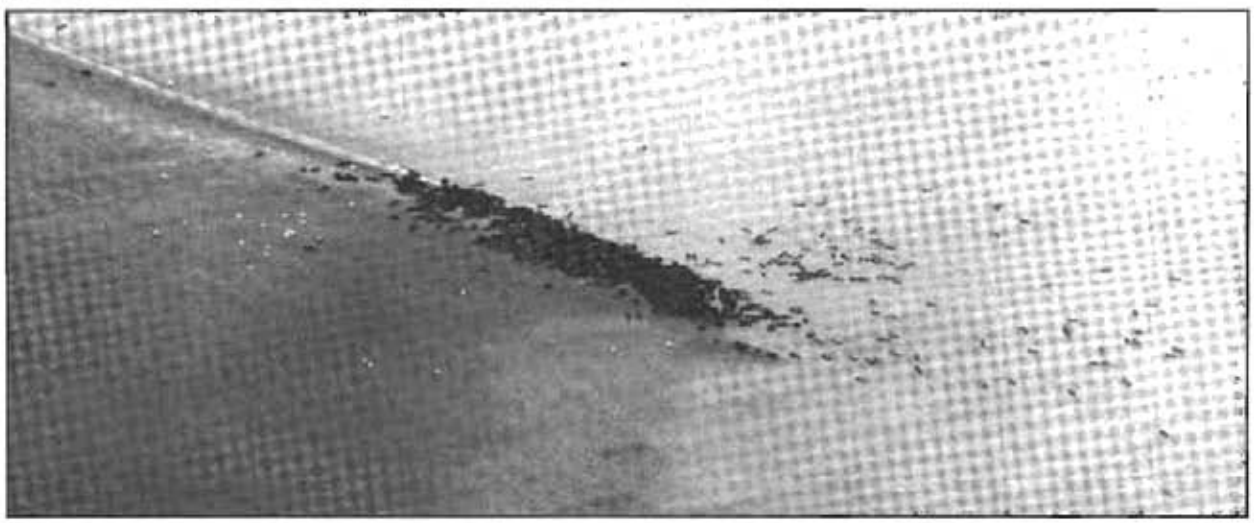


Fig. 27. Large aggregations of sea otters: (A) Western Bristol Bay (K. B. Schneider); (B) Prince William Sound (C. Monnett).

individually, often away from resting areas. Parturition and mating also tend to occur away from others. Mothers with newborn pups are frequently solitary and may rest apart from other animals for a short time following parturition (Sandegren et al. 1973; Jameson, personal communication). Sometimes territorial males tend to rest a short distance from the main female raft, while at other times they rest within the raft (C. Deutsch, unpublished data; Riedman, Staedler,

and Estes, unpublished data). In California, large white-headed males often seem to rest apart from male groups (Bolin 1938; Siniff and Ralls, unpublished data) and in Prince William Sound (Garshelis et al. 1984).

Many otters prefer particular rafting sites, and some return frequently to specific foraging areas as well (Loughlin 1977). Several individual males have been observed habitually resting in the same kelp bed in their respective territories over a period of years in California (Jameson 1989) and in Prince William Sound, Alaska (Garshelis et al. 1984). It is not known if otters recognize and preferentially associate or rest with the same individuals over time, although this aspect of social behavior is currently under investigation in the northern range of California (Riedman, Staedler, and Estes, unpublished data). In Prince William Sound, large male groups are characterized by a high degree of fluidity, with single otters or small groups often breaking off from one raft and joining another or forming a new raft. Interactions in male groups in California and Alaska include frequent mock fights and mock copulations (e.g., Garshelis et al. 1984). Occasionally, apparently altruistic behavior among otters in Prince William Sound and California has been observed during capture operations. Otters may accumulate around the netted animals, vocalizing, exhibiting distress, and sometimes attempting to free the captive otters, which increases the risk of being caught themselves (Garshelis et al. 1984; J. A. Ames, C. Deutsch, and M. Riedman, unpublished data). In California, mothers whose pups have been captured always remain near the boat and repeatedly vocalize. One mother actually climbed into a skiff to retrieve her pup as researchers were tagging it (Riedman and Ames, unpublished data).

Packard and Ribic (1982) compiled an ethogram for sea otters, classifying the behavior of otters observed in California and Alaska into 43 discrete action patterns. Each action pattern was associated with a number of broad functional activity categories, including resting, feeding, grooming, locomotion, and interactions. Some of the behavioral patterns occurred in the context of several activities. They concluded that, while the general activity categories of feeding and resting were distinctive enough to allow reliable identification by observers, the categories of grooming, locomotion, and interaction showed considerably more overlap. Table 5 summarizes and briefly defines the various action patterns occurring within each general activity category as presented by Packard and Ribic (1982).

Communication and Vocalization

The common and investigatory nosing between otters probably involves some form of scent recognition or other chemoreceptive means of communication. Sea otters that are entering, leaving, or simply swimming past a raft, an individual, or a mother and pup pair typically approach and make contact (usually nosing the other otter) with some or all of the otters within the group. Often the interacting otter performs a ritualized head movement termed the "head jerk" by Loughlin (1977). The head jerk involves a rapid, repeated lateral jerking of the head from midline to the side, as the otter nuzzles the recipient's head, chest, abdomen, or anogenital area. An adult male approaching a female will often direct the nuzzling at her genital area, possibly to determine if she is in estrus. A resting otter that is approached and contacted frequently remains relatively passive but may become alert, sniff the other otter, or briefly roll and rock in the kelp. Less common reactions on the part of the disturbed animal include tail block of the anogenital area and lunging and snapping at the intruder (Riedman, Staedler, and Estes, unpublished data).

Loughlin (1977) suggested that the head jerk behavior (or any type of relatively brief investigatory interaction) probably serves to communicate a variety of information. In this respect, an interacting or head-jerking otter might "greet" others, convey information about social status or intent, identify individuals, or determine sex and reproductive status. The nature of head-jerking interactions and other nonvocal forms of communication involving scent or behavioral cues are not well understood. Investigations focusing on nonvocal communicatory interactions among individually identifiable otters are currently in progress in the Monterey area (Riedman et al. 1988*).

Sea otters are generally not considered to be very vocal animals, but many of the adult vocalizations are soft and low in volume and therefore difficult to hear in the field. The loudest and most frequently heard vocalizations are produced by dependent pups. Pups often emit a high-pitched squealing call (sounding similar to the cry of a sea gull) when separated from their mothers. For instance, while the mother is underwater foraging or surfaces a distance away from the pup, the pup may vocalize repeatedly until making contact with its mother again. Mothers also vocalize quite loudly in response to the pup's cries but less frequently than pups do. There seems to be considerable individual variation in the acoustic characteristics of the vocalizations of individually identifiable mother and pup pairs (Staedler, Riedman, McShane, and Williams, unpublished data). Individually distinctive vocalizations would facilitate recognition and help maintain contact between a female and her pup.

Qualitative descriptions of sea otter vocalizations are provided by Fisher (1939), Kenyon (1969), and Sandegren et al. (1973). Kenyon (1969) described eight types of vocalizations: baby cry, scream, whistle or whine, coo, grunt, snarl or growl, hiss, and bark. The baby cry, which is produced by dependent pups, has been previously described. A scream is emitted by a mother separated from

Table 5. *Sea Otter (*Enhydra lutris*) behavioral action patterns occurring within general activity categories (from Packard and Ribic 1982).*

Behavior	General description
	Locomotion
Diving	From a belly-down position, the otter submerges head then feet (this dive usually used while feeding) *Low intensity:* arching of the back is minimal *High intensity:* otter leaps out of water with arched torso clearly visible
Folding dive	From a belly-up position, the rear feet and shoulders move toward the center of the body and the otter sinks backward into the water
Porpoising	As the otter swims just below the surface, the arched back repeatedly appears on the surface; general movement is in the forward direction (contrasted with a feeding dive) *Low intensity:* back just breaks the water surface *High intensity:* the otter repeatedly leaps out of the water with back arched in an inverted U
Rowing	Floating belly up, otter folds ventrally in a V shape then straightens: may be repeated; otter does not submerge
Sculling	Belly up, the otter moves along the surface propelled by movement of the tail and (or) feet
Sidestroking	The otter moves along the surface on its side; one foot may be waved above surface and head may be oriented toward an object
Swimming	Belly down; the head and back are visible moving along the surface
Underwater swimming	Body is totally submerged; the otter reappears at a distance at a location in line with previous direction of movement
	Feeding
Eating	While floating on the back, the forepaws are brought repeatedly to the mouth; object may be shoved into the mouth or pieces bitten off
Periscoping	Only the shoulders and head are visible above the water as the otter takes a few seconds to look around: usually precedes a high-intensity dive
Pounding	Rapid pounding movements are made onto the chest with or without an object held between the forepaws; a hard object may be balanced on the chest as the otter floats on its back; observer can often hear pounding
Submerging	Body is totally submerged; the otter reappears at a short distance not in line with previous direction of movement
	Grooming and Resting
Dunking	While floating on the back, the otter briefly dips the head in and out of the water; the chin is pushed forward, and the back of the head moves dorsally
Floating	Otter floats on the surface, belly up, rear feet up, no sculling, feeding, or grooming movements *Low intensity:* body motionless *High intensity:* slight movement of paws, head, or feet
Hanging	Belly down with both rear and head submerged; the arched back remains visible at the surface but motionless for a few seconds as the otter apparently grooms its belly
Logrolling	From a belly-up position, the otter rotates to the side like a rolling log; differs from rocking in that feet and paws are submerged
Looking	Belly up or on its side, the otter turns its head in various directions *Low intensity:* slow, occasional head turns *High intensity:* rapid agitated movements of head from side to side
Nibbling or licking	Mouth contact is made with some part of the otter's own body, in a nibbling or licking movement; commonly directed toward paws, belly, feet, tail
Rocking	From a belly-up position, the otter does a side roll with torso arched such that the feet and paws remain out of the water *Low intensity:* otter rocks 180° from side to side *High intensity:* otter rolls 360°
Rubbing	Rear feet rub some area of otter's own body *Low intensity:* both rear feet are rubbed slowly against each other in a "hand-washing" movement *High intensity:* rapid scratching movement of one foot directed toward back, neck, or side of body
Shaking	The head is rotated rapidly from side to side in a typical shaking movement; water flies; the muzzle may be outstretched
Somersaulting	Full 360° forward roll with the head tucked close to the belly; often only the curved back is visible until the head reappears at the end of the roll

Table 5. *Continued*

Behavior	General description
Stroking	Front paws repeatedly stroke some area of the otter's own body; may vary in intensity (rapidity of strokes); commonly directed toward chest, head, rear feet, belly, tail, flank, back
Tuckrolling	Head is brought toward chest but bent over to side while otter does a 360° side roll; intermediate between a somersault and a logroll
	Interaction
Begging	Otter remains near the side or head of a feeding otter; head is oriented toward the feeding otter; paws may or may not make contact
Biting	Otter closes jaw briefly on body of opponent; more intense and not as prolonged as grasping; may be repeated
Chasing	Rapid swimming with one otter behind another
Chinning	The otter swims slowly toward another and places chin on chest, belly, or near the head of the other otter
Clasping	Female uses front arms to hold pup to her chest; the pup is usually clasped around the chest, neck or head, and becomes limp
Gaping	Otter holds the mouth open, usually oriented toward partner's head *Low intensity:* brief duration, quality of a threat; may lunge without making contact *High intensity:* prolonged interaction, each otter parrying lunges made by the other
Giving	Holding food or another object, otter moves paws toward another otter; the object is relinquished when the other otter takes it
Grabbing	Jaws are closed on the body of another otter, maintaining prolonged contact Female grabs pup by neck Male grabs female by nose
Interfering	Otter attempts to move body between two other interacting otters
Lunging	Sudden forward body movement toward another otter *Low intensity:* no contact *High intensity:* lunge and nip, mouth contact
Mutual porpoising	Porpoising as described under Locomotion, synchronously or in close sequence with a partner moving in same direction
Nosing	Muzzle contact made with another otter; difficult to distinguish between nibbling and sniffing as the two movements are often intermixed
Pawing	With one forepaw, the otter reaches out to contact its partner; may be a shoving or patting movement
Riding	The otter places its body on the belly of another otter by swimming up slowly or by rolling sideways onto its partner; the other otter may move away or remain stationary *Low intensity:* front half of body covers head and front half of partner's body *High intensity:* full body contact
Shoving	Otter forcefully pushes another otter away with forepaws
Splashing	Belly up, otter moves partly submerged front paws away from body towards another animal, making water splash
Suckling	Pup has mouth in area of female's nipples *Low intensity:* suckling interrupted *High intensity:* continuous contact with nipples
Tumbling	Two otters roll over and over each other; the arched backs are usually visible, with an occasional glimpse of feet, tails, or heads. The body contact is highly variable: sometimes it appears they are wrestling, at other times making jaw contact
Wrestling	In a vertical position, two otters actively grasp each other with forearms around the head and shoulders, then twist to break the hold

her pup or by an adult in extreme distress. Whistling or whining sounds seem to be produced when the otter is mildly distressed or frustrated. For instance, older pups may whine when not allowed to suckle from their mothers (Riedman, personal observation). In another case, an adult male was heard to whine when he could not reach an estrous female who was hauled out on an offshore rock (Deutsch, personal communication). A group of 10 male California sea otters, recorded by California Department of Fish and Game biologists while the animals were being temporarily held together in an outdoor pen, frequently emitted extremely loud and unusual whines and high-pitched whistles, sounding somewhat like the abovewater whistling produced by dolphins.

Adults appear to make cooing sounds when "satisfied or content," according to Kenyon (1969), although these

sounds could also be used in other situations. Cooing appears to be generated in the throat, and the mouth is generally closed when the sounds are emitted. Cooing is heard among pair-bonded adults, as well as females grooming their pups. Kenyon (1969) also noted that females may coo "while eating food that is particularly pleasing." Soft grunting sounds also seem to convey satisfaction, according to Kenyon (1969), and may be produced when the otter is eating. Kenyon believed that grunting in the male is equivalent to cooing in the female. Growling or snarling sounds may be produced when a wild otter has been captured. Adults and dependent pups may hiss at humans when frightened after being captured. Barking is an uncommon vocalization. Kenyon (1969) heard a captive yearling male produce a high-pitched bark that trailed off into a whistle in apparent frustration when trapped in an empty pool. A study of the acoustic repertoire of wild California sea otters is in progress (Staedler, Riedman, McShane, and Williams, unpublished data).

Sexual Segregation

Sea otters exhibit a high degree of sexual segregation in California and in Alaska, which varies seasonally to some extent. Females and males generally rest in separate areas (often called female and male areas), with the exception of solitary, adult males that maintain territories within female areas in California (Peterson and Odemar 1969; Wild and Ames 1974; Loughlin 1977, 1979; Jameson, unpublished data) and in Alaska (Lensink 1962; Kenyon 1969; Schneider 1978*; Garshelis et al. 1984).

In Alaska, male groups are usually situated in areas with more abundant food resources but that are less protected from stormy weather than female areas (Schneider 1978*; Garshelis et al. 1984). 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. However, groups of juvenile males may occur well offshore in exposed areas in California (Ralls et al. 1988a*). In California (Peterson and Odemar 1969; Wild and Ames 1974; Benech 1981*; Estes and Jameson 1983a*) and in Alaska (Garshelis et al. 1984), male otters are the first animals to colonize unoccupied habitat; therefore, male areas generally occur at the edges of the range where expansion is taking place. The longest distance between male areas is about 150 km in Prince William Sound and about 120 km in California—where the populations are expanding—and 15 km or less at Amchitka Island—where the population is at equilibrium density.

Sex and Age Composition in California

Sex and age composition of the California population varies throughout the range in relation to general geographic location and time of year. The center of the range between Cayucos and Monterey is occupied primarily by females (all ages) and pups as well as territorial adult males (that move into female areas in summer and fall) and recently weaned juvenile males, some of which remain in female areas until they are 2–3 years old. The southern and northern peripheries of the range (south of Cayucos and north of Monterey) are inhabited mainly by nonreproductive, immature males throughout the year, and adult males that move out of the center of the range during the winter–spring nonbreeding season (Benech 1981; Estes and Jameson 1983a*; Jameson 1989). In some male groups at the southern end of the range in winter and spring, Jameson (1989) resighted 76% of the adult males that had occupied breeding areas near Point Piedras Blancas during the summer–fall period.

Solitary adult males—at least those from the Piedras Blancas area—return to the center of the range in spring and remain there throughout the summer and fall breeding season, when pup density is low and the number of estrous females is presumably high (Benech 1981*; Estes and Jameson 1983a*; Jameson 1989). Seasonal fluctuations in the sizes of peripheral male groups reflect these movements (Benech 1979*, 1981*; Estes, unpublished data). Peak male densities occur in female areas during late summer to early fall, when ratios of one male per six independent otters are found. Although the breeding season peaks from July to October in the Piedras Blancas area, adult males may be found in the center of the range from April to December. Along the northern Monterey peninsula, adult males occupy territories in female areas throughout the year (Loughlin 1977, 1980; Deutsch, unpublished data; Riedman, Staedler, and Estes, unpublished data; Lyons, personal communication).

While sexual segregation is well defined, distinct female and male areas both locally and throughout major portions of the range are not absolute. A nonterritorial male, for instance, may enter a female raft and interact with all females present (Loughlin 1977; Benech 1981*). Jameson (1989) found that some juvenile and subadult males may occupy female areas in the center of the range throughout the year, although they do not usually associate with adult females. Correspondingly, a few adult females may be found at either end of the range. Groups containing females and pups are located between Point Buchon and Point San Luis to the south (Benech 1981*) and near Santa Cruz and Sandhill Bluff to the north (Bonnell et al. 1983*; Estes and Riedman, unpublished data; Ames and Hardy, personal communication). Locally

established distinct male and female rafting sites may be separated by a minimum distance of 1–4 km or more, as they were in the late 1970's near Monterey (Loughlin 1977) and Point Buchon (Benech 1981*).

Sex and Age Composition in Alaska

Spatial segregation of the sexes also occurs throughout the range in Alaska. At Amchitka Island, at least four (and probably seven) geographically distinct male areas exist throughout the year (Estes, unpublished data). In the female areas, an estimated 95% of the animals caught in nets were females, while about 98% of the otters caught in male areas were males (Kenyon 1969). Sexual segregation also occurs in the U.S.S.R.'s Commander Islands (Marakov 1965).

Garshelis (1983) and Garshelis et al. (1984) investigated social organization of sea otters in Prince William Sound and found that predominantly male areas were located at the front of the expanding population, while females inhabited areas that had been occupied for longer periods. Animals captured in the male areas from May to August indicated a sex ratio of 97% males. Censuses conducted in female areas (at Gibbon Anchorage on Green Island) varied seasonally from a high of 33% males during the breeding season in July and August to <1% males in January and February.

Unoccupied habitat in Prince William Sound was initially colonized by large, solitary, and usually white-headed males. After months or even years, groups of younger males suddenly began to occupy the new areas. Garshelis et al. (1984) believed that older males routinely explored new potential breeding territories, often returning to established areas. The newly occupied areas were therefore eventually occupied by large groups of males, followed by females and pups after a period of years. Subsequent initial occupation of male areas by females may proceed slowly due to harassment of the few females by males in the form of food stealing and sexual interactions (Garshelis et al. 1984). As the proportion of sexually available females within the male areas gradually expands, the establishment of territories by dominant males, along with diminishing food resources, may collectively encourage most males to abandon the area and move into adjacent unoccupied habitat again (Garshelis et al. 1984).

According to Garshelis et al. (1984), it is to the female's advantage to limit her movements and remain in a sheltered area to raise her pup. Conversely, males not constrained by the burden of parental care are able to travel long distances to locate new habitat with abundant food resources but that is often highly exposed to rough seas.

Home Range and Movements

California

Home range has been defined as the area traveled by an animal during its routine activities (Jewell 1966). However, when considering home range and movements of sea otters, it is important to note that the dimensions of the home range may vary in space and time—that is, the home range sizes recorded in various studies can change according to the duration of the study and time of year. The importance of this point was emphasized by studies in Alaska (Garshelis and Garshelis 1984; Monnett and Rotterman 1988a*) and California (Ralls et al. 1988a*), both of which showed that sea otter home ranges consisted of several heavily used areas connected by travel corridors. In addition, sizes of home range and distance of movements depend on the portion of the range in which the animals were marked and subsequently observed. For example, distances of yearly movements by adult males tagged in the center of the range would probably be longer than those recorded for males tagged closer to the peripheral groups located near either end of the range. A general pattern observed by Ralls et al. (1988a*) in California for all age or sex classes was that individuals tended to remain in one area for extended periods, with occasional sudden long-distance movements. These movements occurred at all times of the year.

Males. The size of an adult male sea otter's home range seems to vary seasonally in California. Most of the time males remain in the same area; however, Ralls et al. (1988a*) found that both territorial and nonterritorial males occasionally make long-distance trips throughout the year. Short-period (18–36 h) movements of radio-tagged otters in the central and southern parts of the range averaged about 1 km for adult males and 2.3 km for juvenile males, and although the longest movement during this time was 47.5 km by an adult male, movements of >10 km were rare (Ralls et al. 1988a*). The area used by an individual in one day ranged from 10 ha to more than 1,000 ha. In the summer–fall period, which encompasses the breeding season in California, resident adult male sea otters (territorial and nonterritorial) have smaller home ranges than resident adult females (Loughlin 1977, 1980; Ribic 1982a; Jameson 1983a, 1989). The most comprehensive long-term study of male home range and movements was conducted by Jameson (1989), who visually monitored home range sizes and movements of 19 males tagged near Point Piedras Blancas over 6 years. He found that territorial adult males occupied a mean home range of 40.3 ha (N = 10; SE = 3.97) in the summer–fall period (at which time home range was considered equivalent to territory size), with a mean coastline length of 1.1 km (N = 13; SE = 0.44). The winter–spring (1 December to 30 May) mean home range size of territorial adult

males that remained in female areas was larger at 78.0 ha (N = 5; SE = 7.24), with a mean coastline length of 2.16 km (SE = 0.21).

The annual home range and life range sizes of adult, subadult, and juvenile males are substantially larger than those of adult and subadult females. The larger yearly male home ranges apparently reflect the long-distance male movements of 60–100 km or more to either end of the range that occur seasonally (U.S. Fish and Wildlife Service 1980*; Estes and Jameson 1983a*; Jameson 1983a; Jameson 1989). Jameson (1989) reported that 80.1 km (N = 13; SE = 4.17) was the mean seasonal distance traveled south from female areas in the vicinity of Point Piedras Blancas to peripheral male groups located near Point San Luis, although possible movements of up to 150 km were recorded for one adult male. The mean distance of 80.1 km was considered equivalent to life range, which was calculated as the number of kilometers of coastline known to have been used within the entire study area (Jameson 1989). As mentioned previously, however, the distance traveled seasonally by marked males is dependent on the current population distribution and the geographic location of the female area where each male was tagged and subsequently monitored.

Loughlin (1977, 1980) determined home range sizes along the Monterey peninsula, using radiotelemetry and visual observations conducted at intervals throughout the year. He found that territorial and nonterritorial males had a mean home range size of 35 ha (N = 4, SE = 8.8) and 44 ha (N = 7, SE = 13.4), respectively, while the mean home range size of adult females was substantially larger at 80 ha. A considerable amount of individual variation with respect to home range size was evident.

Using radiotelemetry, Ribic (1982a) assessed home range sizes of sea otters near San Simeon in fall 1978 and 1979. She categorized males as residents or nonresidents. Her results indicated that the home range sizes of resident males averaged 460 ha (N = 5, SD = 0.8), while the average home range size of resident females was 680 ha (N = 4, SD = 2.3). The comparatively larger home range sizes of resident adult males reported by Ribic seems due to differences in methods of calculating home range area and in the timing of Ribic's study period (early fall to early winter), both of which may have contributed to an overestimation of range. Both Ribic (1982a) and Jameson (1989) concluded that adult male California sea otters use two distinct home ranges (in the center of the range within female areas and at the end of the range within male groups), connected by a migration corridor that can be traveled in a brief time.

Ralls et al. (1988a*) implanted radio transmitters in seven adult males and five juvenile males in central California: four of these animals were associated with a male group in Morro Bay. All these males were relatively sedentary or moved only a short distance each day but occasionally made long-distance trips. The nonterritorial males in Morro Bay remained with the male group in this area most of the time, although they periodically moved a distance of roughly 40 km (to the San Simeon area) or about 10 km (to the Cayucos area where another male group was located).

Five territorial males near Point Sur spent most of their time within a small area of less than a few kilometers, although two males made long-distance trips (>20 km) away from their territories. One otter traveled from Point Sur to Moss Landing (a distance of about 60 km); however, he was shot and found dead near the mouth of the Salinas River. The other male, which maintained a territory near Pfeiffer Point, made one trip to an area just south of Grimes Point (8 km) and returned the following day. His second trip was to the Santa Cruz area, where he remained for about two weeks before returning to his territory. This 72 kilometers was the maximum distance traveled by a territorial male. Juvenile males tended to range farther from shore than did adult males.

Females. Less information is available concerning female home range size and movement patterns, although preliminary data indicate that compared to males, most adult females are sedentary. Near San Simeon, females may use an average of 18 km (N = 22) of coastline throughout their life (Jameson, personal communication). As mentioned previously, females seem to have smaller annual or lifetime home ranges than males; however, female home ranges are about 1.5–2 times larger than those of resident adult males during the breeding season. Ralls et al. (1988a*) found that adult females tended to make less extreme movements than males, and they traveled average distances that were intermediate in length compared with those traveled by males, since males either remained within a limited area or made long-distance movements. In California, 7 of 13 adult females, and 6 of 9 juvenile females moved maximum distances of >20 km.

Female otters are capable of traveling long distances, however, and three tagged females in California are known to have moved between the southern and northern parts of the range. One adult female tagged near San Simeon traveled a distance of 110 km north to Point Lobos (Jameson, personal communication), and a young female tagged near Cayucos moved a distance of ≥160 km to the northern Monterey peninsula (Riedman, Staedler, and Estes, unpublished data). The third adult female, who was originally tagged in Monterey, moved to San Simeon and returned to Monterey, a round-trip distance of about 280 km. The female was last sighted in Monterey in May 1976 after losing her 2-month-old pup in April. She was observed about 1 year later near San Simeon with a second pup of about 1–3 months, which seemed to have been weaned successfully. She was sighted about 7 months later in Monterey with a 1.5-month-old pup (Loughlin et al. 1981). Riedman et al.

(1988*) found that three tagged adult females routinely traveled across Monterey Bay between Monterey and Santa Cruz (a distance of 40–50 km, depending on the route taken) for over 4 years. These females tended to spend several months in each area, and often returned to Monterey to give birth and raise their pups. Reasons are unclear for long-distance travel by female sea otters in California, although Ralls et al. (1988a*) suggested that both adult and juvenile females travel long distances in search of areas where they can become residents. Some females may also move moderately long distances when weaning their pups (Riedman, Staedler, and Estes, unpublished data).

Dispersal of Juveniles. Dispersal and movement patterns of juvenile sea otters and newly weaned pups of both sexes are currently under investigation in the southern (Jameson, unpublished data), central (Ralls et al. 1985*), and northern (Riedman, Staedler, and Estes, unpublished data) ranges in California. Juvenile males seem to disperse greater distances from their natal areas than juvenile females, although there are exceptions to this pattern. Juvenile males in the San Simeon area seem to leave the natal area (which contains a high number of females and pups) from about 6 months to 2.5 years after weaning to join male groups at either end of the range (Jameson, unpublished data). Most juvenile males in the Monterey area leave the natal area immediately after weaning (Riedman, Staedler, and Estes, unpublished data). Jameson (1983b, and unpublished data) resighted two juvenile males 64–80 km south of their natal area within 2 weeks of weaning. At least 30% of the juvenile males tagged in the center of the range have been subsequently resighted in male groups (Jameson 1989). Seven juvenile males moved an average distance of 77 km (SE = 8.86) south of the natal area near Piedras Blancas to male groups. Another juvenile male, which weighed 12.3 kg at the time of capture, moved 187 km north from Piedras Blancas to join a male group near Soquel Point near Santa Cruz. Nearly 2 years elapsed between sightings of this male at Piedras Blancas and Soquel Point. Subsequent observations suggest that the male has remained in the Soquel Point area (Jameson, personal communication).

Ralls et al. (1985*) reported that the only newly independent juvenile implanted with a radio transmitter, a male, traveled more widely than any other adult sea otter monitored. The juvenile male was captured near Torre Canyon in mid-March. One month later he traveled slowly north, nearly to Yankee Point, after which he moved south to Pacific Valley. He then moved north again to Moss Landing (about 120 km from Pacific Valley), and soon moved south again. At latest report, the young male had not moved into a predominantly male area.

In contrast, recently weaned females often tend to remain near the area in which they were born. In the San Simeon area, one newly weaned female remained along a 5-km length of coastline for at least 2 years (Jameson, unpublished data). In Monterey, several tagged juvenile females remained in the vicinity of their natal area for at least 3–4 years (Riedman, Staedler, and Estes, unpublished data). In fact, since the late 1970's, many adult females weaned near Monterey still occupy the same area as their mothers, and some of these females have given birth to their own pups. Some degree of matrilineal kin relationships therefore seems to exist in this area. Riedman, Staedler, and Estes (unpublished data) observed several cases in which juvenile and adult offspring in the Monterey area interacted with their mothers in some way.

Daily Movements. Localized, daily movement patterns vary in relation to territorial status of males and whether or not females have a pup. Most movements away from habitual rafting sites are associated with foraging activity. Females without pups and males typically leave their resting areas, feed individually, and subsequently return to the resting areas. Territorial males generally forage within their territories or well offshore. Before territorial males return to their resting sites after feeding, they often patrol the boundaries of their territories and travel to female rafting areas, where they may investigate each female in the raft (Loughlin 1977, 1980).

Many females with pups, however, do not always return to their previous resting sites after foraging, but instead may continue to rest and feed, gradually returning to their original resting sites within 12–48 h (Loughlin 1977, 1980; Jameson, unpublished data; Riedman, Staedler, and Estes, unpublished data). Sandegren et al. (1973) found that the location of resting groups of females with pups changed daily. However, some females with pups in Monterey move short distances and rest in different sites from day to day, whereas others consistently rest and sometimes forage in the same areas, traveling very little (Riedman, Staedler, and Estes, unpublished data).

Alaska

Movements and home range sizes of Alaskan sea otters were first investigated in the Aleutian Islands by Lensink (1962) and Kenyon (1969), who tentatively concluded that a female's home range included 8–16 km of coastline and that males may have larger home ranges than females. Lensink (1962) reported that movements in the Aleutian Islands were related to season and weather conditions. In the Commander Islands of the Soviet Union, movements of otters were also related to weather, season, time of day, and human-caused disturbance (Barabash-Nikiforov 1947; Barabash-Nikiforov et al. 1968). As in California, movement patterns and home range sizes of Alaskan otters reported in various studies probably depended on the location of the study area, time of year, and duration of the study.

Males. Studies conducted by Garshelis (1983), Garshelis and Garshelis (1984), and Ralls et al. (1985*)

provided detailed information on movement patterns of sea otters in Prince William Sound (Fig. 27). Comparable information is not available from other areas of Alaska. Seasonal male movements seemed to vary in relation to the time each study area was occupied by otters. In a new area where food resources were relatively abundant, territorial males were fairly sedentary and traveled only short distances—generally <25 km (Ralls et al. 1985*). In contrast, Garshelis et al. (1984) recorded long-distance movements of >100 km for five adult territorial males that left Gibbon Anchorage at Green Island, presumably an area with reduced food resources that had been occupied by otters for a long time. The males traveled to male areas in northeastern Prince William Sound, where food was more abundant. These differences may simply occur because newer habitats were closer to peripheral male groups than areas that were occupied longer. As in California, some males moved between male and female areas throughout the year.

Males in northeastern Prince William Sound also moved to and from male areas relative to season, weather conditions, and boat traffic associated with commercial fisheries (Garshelis and Garshelis 1984). For instance, male groups were present in Orca Inlet only in winter. Throughout much of the remaining year, heavy boat traffic in Orca Inlet apparently disrupted the otters and caused them to move. Males were also attracted to Orca Inlet mudbars, where they frequently hauled out during stormy winter months. Unlike females, males often traveled in groups between areas (Garshelis and Garshelis 1984).

As in California, the home ranges of male otters in Prince William Sound consisted of peripheral male areas and breeding territories within female areas, connected by travel routes or migration corridors. Seasonal home range sizes in male areas seem to vary in habitat characteristics. For example, Garshelis and Garshelis (1984) reported that males in Nelson Bay had significantly larger home ranges ($\bar{x}$ = 11.0 km; SE = 0.7; N = 13) than Simpson Bay males ($\bar{x}$ = 4.6 km; SE = 0.5; N = 4). They attributed this to the fact that Nelson Bay is larger than Simpson Bay, and provides more available habitat with greater distances between feeding and resting areas.

Garshelis and Garshelis (1984) suggested that annual and lifetime home ranges of males may be larger than those of females and may include most of Prince William Sound. The seasonal and sexual variation in home range size may be similar between Prince William Sound and California in that males have larger annual or lifetime home ranges—but smaller seasonal home ranges (consisting of defensible territories)—than females.

Females. Female movement patterns in Prince William Sound seem to vary in relation to such interrelated factors as duration of occupation (by otters), weather conditions, season, reproductive status, and age of pup. At Green Island, where the population has been long established, females with large pups began moving into Gibbon Anchorage in early fall, apparently because shallow-water feeding areas in Gibbon Anchorage facilitated independent foraging by pups. Before August, females with small pups too young to forage successfully remained in deeper water with more abundant or higher quality food. In fall and winter, stormy weather also apparently caused independent females and mothers with small pups to move into protected areas such as Gibbon Anchorage (Garshelis and Garshelis 1984).

Accordingly, the size of females' home ranges at Green Island appeared to vary as a function of reproductive status and age of pup (Garshelis and Garshelis 1984). Females without pups and those with pups 3 months old had larger average home range sizes ($\bar{x}$ = 4.8 km; SE = 0.9; N = 7 and $\bar{x}$ = 4.5 km; SE = 1.8; N = 2, respectively) than females with pups older than 3 months ($\bar{x}$ = 1.0 km; SE = 0.2; N = 6). Garshelis and Garshelis (1984) speculated that the more sedentary behavior of females with large pups allowed the pups to become familiar with specific feeding areas. Such feeding areas were often located within male territories, so that constant attempts by the male to prevent the pair from leaving also may have influenced the female's sedentary behavior. Independent females and those with small pups were not restricted to shallow feeding areas. Garshelis and Garshelis (1984) believed that some females moved more extensively in other areas, so that life ranges were larger than those recorded in their study area.

Through the use of radiotelemetry, Monnett and Rotterman (1988a*) found that adult female sea otters in Prince William Sound moved distances of 30–80 km, traversing expanses of deep water and moving between major bays and fjords. In contrast with central California, where adult females tend to remain fairly sedentary (except for occasional long-range movements), the adult females in Prince William Sound undertake extensive seasonal movements. These females bear their pups and nurse them in the central part of the sound, wean their pups and copulate in the deep fjords of the north-central part of the sound, and then move far to the east to spend winter. These complex patterns, compared with those documented in central California by Ralls et al. (1988a*), are correlated with—and possibly caused by—differences in habitat complexity between the two areas; Prince William Sound may present a more variable large-scale mosaic of habitats to sea otters, and the otters may benefit by moving among the mosaic patches to meet specific needs.

Dispersal of Juveniles. As in California, juvenile male sea otters in Prince William Sound tend to disperse greater distances than juvenile females. Monnett and Rotterman (1988a*) found that juveniles tended to move away from the natal area immediately after weaning, although, on average, males moved farther than females; the greatest distance traveled by a juvenile male from his natal loca-

tion in Prince William Sound was about 120 km; the greatest distance moved by a female was 38 km. Movement patterns of recently weaned females were similar to those of older independent females, although the average home range sizes of juvenile females ($\bar{x}$ = 7.6 km; SE = 1.6; N = 3) were larger than those of solitary adult females ($\bar{x}$ = 4.8; SE = 0.9; N = 7; Garshelis and Garshelis 1984).

Garshelis et al. (1984) found that male dispersal from female areas often took place shortly after weaning; however, some males may have delayed dispersal until 2 years of age or made interim stops on the way to male areas. Despite its unfamiliarity with northeastern Prince William Sound, one juvenile male born near Green Island traveled 100 km to a male area. Newly independent males may follow older males to distant male areas and remain there at least until breeding age (Garshelis et al. 1984).

Daily Movements. As in California, otters in Prince William Sound and the Aleutian Islands use different areas for resting and feeding (Lensink 1962; Garshelis and Garshelis 1984). Daily home ranges of males in northeastern Prince William Sound were clustered within five separate bays or coves. Although males moved among these areas, they tended to remain in the same area on any given day (Garshelis and Garshelis 1984). Daily home ranges of females near Green Island were clustered within six areas delineated by distinct topographical boundaries. Females accompanied by pups remained in these areas longer than solitary females. Females moved among areas somewhat more frequently than the males, probably because male areas were larger and separated by greater distances than female areas. The movement of both sexes between areas tended to occur irregularly (Garshelis and Garshelis 1984).

Summary of Movement Patterns

In conclusion, information from studies of sea otters in Alaska and California suggested that complex relations exist between activity budgets, movement patterns, habitat characteristics, and the probability of survival, and that these may differ fundamentally between juvenile male otters and juvenile female otters. Postweaning dispersal tends to be greater in juvenile males than females. Although the reason for this difference is not known, it probably results from the sea otter's polygynous mating system and the fact that adult males maintain territories in most areas inhabited by adult females. Whether the territorial males compete for food, females, or both is not known, although it seems likely that males compete for access to mates. However, aggressive behavior by territorial males seems to drive juvenile and subordinate males away from the female areas. The result seems to be that juvenile males are forced into areas not inhabited by territorial males, whereas juvenile females are not. These juvenile males ultimately join male groups, whereas juvenile females tend to remain nearer the area of their birth. In central California and Prince William Sound, male areas tend to occur at the peripheries of the ranges. This is also true of growing populations in the western Aleutian Islands (Estes, unpublished data). These male groups are spatially labile, moving gradually outward as adult females expand their range. The distance separating male groups gradually becomes greater, requiring increasingly longer distance dispersal by juvenile males weaned near the center of the range. However, these peripheral groups are juxtaposed with areas in which food resources are comparatively abundant because they have not been heavily exploited by foraging sea otters. Therefore, we conjecture that juvenile males experience higher travel costs than do juvenile females; however, males also benefit from foraging on more abundant food resources. Sex-specific differences in activity budgets and probabilities of survival seem to be related to these movement patterns. Compared with juvenile males, females spend more time foraging and suffer higher rates of mortality (Monnett and Rotterman 1988b*; Ralls et al. 1988a*; Siniff and Ralls 1988*).

These patterns, implicitly assumed to be species characteristics, have been variously interpreted. Ralls et al. (1988a*) suggested that sex-related differences between juvenile males and females may serve to benefit male reproductive opportunities and female feeding opportunities—that is, the extensive movements of juvenile males may allow them to search for and assess available territories, whereas the more limited movements of juvenile females may result in a detailed familiarity with food resources within the smaller, natal area. Monnett and Rotterman (1988b*) speculated that these differences are the consequence of higher parental investment in males than females, as predicted by Trivers and Willard (1973). Garshelis et al. (1984) suggested that young males aggregate in male areas because of social benefits derived from gregariousness. Each of these explanations presumes sex-related social benefits to the observed patterns, which may be true. However, none of the explanations recognizes that (as we suggest) the patterns are derived from adult male aggression, a fundamental outcome of the sea otter's polygynous mating system and not unlike the juvenile dispersion patterns observed in numerous species of polygynous mammals.

Limited data on sex-specific distribution and mortality patterns from Amchitka Island suggest to us that whereas behavioral processes related to the sea otter's polygynous mating system may be fundamental to all or most sea otter populations, some of the behavioral and demographic consequences of these processes may vary, depending on whether the population is at or near carrying capacity or has access to unoccupied habitat into which it can grow. Unfortunately, we have no data on activity budgets or movement patterns for different age or sex categories at Amchitka Island. However, results from Kenyon's (1969)

long-term studies at Amchitka indicate two intriguing differences from the patterns reported from central California and Prince William Sound. One difference is that male groups are interspersed within female areas (there are no range peripheries where they could form), and these male areas tend to be separated by fairly short distances (11–19 km; Kenyon 1969; Estes, unpublished data). All male areas that are presently known at Amchitka Island occur near exposed points with extensive shallow habitat extending offshore. We presume that, compared with central California and Prince William Sound, dispersing juvenile males are required to travel shorter average distances before encountering a male group, and these male groups are not juxtaposed with rich food resources. The costs of male dispersal may therefore be less than they are in expanding populations, but juvenile males derive no foraging benefits by occupying these areas. Indeed, male groups may be constrained to form in habitats unsuitable for adult females. The second difference is that the juvenile mortality rate is higher in males than females, based on Kenyon's (1969) analysis of beached carcasses. As Kenyon pointed out, this could be due to biases in sex determination. However, a slightly male-biased sex ratio persists even when all the indeterminate juveniles from Kenyon's sample are assumed to be females. Although more data from Amchitka Island are needed to substantiate these patterns, we expect to find fundamental sex-related differences in juvenile activity, movement, and survival between sea otter populations that are still growing and those that are at or near equilibrium.

Reproduction

Seasonal Phases of Breeding

California

Although mating and pupping among sea otters take place throughout the year in California, a peak period of pupping tends to occur from January to March (Fisher 1940; Vandevere 1970*, 1972*, 1979*; Sandegren et al. 1973; Estes and Jameson 1983a*; Siniff and Ralls 1988*; Ames, unpublished data; Jameson, unpublished data). A secondary but equally pronounced pupping peak appears to occur in late summer to early fall (Siniff and Ralls 1988*; Jameson, unpublished data: Riedman, Staedler, and Estes, unpublished data; Vandevere, personal communication). This second pupping peak may stem from elevated pup mortality during the winter pupping peak. The rationale for this suggestion is as follows: Because the probability of mortality declines with increasing age of the pup (Jameson, personal communication; Riedman, Staedler, and Estes, unpublished data), the greatest incidence of pup mortality would occur during winter, when small pups are most numerous and storm activity is greatest. Furthermore, females tend to come into estrus soon after losing their pups (Riedman, Staedler, and Estes unpublished data); if females successfully mate shortly thereafter, they would give birth in early fall, after a gestation of about 6 months (Wendell et al. 1984).

The proportion of females that lose their young pups seems highest in winters with severe storms or prolonged inclement weather and sea conditions. The late summer to early fall secondary pupping peak may therefore be more pronounced during years when winter storms are especially severe. For example, due to anomalies associated with the 1982–83 "El Niño" event, winter 1983 was atypically severe in the high frequency and severity of storms, large swells, and the resultant reduction in the kelp canopy from late January to April (Dayton and Tegner 1984). The number of pups counted throughout the range in spring 1983 was low (9.6% of the total population), compared with spring 1982 (16.5%) and 1985 (17.4%), suggesting that pup loss was high in winter 1983 (California Department of Fish and Game and U.S. Fish and Wildlife Service, unpublished data). In addition, there appeared to be a sudden and pronounced increase in mating activity during April and May of 1983 in the Soberanes Point area, as would be expected if a high proportion of females lost their pups during the preceding winter (Riedman, unpublished data). In spring 1984, the proportion of pups in the population was still low (9.4%), indicating that the suggested shift in reproductive events persisted for 2 years in the population.

Indirect evidence suggests that the mating season peaks from July to October in the southern part of the range near San Simeon, although moderate densities of adult males occur within female areas from April through December there (Jameson 1989). In the Monterey area, the frequency of mating activity among territorial males generally appears to increase from September through November (Deutsch, unpublished data; Riedman, Staedler, and Estes, unpublished data). The general yearly reproductive pattern in California therefore consists of a winter pupping season and summer–fall breeding season.

Alaska

Mating and pupping also occur throughout the year in Alaska. However, the breeding and pupping seasons peak about 2–3 months later in Alaska than in California. In addition, reproductive events seem to be temporally synchronized to a greater degree in Alaska than in California. The mating season in Prince William Sound peaks during September and October (Garshelis et al. 1984). In Prince William Sound, most pups are born in May; the peak of weaning is about mid-November and, in contrast with central California, few births occur in late fall and winter. There are no sex differences in the seasonal distributions

of birth or weaning times (Monnett and Rotterman 1988b*).

Studies conducted at Amchitka Island in the 1960's by Kenyon (1969) indicated that, similar to Prince William Sound, the pupping season peaked in early summer, whereas the mating season peaked in late fall and winter. Schneider's (1973a*) extensive study and analysis of sea otter reproductive tracts from the central and western Aleutian Islands indicated a mating peak during October–December and a pupping peak in May and June. However, the seasonal pattern of increase and decline in both breeding and pupping was thought by Schneider (1973a*) to be broad, spanning perhaps 4–5 months each.

Mating Behavior

Sea otters seem to exhibit a variable degree of polygyny, although many aspects of their mating system remain unclear. A male may copulate or form a pair-bond with several females successively throughout the year. Females often mate with only one male during a given estrus period, especially if they form pair-bonds. However, some females occasionally mate with more than one male during one estrus. Garshelis et al. (1984) observed at least one female that copulated with two different males in Prince William Sound, and Riedman, Staedler, and Estes (unpublished data) documented several cases in which a female mated or formed a pair-bond with two or more males during estrus. Mating may take place with or without the formation of pair-bonds in California (Vandevere 1970*, 1973a*; Loughlin 1977, 1980; Deutsch, personal communication) and in Prince William Sound, Alaska (Garshelis et al. 1984). In contrast, Kenyon (1969) observed copulation only during the 3 to 4 days of pair-bonding in the Aleutian Islands, although his observations probably were less extensive than those in California or Prince William Sound.

The duration of pair-bonding typically lasts from 1–4 days, with a mean of about 3 days, in California (Vandevere 1970*; Deutsch, unpublished data; Riedman, Staedler, and Estes, unpublished data) and in Alaska (Kenyon 1969; Garshelis et al. 1984). However, the pair-bonding period has been observed to last up to 10 days in the Monterey area (Riedman, Staedler, and Estes, unpublished data). During pair-bonding, the mated pair conduct all activities in close proximity. Several copulations may take place throughout pair-bonding (Kenyon 1969; Vandevere 1970*; Deutsch, personal communication; Riedman, Staedler, and Estes, unpublished data). However, Garshelis et al. (1984) observed up to four subsequent copulations only on the day of initial copulation, even though in some instances the pair-bonds persisted up to 3 days. The pair-bond is often terminated by departure of the female from the male's territory, during which time the male may attempt to prevent the female from leaving (Kenyon 1969; Vandevere 1970*, 1973a*; Garshelis et al. 1984; Deutsch, personal communication). Formation of pair-bonds with estrous females may be advantageous to males, since it prevents females from copulating with other males and because the repeated copulations that occur during pair-bonding increase the likelihood of successful insemination.

It seems that a female's sexual receptivity ends after pair-bond dissolution, suggesting that estrus, on average, lasts 3–4 days. In Prince William Sound, previously pair-bonded females did not interact sexually with other males after leaving their mate's territory. Other females remained within their mate's territory for up to 24 days after copulation but did not interact sexually with the territorial male (Garshelis et al. 1984). In California, females usually do nor appear to be sexually receptive after pair-bonding, whether or not they subsequently remain in their mate's territory (Deutsch, personal communication; Riedman, Staedler, and Estes, unpublished data). In Monterey, however, several cases have been observed in which a female continued for several weeks to mate or pair-bond with various males, suggesting that her estrus period was prolonged until she was successfully inseminated (Riedman, Staedler, and Estes, unpublished data). Most of these females were aged, which leads us to speculate that aged females may experience difficulties conceiving or may miscarry soon after conception.

Although pups still may be present with females during subsequent sexual interactions, successful copulation seems to rarely or never occur before the pup has been weaned. Females with large pups are sometimes closely "tended" by a male for several days. During the tending period, the male occasionally swims, feeds with, and otherwise interacts with the female and pup pair, and occasionally the male may attempt to copulate with the female. In Prince William Sound, Calkins (1972), Calkins and Lent (1975), and Garshelis et al. (1984) observed mother and pup pairs that were tended by males for a number of days, when, at various times, copulation was unsuccessfully attempted. Garshelis et al. (1984) reported that 42% of sexual interactions involved mothers with a pup. Kenyon (1969), also, observed males sexually interacting and attempting to copulate with a female accompanied by a pup; copulation was never successfully completed.

In California, tending by territorial males of mothers with large pups—and sometimes with small pups (<3 months)—has been observed on many occasions. The males generally follow the pair closely for a variable period (several minutes to a few hours) on a given day, often tending the same pair for several days. It is not clear why males would tend mothers with small pups, since

they would not be sexually receptive. Possibly the females were experiencing an incomplete estrus cycle (one that would not result in pregnancy), such as that described by Schneider (1978) in Alaska. Males often engage in nuzzling, biting, tumbling, and rough play with the female and her pup. Frequently during such interactions, pups seem to exhibit distress, vocalizing repeatedly and trying to climb onto their mother or to pull her away from the male. Occasionally, pups seem to interact in a playful manner with the male. The mothers generally attempt to swim away from the attending male. As in Alaska, copulations are occasionally attempted but are not successful (Riedman, Staedler, and Estes, unpublished data; Deutsch, personal communication).

Copulation occurs exclusively in the water and is usually initiated by the male, although females have been observed to initiate copulatory activity on occasion (Kenyon 1969; Deutsch, personal communication). Coitus is preceded and followed by mutual nuzzling, pawing, tumbling, and otherwise highly synchronous activity. During a typical copulation, the male clasps the female from behind and grasps her face or nose with his teeth, after which the pair alternately rests and vigorously spins around their longitudinal axis (Kenyon 1969; Vandevere 1969*, 1970*). Copulations commonly last 15–30 min, although duration is variable. In Prince William Sound, Garshelis et al. (1984) observed copulations lasting from 15 s to 38 min. Kenyon reports that copulation may last up to 35 min; in California, most copulations have been reported to last 20–30 min, although briefer copulations have occurred (Estes, Staedler, and Riedman, unpublished data; Duetsch, personal communication; Jameson, personal communication). There are no reliable cues to enable a field observer to determine if and when ejaculation occurs. Interestingly, the briefer copulations frequently take place with young females (Garshelis et al. 1984).

A female's bloody nose indicates recent mating activity (Brosseau et al. 1975), and the resultant scars may aid in

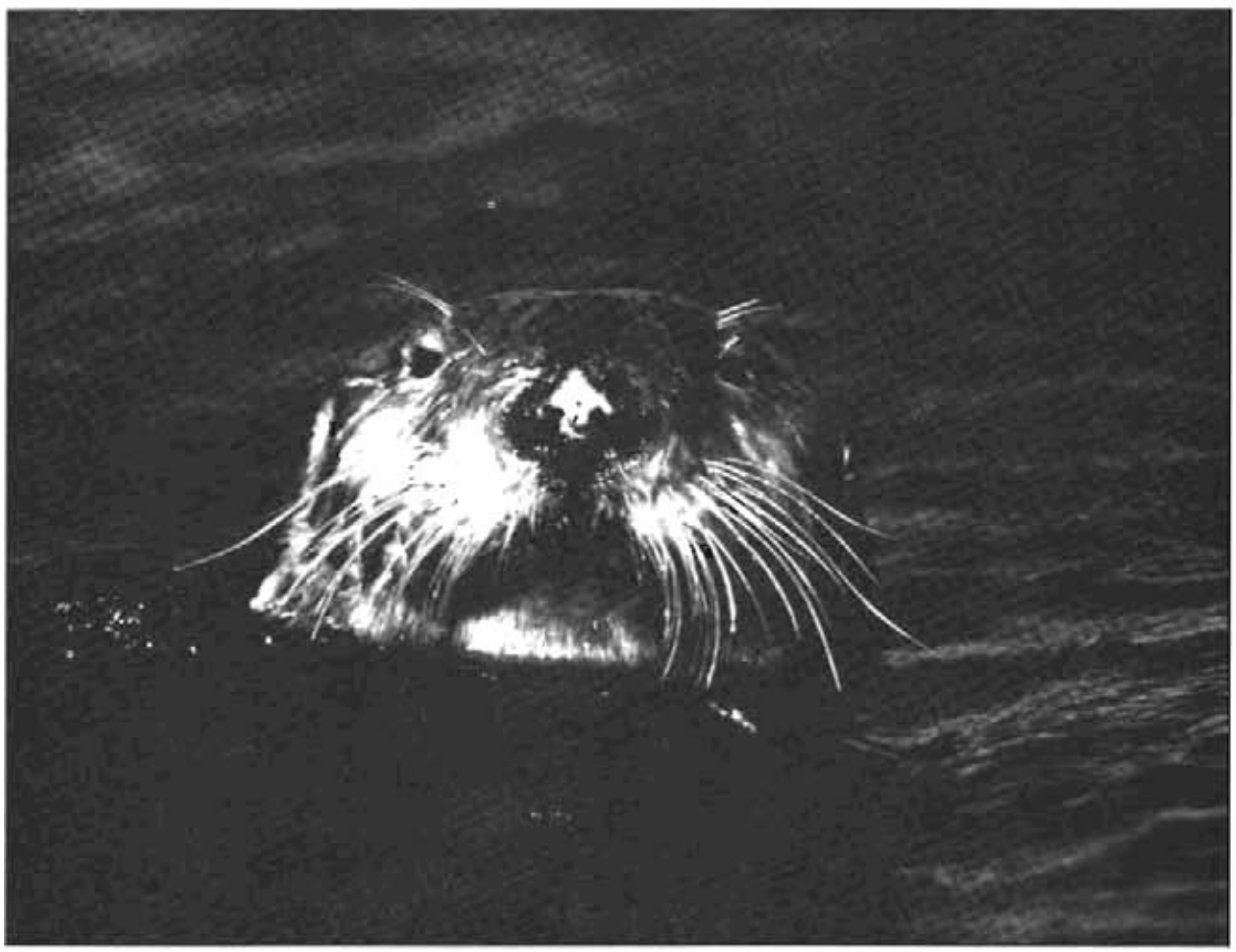


Fig. 28. Female California sea otter with distinctive nose scar acquired during mating activity (F. Bavendam).

individual identification of adult females (Foott 1971; Fig. 28). Nose scars also indicate that a female is sexually mature, although some multiparous females have very little or no scarring. Interestingly, certain territorial males in the Monterey area tended to be consistently rougher on females' noses than other males were during mating. These females often sustained extremely serious nose and facial lacerations. In two cases, most of the nose was removed (Ames, Riedman, and Staedler, unpublished data). Ames et al. (unpublished manuscript) reported that complications stemming from severe nose or facial injuries inflicted during copulation may cause death in some females, and they speculated that some of the youngest and oldest females may be drowned during vigorous mating bouts. Garshelis et al. (1984) observed one female that died shortly after a forced copulation in Prince William Sound. On two separate occasions, one tagged male who held a territory along the northern Monterey peninsula was observed copulating with a tagged dead female. In the first case, he appeared to have accidentally killed her during an attempted copulation, at which time she was accompanied by a large pup approaching weaning age. In the second case, it was not known whether the male killed the female, but she had a pup that was much too young to be weaned (Riedman, Staedler, and Estes, in preparation). Jameson (personal communication) also observed a male holding and guarding a female carcass.

Reproduction in the Male

Reproductive Physiology

Although limited in scope, studies of male reproductive physiology have taken place primarily in Alaska. Schneider (1978*) concluded that Alaskan males did not reach sexual maturity for 5–6 years, and became active breeders several years later. Males 2–6 years old were rarely found in female areas during the breeding season (Schneider 1972b*). Garshelis (1983) found that no males aged <6 years bred successfully. According to Johnson (cited in Ralls et al. 1983), Alaskan males did not hold territories until 8–10 years of age. The onset of sexual maturity and the age that males become reproductively active in California has not been established. Green (1978) suggested that California males reach sexual maturity at about 5 years but probably do not establish territories or actively breed for 2–3 or more years after reaching puberty. Spermatogenesis in the Alaskan population occurs throughout the year, although individuals probably produce sperm on an intermittent basis (Lensink 1962). Old males shown no signs of diminished sperm production (Kenyon 1969).

Territoriality

California. In California, adult males establish and maintain territories in areas of high female density, seasonally (Vandevere 1970*; Jameson 1989) and, sometimes, throughout the year (Loughlin 1977, 1980; Riedman et al. 1988*; Deutsch, personal communication). Territorial maintenance is probably associated with the availability of good habitat (e.g., food, protected resting sites) and an adequate number of estrous females, both of which vary seasonally.

The best territories in California include canopy-forming kelp (especially *Macrocystis pyrifera*), sheltered areas for resting, and adequate food resources. The density, distribution, and configuration of the kelp canopy, as well as topographical features of the coastline, may play a role in delineating territorial boundaries. In the southern part of the range, the seasonal kelp canopy reduction that occurs in winter and spring may diminish the potential number of male territories in preferred locations and intensify competition for the remaining available sites. Jameson (1989) found that the kelp canopy in an area near Point Piedras Blancas diminished from 150 ha in late summer to 8.3 ha during the following winter, with most winter kelp concentrated in one-fifth the area of the summer kelp distribution.

The number of potentially sexually receptive females varies seasonally, as does the density and distribution of reproductively active males that maintain territories within female areas. Observations from the southern part of the range (Jameson 1983b) showed that throughout the summer–fall breeding season, when the number of estrous females was potentially high, males held territories within female areas. Jameson (1989) found that the number of territorial males in female areas peaked in late summer, with a mean arrival date of 28 May and a mean departure date of 21 December. During the winter–spring pupping season, most adult males leave female areas to join male groups at the southern end of the range, evidently because of increased competition for suitable territories, as well as the presence of fewer estrous females at this time of year.

In contrast, Loughlin (1977, 1980) found that territorial males remained in female areas throughout the year in the northern part of the range near Monterey. He identified seven territorial males and reported that at least two of these maintained territories continuously for 1 year or longer. Recent observations of territorial males along the northern Monterey peninsula confirmed Loughlin's findings that territories are maintained throughout the year in this area; many of these males have remained in their territory for several years (Riedman et al. 1988*; Deutsch, personal communication).

In summary, whether or not territories are maintained on a year-round or seasonal basis in female areas may be related to the following variables: topography, exposure to storms, abundance and distribution of kelp beds, abundance of food resources, number of sexually receptive females, and distance from peripheral male groups. The length of time throughout the year that territories are

maintained may vary depending on reproductive benefits or mating opportunities compared with costs of territorial maintenance. There may be more opportunities for males to mate throughout the year in Monterey. As Jameson (1989) pointed out, the northern side of the Monterey peninsula is more sheltered from storms than his study area near Point Piedras Blancas, and the seasonal kelp canopy reduction in Monterey seems to be not as pronounced. In addition, the kelp beds off northern Monterey do not extend as far offshore as they do in the Piedras Blancas area, and onshore–offshore "layering" of territories does not occur in Monterey Bay.

Individual adult males show long-term site fidelity, returning each year to the same territory (Loughlin 1977; Jameson 1989). Several males near Point Piedras Blancas held the same territory each breeding season for up to 6 years, and each territorial male habitually rested within several meters of the same site after returning to his territory (Jameson 1983b, 1989). Along the northern Monterey peninsula, two males held the same territories for at least 7 and 8 years before their deaths, and another male occupied a territory he has held for at least 9 years (Deutsch, unpublished data; Riedman, Staedler, and Estes, unpublished data).

Territorial males near Monterey seem to rest exclusively within their territories, although they sometimes leave their territories to feed or search for estrous females, occasionally trespassing through another male's territory. For instance, territorial males are sometimes observed feeding beyond the edge of the kelp bed up to several hundred meters offshore of their territories (Deutsch, unpublished data; Riedman, Staedler, and Estes, unpublished data). Territorial males have also been observed in another male's territory attempting to drag a female back to the first male's territory; two males seem to employ this mating strategy more often than other otters (Deutsch, unpublished data; Riedman, Staedler, and Estes, unpublished data). Females and dependent pups are allowed to rest within the territorial boundaries while other males generally are not. Resting females, however, are sometimes disturbed by a resident male attempting to steal food or initiate mating activity. Transient males are usually permitted to pass through or feed within a territory.

Males often patrol the boundaries of their territories, sometimes seeming to advertising their presence with pronounced displays of splashing and grooming. Fights involving one or more territorial males are seen infrequently; they typically involve lunging, pushing, and shoving motions directed toward the opponent's chest, face, and neck (Fisher 1939; Vandevere 1970*; Loughlin 1977, 1980).

The elements of mating success in California males (i.e., correlations with size, age, and territory quality) have not been determined. Jameson (1989) found that the weights of territorial males averaged 30 kg (N = 10), which is similar to the overall average weight of 29 kg reported for adult males in California (Woodhouse et al. 1977*; Ames, unpublished data). The average weight of transient males in Jameson's study was about 29 kg (N = 12), although it was possible that some of the transient males were actually territorial males moving to or from their territories at the time they were captured.

Alaska. In Alaska, territories are also maintained seasonally (Schneider 1972b*, 1978*; Garshelis 1983; Garshelis et al. 1984) and, to a lesser extent, throughout the year (Lensink 1962; Sinha et al. 1966; Antrim and Cornell 1980). However, with the exception of Garshelis's work, less information is available on male territories in Alaska. Kenyon (1969) did not observe obvious male territorial behavior on Amchitka Island, although lone adult male otters were repeatedly seen in the same locations in a female area, and numerous instances of pair-bonding were observed. He surmised that males traveled from male to female areas when actively searching for estrous females, without necessarily maintaining distinct territories in the female areas. However, Kenyon did not observe individually marked males, and it is likely that territories are maintained at Amchitka.

Garshelis (1983) and Garshelis et al. (1984), who worked in Prince William Sound, presented the most recent and comprehensive study of male territoriality in Alaskan sea otters. They identified four criteria for characterizing territory quality: availablity of food resources, territory size, degree of enclosure (protected versus open area), and accessibility or defensibility of territory entrances. The presence of abundant food resources may attract females to particular territories, although this is difficult to measure due to the patchy distribution of prey. Females with pups preferred territories with shallow-water areas and mussel (*M. edulis*) beds where pups could forage easily. Females also seemed attracted to well-enclosed and protected territories. Female–pup pairs often entered sheltered territories to rest during stormy weather, which occurred frequently during the fall breeding season. In addition, territories with narrower entranceways—if they were not obstructed by other territories—could be more easily guarded to prevent other males from entering or females from leaving. Simply by virtue of their size, larger territories were more likely than smaller territories to contain adequate food resources and protected resting areas.

Garshelis et al. (1984) found that the average territory size at midtide was 23 ha (N = 12), ranging from 4 to 50 ha, which was somewhat smaller than the 35–40 ha mean reported in California (Loughlin 1980; Jameson 1989). Calkins and Lent (1975) reported territory sizes for two males in Prince William Sound to be 75 ha and 125 ha.

Mating success of individual males in Prince William Sound varied with territory quality, duration of territory occupation, age, and size of the male (Garshelis et al.

1984). Territory quality (ranked by the four qualities mentioned) was significantly correlated with the number of copulations and pair-bonds formed with the different females observed within each territory. Mating success was also correlated with the length of time a male occupied his territory. Only males that spent >2 months in their territories mated more than once and formed multiple pair-bonds. Conversely, mating success was low for males that occupied their territory for <1 month (although mating success was not determined for males when they were not in their territories). Males that remained <1 month occupied the poorest quality territories.

Large males held higher quality territories than did smaller (and presumably younger) males in Prince William Sound. Territorial males ranged in age from 6 years to >12 years (N = 7). Males weighing less than 34 kg occupied the poorest quality territories, while the best territories were occupied by the heavier, older males. Garshelis et al. (1984) suggested that females may choose a mate not only on the basis of territory quality but size and age of the male. Indirect evidence suggests that males typically develop a white-headed appearance at about 6 years, while females do so at 8–9 years (Garshelis 1984). Garshelis et al. (1984) speculated that earlier development of white-headedness in males may have evolved with the attraction of females to older-looking males. Individual males in Prince William Sound exhibited site fidelity to their territory, as occurs among California males. Several males in Prince William Sound returned to the same territories for 2–9 years. However, one male switched to the highest-rated territory after its occupant died (Garshelis et al. 1984). No displacement of territory holders by other males occurred. All cases of territorial desertion were evidently voluntary.

Territorial and agonistic behavior of sea otters in Prince William Sound appears to be similar to that observed in California. Territorial males often patrolled the boundaries of their territories with vigorous and highly visible grooming, kicking, and splashing (Calkins and Lent 1975; Garshelis et al. 1984). Most territorial males left their territories for brief feeding excursions (generally lasting <10 h, but up to 2 days), during which time territorial encroachment by other males was most common. Territory holders frequently rested in the main entranceway of their territories at dusk, when transient males often entered the study area (Garshelis et al. 1984). Actual fighting between males as well as territorial trespassing by transient or other territorial males was infrequently observed. Territory holders usually repulsed trespassers without actual contact or by brief aggressive interactions (lasting <5 s), although one vigorous fight lasted 9 min (Garshelis et al. 1984). Calkins and Lent (1975) observed two brief fights (in defense of territory) in addition to numerous chases of the intruding male from the trespassed territory.

Although the breeding season in Prince William Sound peaks in fall, some males established territories as early as April or May. However, before August, territories were not rigorously maintained, and the territory holders often left their territories for up to 2 weeks in spring and early summer to feed in areas where food resources were apparently more abundant. By September, territories were well defined; most territories were vacated by December. In winter, several territorial males occasionally returned to female areas, evidently in search of estrous females that became receptive after the main fall breeding season (Garshelis et al. 1984).

Reproduction in the Female

Reproductive Physiology

In Alaska, most females reach reproductive maturity (enter their first estrus) between 4 and 5 years of age, although some females enter their first estrus as early as 3 years (Kenyon 1969; Schneider 1972a*, 1973a*; Garshelis 1983; Garshelis et al. 1984; Calkins and Schneider 1984*; Jameson and Johnson, unpublished manuscript). Although comparatively little information is available concerning the onset of sexual maturity in female California sea otters, preliminary observations indicated a similarity with Alaska (Wendell et al. 1984; Jameson and Johnson, unpublished manuscript). Wendell et al. (1984) reported that one female gave birth for the first time at 4 years. Jameson and Johnson (unpublished manuscript) found that 67% (6 of 9) of the California females they observed mated for the first time after reaching 4 years of age. Of nine females, two pupped for the first time in their third year of life, one in the fourth year, four in the fifth year, one in the sixth year, and one in her seventh year. Two females in Monterey mated for the first time at about 2 years of age, and one of these females gave birth at 2.5 years, although her pup died soon after birth (Riedman et al. 1988*). Jameson and Johnson (unpublished manuscript) found that 50% (N = 6) of females with first pups lost their offspring before weaning.

Primiparous and multiparous females seem to come into estrus and mate <1 day to a few weeks after weaning their pups in Alaska (Schneider 1978*) and in California (Jameson and Johnson, unpublished data; Riedman et al. 1988*). Preliminary observations in the Monterey area suggested that a female often comes into estrus immediately after weaning her pup, at which time she copulates or forms a pair-bond (Riedman et al. 1988*; Deutsch, unpublished data). Jameson and Johnson (unpublished manuscript) found that the mean interval between separation from pup and copulation was 2.7 days for six Prince William Sound females (<1 day for four of these females). Females in the Monterey Bay area that have lost their pups (usually <2 weeks after parturition)

came into estrus again and copulated about 1-4 weeks after the pup's death (Riedman et al. 1988*). When captive Alaska females at the Tacoma Aquarium lost their pups before weaning, each female came into estrus within a month after her pup died (Brosseau et al. 1975).

Observations from Alaska and California suggested that the average period of female sexual receptivity (duration of estrus) seems to be 3–4 days (Garshelis et al. 1984; Riedman et al. 1988*; Jameson, unpublished data; Deutsch, personal communication). Yet several California females, especially older individuals, seemed to come into estrus 2–3 or more times within 2–3 months or possibly remained in estrus throughout this period until they were successfully impregnated, suggesting that aged females possibly experienced problems in successfully conceiving or maintaining early pregnancy (Riedman et al. 1988*). According to Brosseau et al. (1975), captive Alaska females seemed to be in estrus for about 5 days; if conception did not occur, females seemed to come into estrus again within 5 weeks. It is not known for certain whether a female would remain in estrus if she did not copulate, if the duration of estrus is variable as to when and how often the female copulates or what factors or mechanisms stimulate ovulation and the onset of estrus. Ovulation is induced by mating activity in other mustelids, yet the cessation of lactation stimulates ovulation in many other mammals (Cowie 1972) and may do so in sea otters. However, Schneider (1978*) found that a fairly high proportion of females with pups in Alaska began estrus, although most failed to produce a successful pregnancy. In California and Alaska, observations of mother and pup pairs indicated that females rarely copulate while still accompanied by a pup (Kenyon 1969; Calkins and Lent 1975; Garshelis et al. 1984; Riedman, Staedler, and Estes, unpublished data; Deutsch, personal communication).

Like all marine mammal species, sea otters give birth to a single pup (Estes 1979). Twinning is rare, but it has been reported occasionally. No case has been documented in which a female raised both pups successfully. Williams et al. (1980) found an adult female that evidently died while giving birth to twin fetuses (same incident described in Wild and Ames 1974). Jameson and Bodkin (1986) observed a female that probably had recently given birth to live twins. Although initially she nursed and cared for both pups, one (a 1.1-kg female) was abandoned about 24 h following birth and was taken to the Monterey Bay Aquarium, where she is currently (October 1990) a healthy 6-year-old juvenile.

In the Aleutian Islands, Kenyon (1969) found no twin fetuses in 178 female reproductive tracts. Sinha et al. (1966) also found no evidence of twinning in 83 pregnant females. Both Kenyon (1969) and Sinha et al. (1966) found reproductive tracts containing two corpora lutea although only one fetus was present. Schneider (1972a*) examined 565 reproductive tracts and found 24 cases of multiple ovulations. Of these, five resulted in twin fetuses and one in triplet fetuses; most of the fetuses were relatively large-sized and appeared to have developed normally. These data indicate that more than one ovulation took place in 4.2% of the estrus cycles, and about half of these resulted in the development of more than one fetus. In the Commander Islands, Barabash-Nikiforov (1947) found twin embryos in utero, and cited two similar cases reported by Japanese traders.

It is highly unlikely that a mother could successfully raise two newborn pups at once. However, a number of observations of females accompanied by two pups of different as well as similar ages have been made in the Commander Islands (Barabash-Nikiforov 1947; Barabash-Nikiforov et al. 1968) and in Alaska (Snow 1910; Lensink 1962; Kenyon 1969; Garshelis 1983). It is unclear whether one of the pups was an orphan or the female's pup from a current or previous birth.

Sea otters undergo a period of delayed implantation (Sinha et al. 1966). The unimplanted gestation period in Alaska has been estimated to last from a minimum of 3.5–4.5 months (Schneider 1972a*, 1973a*, 1978*) to 7–8 months (Kenyon 1969). There is more recent evidence indicating that the length of preimplanted pregnancy may be variable (Kenyon 1981) and, in some instances, brief (less than 1–2 months), especially in California (Loughlin et al. 1981). Detailed gross and microanatomical descriptions of the female reproductive tract are provided by Sinha et al. (1966) and Kenyon (1969).

The composition of sea otter milk is similar to that of other marine and aquatic mammal species in its high fat and low lactose content (Estes 1989). Fat and protein content of four milk samples taken in California ranged from about 21–26% and 9–12%, respectively (Jenness et al. 1981). The fat content of sea otter milk is considerably higher than that of other mustelids, such as badgers (*Taxidea taxus*; Jenness, unpublished data) and ferrets (*Mustela putorius*; Jenness and Sloan 1970), in which milk fat content has been reported to be 9.5 and 8%. However, many phocid seals and cetaceans have higher average concentrations of milk fat than sea otters, exceeding 50% in some stages of lactation (Riedman 1990). The high proportion of fat and protein in the milk provides a high-energy diet and promotes rapid tissue growth in the pup, which is important for survival in the marine environment.

It is unknown if changes in milk composition occur throughout lactation in sea otters. In other mammals that feed throughout lactation, fat and protein content tend to remain constant during the nursing period (e.g., northern fur seal; Ashworth et al. 1966) or increase slightly (e.g., black-tailed deer, *Odocoileus hemionus*; Mueller and Sadleir 1977). Therefore, pronounced increases in milk fat composition over time probably do not occur in sea otters as they do in fasting and lactating marine mammals.

such as northern elephant seals (*Mirounga angustirostris*; Riedman and Ortiz 1979).

Temporal Parameters Characterizing the Reproductive Cycle

There seems to be a potential for considerable individual as well as geographical variation and plasticity in the temporal phases of the female sea otter's reproductive cycle. Evidence from California indicated that most adult females give birth to one pup each year, with the reproductive cycle ranging from 11 to 14 months (Vandevere 1978*, 1979*; Jameson and Johnson 1979, Loughlin et al. 1981; Estes and Jameson 1983a*; Wendell et al. 1984; Siniff and Ralls 1988*; Jameson and Johnson, unpublished manuscript). Jameson and Johnson (unpublished manuscript) calculated a reproductive cycle or mean pupping interval of 12.4 months (N = 11; SE = 0.20). The natality rate among California females is estimated to be 85–90% (Jameson and Johnson, unpublished manuscript). Siniff and Ralls (1988*) radio-tagged adult females in California and found them to produce 0.87–0.90 pups per year. These and other data (Loughlin et al. 1981; Wendell et al. 1984; Riedman, Staedler, and Estes, unpublished data) indicate that adult female California sea otters most frequently give birth annually.

Lensink (1962) believed that females at Amchitka Island gave birth every 2 years, while Kanaga Island females gave birth each year. He suggested that geographical differences in reproductive cycles might account for the higher proportion of pups in the Kanaga Island population. On the basis of histological and gross morphological examination of female urogenital tracts, Chapman (in Kenyon 1969), Kenyon (1969), and Schneider (1971*) estimated that the reproductive cycle of females in the Aleutian Islands was about 2 years. Kenyon (1982) suggested that females in Alaska gave birth every 2 years in areas of high population density.

Most females observed by Garshelis (1983) in Prince William Sound (seven of eight) gave birth every 2 years, whereas one female pupped annually. Yet Garshelis estimated that pup dependency lasted only 5–6 months. He concluded that, although females are capable of reproducing annually, they rarely do so under food-stressed conditions. Garshelis et al. (1984) speculated that poor physical condition may lengthen reproductive cycles in some females by causing delayed estrus, delayed implantation, or resorption of the embryo. Jameson and Johnson (unpublished manuscript) found that 77% (17 of 22) of the females in Prince William Sound pupped annually, but the remaining 5 females may have had longer reproductive cycles.

The most accurate estimates of gestation length in sea otters have been derived from observations of marked individual females in California. The gestation period there has been estimated at 4–6 months (Loughlin et al. 1981) and 6 months (Estes and Jameson 1983a*; Jameson and Johnson, unpublished manuscript). Assuming that copulation occurred soon after weaning, Jameson and Johnson (unpublished manuscript) estimated maximum gestation periods for 22 pups (born to 13 females) and found a range of 5.0–7.8 months, with a mean of 6.0 months. They suggested that the 6-month gestation period consists of an implanted phase of 4 months and an unimplanted phase of 2–3 months. Among California otters, variation seems to occur in gestation length over time between successive reproductive cycles. The length of gestation periods may generally vary at the population level in California, Prince William Sound, and the Aleutian Islands; however, with the limited information and rough estimates of gestation lengths from early studies in Alaska, and because of the different methodologies employed in Alaska and California, it is difficult to establish that such differences exist.

In Alaska, estimates of gestation length were derived from examination of ovaries and conceptuses of reproductive tracts rather than by observation of marked individuals. In the Aleutian Islands, Kenyon (1969) and Chapman (in Kenyon 1969) estimated gestation to be 10–12 months, with the implanted period lasting 4.5–5.5 months; however, these estimates were based on assumptions that the fetal growth rate during the implanted pregnancy was similar to that of river otters, and that the timing of the peak mating and pupping seasons was representative of all of the reproductive tracts sampled. They note that the estimates of gestation period may be high due to sampling errors. Schneider (1973a*) estimated that females in the Aleutian Islands had a gestation of 7.5 months with an implanted period of about 3.8 months. He also based his estimate on another estimate of peak breeding and pupping periods derived by analyzing reproductive tracts. Barabash-Nikiforov (1947) assumed that the gestation in Commander Island sea otters was about 8–9 months, based on the timing of mating and pupping seasons, stage of development of the pup at birth, and one captive female that mated and gave birth 8 months later.

According to Wendell et al. (1984), pup dependency periods in California were 5–8 months, although most pups seemed to be weaned at around 6 months. Riedman et al. (1988*) found that pup dependency varied from 4.5–9.5 months. Jameson and Johnson (unpublished manuscript) followed 23 females in the southern part of the range near Point Piedras Blancas and found that pup dependency lasted 5.0–7.5 months, averaging 6.1 months. Estes and Jameson (1983a*) estimated that pup dependency periods were about 6 months. Payne and Jameson (1984) also calculated a mean pup dependency of 6 months; they presented ontogenetic information on pup development showing that 6-month-old pups are self-sufficient in all activities and seem capable of surviv-

ing on their own. It seems likely that pups abandoned or otherwise orphaned at <4.0–4.5 months do not survive on their own in California, although in Prince William Sound, Monnett and Rotterman (1988b*) found that pups survived when weaned only an estimated 2.5 months after birth. Loughlin et al. (1981) reported pup dependency periods of 8.0–8.5 months for three female and pup pairs and 3.5–6.0 months for two others.

In Alaska, the duration of pup dependency often seems longer than that observed in California. Kenyon (1969) believed that Aleutian Island females cared for their pups for a least 1 year—possibly longer in some cases. Schneider (1971*) suggested that pup dependency periods in the Aleutian Islands were also about 1 year. In Prince William Sound, Jameson and Johnson (1979*) estimated that the duration of pup dependency was 6 months or longer. From radio-tagged adult females in Prince William Sound, the average duration of pup dependency was estimated to be 169 days (5.6 months), although this varied from 76 to 333 days (2.7–12.0 months: $N = 23$). No sex differences were detected in the duration of pup dependency (Monnett and Rotterman 1988b*). Garshelis et al. (1984) similarly found that pup dependency periods of 5–6 months seemed to be common in Prince William Sound, although he thought most females gave birth only every 2 years. In the Commander Islands, pup dependency seemed to be 6–7 months (Barabash-Nikiforov et al. 1968).

It is unclear why pup dependency periods are so variable among females in the same area, although Monnett and Rotterman (1988b*) suggested that variables such as the abundance of food and a female's age and health may influence the duration of dependency periods. Observations in the Monterey area suggest that a female's weight may be related to the length of time she cares for her pup, and long-term research in the Monterey area may be able to show how a female's age, diet, and foraging behavior untimately influence the length of her pup dependency periods and reproductive success (Riedman, Estes, and Staedler, unpublished data).

Fig. 29. California sea otter mother nursing small pup about 1 month of age (D. Buchich).

Maternal Care and Pup Development

Parental care is provided exclusively by the female. Maternal behavior in California sea otters has been described by Fisher (1940), Limbaugh (1961), and Davis (1979), but various aspects of pup development and maternal care have been quantified or studied in greater detail (Vandevere 1972*; Sandegren et al. 1973; Payne and Jameson 1984; Staedler 1987; Riedman et al. 1988*; Faurot, unpublished data). Kenyon (1969) provides a detailed description of maternal and filial behavior among Alaskan sea otters.

Observations from California indicate that parturition occurs both in the water (Sandegren et al. 1973; Riedman, unpublished data) and on land (Woodward 1981b; Jameson 1983a). Jameson (1983a) suggested that females may give birth on land in areas where kelp beds are sparse. Barabash-Nikiforov (1947) believed that birth occurred on land in the Commander Islands. He observed one female that gave birth on land, and he found placentas on the shore on two other occasions. Intensive postpartum grooming of the pup by its mother begins immediately after birth (Sandegren et al. 1973; Woodward 1981a*; Jameson 1983a).

Mothers with newborns often tend to avoid other otters (Fig. 29). Within several days of parturition, however, females will associate and rest with otters in rafts containing other female and pup pairs (Sandegren et al. 1973; Jameson, unpublished data). Sandegren et al. (1973) found that during the peak winter pupping season, females with pups behaved aggressively toward other individuals, particularly during winter storms when sheltered resting sites were scarce and kelp beds were sparse. Apparently, competition for such favored resting sites was intensified at this time. During brief periods of inclement weather, mothers with young pups often repeatedly swam in a large circular pattern, slowly traveling downwind and then rapidly swimming upwind. Sandegren et al. (1973) suggested that females may swim in such a pattern in response to their pup's apparent distress during rough sea conditions as waves wash over them—a smooth downwind ride allows the pup to suckle and rest.

A female invests considerable resources in caring for her pup, which is dependent on her for nourishment, grooming, and protection, especially when young. According to Sandegren et al. (1973), mothers nurse their pups an average of six times per day (during daylight), with each nursing bout averaging 9 min. Females with pups at Point Lobos, California, spent 41% of their daylight hours resting, 16% feeding, 20% grooming their pup, 10% grooming themselves, 13% swimming, and 8% nursing their pup (which was always done in conjunction with resting, swimming, or grooming of the pup). During daylight hours, females with smaller pups spent slightly more time nursing and grooming their pups, more time resting, and substantially less time feeding (2%) than females with larger pups (26%; Sandegren et al. 1973). Studies in Monterey also suggested that females with very young pups spent more time resting and less time feeding during the day than other animals (Riedman, Staedler, and Estes, unpublished data; Lyons, personal communication). It is possible that females with young pups spend proportionally more time feeding at night than independent otters or females with large pups. Mothers with large pups, however, appear to spend an equivalent or greater amount of time feeding during the day than independent otters in the northern part of the California range (Sandegren et al. 1973; Lyons, unpublished data; Riedman, Staedler, and Estes, unpublished data) and in Alaska (Garshelis 1983). In addition, females with large pups obtain food not only for themselves but also capture much of the food eaten by their pup as well (Riedman, Staedler, and Estes, unpublished data). However, Ralls and Siniff (1988*) found that females with small pups fed slightly more than females with large pups over a 24-h period in the central and southern parts of the range, although this difference was not significant. Mothers with small pups spent 40.6% of their time resting, 42.71% feeding, and 16.5% engaged in other activities; mothers with large pups spent 48.45% of their time resting, 36% feeding, and 15.5% engaged in other activities. Sandegren et al. (1973) found that the diurnal activity cycle of females with pups was similar to that of independent otters, with activity peaks at dawn and dusk, although observations in Monterey indicated that many females with large pups are active in the middle of the day (Riedman, Staedler, and Estes, unpublished data). Over a 24-h period, Ralls and Siniff (1988*) observed early morning and early evening peaks in feeding activity among mothers with pups.

While pups are young, females remain with their pups constantly unless the mother is diving for food. In some areas of Alaska, bald eagles prey on small pups, apparently capturing them as lone pups float on the surface while their mothers are underwater (Sherrod et al. 1975). Although sightings of pup capture were rare, numerous remains of sea otter pups were discovered at eagle nest sites at Amchitka Island in late spring and early summer, which corresponds with the seasonal peak in sea otter births and the period just before fledging of eagle chicks. Although some of the otter pups may have been obtained by scavenging dead individuals, material examined from some of the nests showed hematomas around talon puncture wounds and other evidence of live procurement. Eagles may cue in on the distinct, piercing vocalization typical of pups separated from their mothers. The extent to which nesting pairs of eagles exploit sea otter pups varies substantially. The remains of one or more pups was found repeatedly in some nests while never occurring in others. At one nest site, nine pups were found over the breeding season.

In 1972 at Amchitka Island, a minimum of 56 pup carcasses were retrieved from 34 nests examined. At that time, there were 71 known active nest sites on the island, and about 35–40% percent of the eagle population was composed of nonbreeding individuals. Thus, pup loss to eagle predation may have affected the dynamics of the sea otter population, even though it contained at least several thousand individuals (Estes 1977). The extent to which similar interactions occur in other areas containing both otters and bald eagles is unknown. It may be that eagle predation on otter pups is restricted to areas where both species are at resource-limited population abundances. In Prince William Sound, coyotes apparently killed several recently weaned pups (Monnett and Rotterman 1988b*).

On numerous occasions, mothers have been observed carrying and sometimes grooming their dead pups for up to several days in Alaska (Kenyon 1969) and in California (Ames, Deutsch, Jameson, Lyons, Riedman, Staedler, unpublished data; Vandevere, personal communication). Most of these pups are either newborns or less than one month old. In some cases, the pup had been dead for several days, and patches of fur and skin were sloughing from the carcass. One adult female (of unknown reproductive status) was seen carrying and manipulating a dead red phalarope (*Phalaropus fulicarius*) as if it were a pup (Vandevere, personal communication); another female that had recently lost her newborn pup held and manipulated an empty beer bottle like a pup (Riedman, Staedler, and Estes, unpublished data).

Payne and Jameson (1984) provided a detailed analysis of the ontogeny of pup growth and behavioral development ($N = 14$ wild California pups, 1 wild Oregon pup, and 3 captive pups); they found that age could be determined approximately by appearance and behavior. For instance, the natal pelage was completely replaced by adult pelage by age 13 weeks. Nourishment was derived primarily from the mother's milk during the first month; by 4 months, the pup subsisted mainly on solid food obtained by the mother. The pup's proficiency in other activities, such as swimming, grooming, and the ability to use tools, also increased gradually with age. By 14 weeks, most pups were able to swim independently, dive proficiently, and groom themselves without help from their mothers. Pups captured and broke open hard-shelled prey, using a rock tool, by 20–24 weeks (Payne and Jameson 1984; Fig. 30). Despite these general correlations between age and the development of various skills, pups of similar ages may show striking differences in behaviors and proficiency in grooming, diving, and foraging skills (Faurot 1987*; Riedman et al. 1988*).

In California (Payne and Jameson 1984) and in Alaska (Kenyon 1969; Schneider 1973a*) females continue to lactate until weaning, at which time—following an average pup dependency period of 6 months—California pups weigh about 12 kg (Jameson, unpublished data), and Aleutian Island pups weigh 12–14 kg (Kenyon 1969; Schneider 1973a*). However, Schneider (1973a*) reported that one male pup reached 17 kg before weaning took place. Preliminary information from California suggests that the pup's weight may be positively correlated with its mother's weight—that is, small females may produce pups that are smaller than average in size at a given age (Riedman, Staedler, Estes, and Ames, unpublished data).

As pups grow older and approach weaning age, interactions between the mother and pup pair seem to change:

Fig. 30. California sea otter mother interacting with large pup, which is attempting to nurse; pup is approaching weaning age, which is 5–8 months (D. Buchich).

for instance, the mother may not offer her pup food as readily and may avoid her pup when it solicits prey (Staedler 1987; Riedman et al. 1988*). Preliminary observations suggest that a mother may shift locations just before, during, or immediately after her pup is weaned in California (Wendell et al. 1984; Jameson, unpublished data; Riedman, Staedler, and Estes unpublished data) and in Prince William Sound, Alaska (Monnett and Rotterman 1988a*). In Prince William Sound, Garshelis et al. (1984) reported three cases in which pups (both male and female) traveled away from their mothers at the time of weaning. Garshelis et al. (1984) suggested that sexual precopulatory interactions between the mother and a male may instigate female and pup separation and play a role in the weaning process.

Observations of eight female and pup pairs in Prince William Sound indicate that a mother in poor health may abandon her pup before it is old enough to survive on its own. Three of the mothers who were in poor physical condition (two of which died 1–2 days after separation) abandoned their pups, which weighed only 6–9 kg at separation (Garshelis 1983). It is possible that periods of severe storms and rough sea conditions also promote premature separation of female and pup pairs in California (Morejohn et al. 1975; Riedman et al. 1988*; Ames unpublished data; Jameson, unpublished data) and at Amchitka Island (Kenyon 1969).

It is unknown to what extent adult females associate with their offspring after weaning. In Prince William Sound, Garshelis (1983) observed one instance in which a female pup, weaned at an estimated 7 kg, reunited with her mother about 1 year after birth. The pup foraged independently throughout winter before rejoining her mother, who did not have a second pup at this time. The mother and pup pair remained together continuously for over 4 months, during which time the juvenile often took food from her mother, especially when the mother captured more food items or larger prey than did the pup. Separation of the pair seemed to be initiated by sexual interactions between the mother and a male. Observations of females accompanied by or caring for two pups of different ages have been made in Alaska (Lensink 1962; Kenyon 1969) and in the Commander Islands (Barabash-Nikiforov 1947; Barabash-Nikiforov et al. 1968), although in all these instances it was unknown if the larger pup was the female's previous offspring or an adopted orphan. Barabash-Nikiforov (1947) reported that "a grown cub often remains with the mother even after a new one is born, so that the mother is seen together with the newborn and a yearling." We regard this as unlikely in view of the infrequent nature of such sightings in subsequent studies.

Along the Monterey peninsula, many females and their adult female offspring (some of which have produced daughters of their own) have resided in the same general vicinity for several years. Riedman et al. (1988*) observed cases in which juvenile or adult female offspring (up to 6 years old) interacted briefly with their mothers, as well as two instances in which pups reunited with their mothers after being separated or weaned. In one of these cases, the mother cared for her pup an additional 2 months after weaning it for about 1 week. In another instance, a 14-kg female, who was not accompanied by a mother when captured in Monterey (and released several kilometers from the capture site), was observed a few days later being nursed and groomed by her apparent mother back at the capture site. In another case a 2-year-old juvenile female was sighted in the same cove with her mother near Point Piños (along the Monterey peninsula), but the pair was not observed to interact during the observation period (Lyons, personal communication). Studies focusing on the existence and nature of relationships between females and their grown offspring are currently in progress in the northern part of the range in California (Riedman et al. 1988*).

Alloparental Care and Adoption in Wild and Captive Sea Otters

An alloparent is an animal, other than the genetic parent, that provides care for conspecific young (Wilson 1975). Most alloparental and fostering behaviors are reported among mammals and birds, where systems of parental care are especially well developed. Because many social mammals live in groups characterized by matrifocal networks, and the primary burden of parental care usually falls on the female, it follows that most cases of alloparenting and adoption in mammals involve female rather than male assistants or foster parents (Riedman 1982).

Parental behavior directed toward nonfilial young superficially seems to be a form of altruism in which the foster parent assists other individuals at its own expense (Hamilton 1964) by investing its limited resources into promoting the survival of another's offspring. However, individuals that care for foreign young may acquire advantages associated with increased inclusive fitness (based on kin selection), parental experience, reciprocal altruism, and exploitation of the fostered young. In many cases, environmental constraints (such as scarce breeding sites or food resources requiring cooperative foraging strategies) seem to influence the occurrence of alloparenting and adoption. In addition, proximate factors incorporating reproductive errors may be involved in some instances of fostering. Often, several selective benefits, along with various environmental pressures or reproductive mistakes, may collectively promote the evolution of alloparental care and adoption (Riedman 1982).

Reproductive mistakes, as well as selective benefits associated with increased parental experience for juvenile female sea otters and reciprocal cooperation in the form

of "babysitting" behavior (allowing potentially increased foraging freedom for females with pups), might seem to theoretically promote the occurrence of some degree of allomothering and adoption among sea otters; however, few instances of alloparental behavior or adoption have actually been observed in the wild. In captivity, the potential for fostering behavior to occur, based on reproductive mistakes made by female sea otters, seems to be relatively high.

Wild Otters. Explanations for the scarcity of foster-parent incidents among wild sea otters include the possibilities that (1) fostering behaviors are difficult to observe in the field and (2) such behaviors actually occur very infrequently. The latter seems more likely. Given their social organization and breeding behavior, fostering opportunities are rare for sea otters, unlike other mammals that give birth synchronously and raise their young in crowded breeding colonies, such as several species of bats (Brosset 1962; Davis et al. 1962), pinnipeds (Riedman and LeBoeuf 1982), and ungulates. Under those more crowded circumstances, mother–pup separations and opportunities for allomothering and adoption of orphaned pups frequently arise.

Among the California population of sea otters, females give birth throughout the year and raise their pups in low-density groups in the water rather than in crowded breeding colonies. The chances of an orphaned sea otter pup encountering a potential foster mother—particularly one that has recently lost her own pup—are probably remote.

However, one well documented adoption in Monterey lasted 2–3 weeks (Staedler and Riedman 1989). The foster mother was a tagged adult female of known history. She cared for a large female pup that had apparently recently lost its mother. The adoptive female nursed, shared food with, and rested with the orphan for at least 2 weeks. However, the orphan, was found dead on a nearby beach 3 weeks after being adopted. (The pup was 30% underweight when it died, probably of starvation.) Staedler and Riedman (1989) attributed this case of adoption to reproductive mistakes on the part of the female, who evidently lost her own pup soon after its birth, several days before she adopted the orphaned pup.

In Alaska, orphaned wild sea otter pups, as well as juveniles, are sometimes observed with a tolerant adult of either sex (Kenyon 1969). In the Monterey area, dependent pups as well as recently weaned juveniles are sometimes observed trying to suckle from mothers with pups or from independent females (Riedman et al. 1988*, Deutsch, personal communication)—for instance, near Monterey, a tagged juvenile weaned in late August near Monterey was observed about 3 months later in its natal area attempting to suckle a tolerant subadult female.

The quality and extent of care given to orphaned pups by accompanying adults is unclear in many cases, although to survive, a young pup requiring milk would certainly need the care of a lactating female. Kenyon (1969) describes one allomothering incident in which a wild adult female cared for two pups of similar size, allowing both pups to nurse. However, most of the maternal care was directed towards only one of the pups, and Kenyon concluded that the other pup was probably an orphan. A number of other cases of females accompanied by two pups of different (as well as similar) ages have been reported in Alaska (Lensink 1962; Garshelis 1983) and in the Commander Islands (Barabash-Nikiforov 1947; Barabash-Nikiforov et al. 1968). In most instances it was not clear if one pup was the female's previous offspring or an orphan, although Barabash-Nikiforov (1947) believed that a grown pup often remained with its mother after she gave birth to a new pup. Kenyon (1969) suggested that in a noncaptive situation, an adult otter that tolerates or cares for an orphaned pup might enhance the pup's chances of surviving; he also speculated that the extent of alloparenting behaviors observed may decrease during stressful conditions (such as during storms or a shortage of food resources).

In California, a form of male exploitation of dependent pups has been occasionally observed; it resembles the exploitive alloparental care that occurs in many species of primates, in which the male with an infant in his possession may derive benefits such as increased social status, protection from aggressive conspecifics, or various reproductive opportunities (Riedman 1982). In sea otters, the benefits resulting from possession of a dependent pup seem to be related to "free" food: many incidents have been observed in which an adult male stole the pup of a foraging female and relinquished the pup only when the mother gave the male her prey (Riedman et al. 1988*; Faurot, Schusterman, and Vandevere, personal communication). However, the male did not actually provide care for the pup (Riedman et al. 1988*).

Captive Otters. Numerous instances of allomaternal care, foster-parenting behaviors, and adoption of pups have been observed among captive Alaskan sea otters at the Seattle Aquarium (C. J. Casson, personal communication), the Vancouver Aquarium, and Point Defiance Zoo and Aquarium (S. Hewlett, personal communication). All of the fostering events occurred naturally—there was no human intervention, and no animals were artifically primed to accept a pup.

At the Seattle Aquarium, all the allomothering incidents occurred at successive intervals between one adult female and four different pups that were unrelated to the female. The adult male never exhibited interest in the pups. All four pups (both males and females) were offspring of the same female, and each pup grew to adult status. During the fostering incidents, the pups' ages varied from 2 months to 10 months. The allomother was observed to care for each of the four pups for short periods of several

minutes while the genetic mother was present. The allomother's caretaking behavior involved grooming the pup, offering the pup solid food, and protecting it from adult males.

Two separate cases of adoption lasting 2–3 days were observed between the adult female and the two most recently born pups. The adoptions took place when the pups were about 7 and 10 months old, at which time their mother temporarily abandoned them. During the 2–3 days of abandonment, the mother seemed to be in estrus and spent most of her time close to, or mating with, the adult male. At this time, the foster mother became the pup's exclusive caretaker, feeding the pup solid food, grooming it, sleeping with it on her chest, and protecting it. Nursing was not observed, although the adopted pup attempted to suckle its fosrer mother several times. After the 2–3 days of mating activity, the genetic mother took the pup away from its foster mother and began to care for it again (Casson, personal communicarion).

At the Vancouver Aquarium, one case of adoption has been observed in which the foster mother stole the 4-month-old pup of another female (who had cared for it successfully up to that point) and adopted it for several months. At the time of adoption, the foster mother had recently lost her own 8-month-old pup. The genetic mother never seemed to offer resistance to the foster mother that took the pup or tried to regain it. The adoption was terminated by the aquarium staff when the foster mother gave birth to her own pup; this allowed her to care for the newborn. The adopted pup was well cared for and apparently healthy and in excellent condition (Hewlett, personal communication).

At the Point Defiance Zoo and Aquarium, it is fairly common for either nonlactating or lactating adult females to care for another female's pup. For example, a 6-year-old, 23-kg adult female (named Cordova) gave birth to a healthy male pup (pup 1) on 16 June 1984 at 9:00 a.m. At about 1:00 p.m. on the same day, another adult female (Nooka) of the same age and weight, stole Cordova's pup and began to care for it. One hour later, Nooka gave birth to her own pup (pup 2). Both adult females ignored pup 2, which was removed from the display and revived twice by the staff from near-drowning. Due to Nooka's persistence in keeping pup 1—and the possibility of injury to the pups in a tug-of-war between the two females—Cordova was separated into a holding pool with pup 2 for the night. Cordova immediately tossed pup 2 against the wall and the impact killed it.

Cordova was returned to the display on 22 June. However, within 24 hours, the adult females (both of whom wanted the pup) managed to mortally injure Nooka's adopted pup with their pulling. The adoption of Cordova's pup by Nooka therefore lasted 7 days, but it might have continued throughout the pup's dependency if it bad survived. During this time, the 8-year-old male (Sitka) and 4-year-old female (Ma-Linke) remained in the display with Nooka and her adopted pup. Although the male showed no interest in the pup (at least during daylight hours, when the staff was present), the young female was allowed to act as allomother and to hold the pup several times.

On 7 August 1984, Ma-Linke gave birth to a healthy male pup. Cordova and Nooka both attempted to steal Ma-Linke's pup, and the newborn was subsequently killed within 24 h because of tugging and pulling by the two adult females.

On 4 February 1985, Nooka delivered a stillborn male pup and was placed on temporary loan to the Seattle Aquarium. On 17 February 1985, Cordova gave birth to a healthy male pup. On 26 March 1985, Ma-Linke gave birth to a female pup. Although both females raised their own young, botb pups were allowed to play on top of Ma-Linke with no apparent concern from Cordova. However, both pups were killed during the night, on separate occasions in early May, probably from injuries inflicted by the adult male Sitka.

Jim Short (personal communication) of the Point Defiance Zoo and Aquarium concludes that if a mother were to be removed from the display, another female would adopt and attempt to raise her pup. An immature female would probably also exhibit interest in the pup, although her level of interest might eventually decline as the pup aged. Adult males seem to either ignore pups or behave aggressively and destructively toward them. It is possible that the killing of young pups by adult male otters parallels the occurrence of infanticide among mammals such as laugurs (*Presbytis* spp.; Sugiyama 1967, Hrdy 1974), lions (*Panthera leo*; Schaller 1972), and bears (McCullough 1981), so that the female that bas lost her offspring comes iuto estrus sooner. Although some of the captive sea otter pups may have been offspring of the male that killed them, this situation would be less likely in the wild. Infanticide by adult males has never been reported among wild sea otters.

Kenyon (1969) documented one case of experimentally induced allomothering that occurred in captivity. A recently captured adult female was placed in an enclosure witb an orphaned juvenile (8.2-kg) female several months old. The juvenile approached the female within a few minutes, and she allowed it to suckle. The female also exhibited protective behavior towards the juvenile, clasping it around the neck when alarmed. The female subsequently nursed and protected the juvenile for 8–9 days, with increasingly longer intervals elapsing between caretaking behaviors. After the ninth day, the female did not allow the juvenile to suckle and often stole its food, although the pair rested in close proximity and clasped one another with their forelegs when alarmed.

Population Dynamics

Historical Distribution and Abundance

Historically, the sea otter's range extended from the northern Japanese archipelago (from at least northern Hokkaido and southern Sakhalin) northward along the east coast of Kamchatka, eastward through the Commander Islands, Aleutian archipelago, and Pribilof Islands to the Alaska Peninsula, and along the Pacific coast of North America south to about central Baja California, Mexico (Fig. 7). The exact southern extent of the range in Baja California is unclear due to the lack of adequate historical records. According to Scammon (1870), sea otters occurred at Isla de Guadalupe and Isla de Cedros. Kenyon (1969) concluded that the sea otter's range extended to Morro Hermoso, about 50 km south of Isla de Cedros. Because of coastal habitat distribution and present day oceanographic conditions, sea otters probably could have lived at least as far south as Punta Abreojos, Baja California. This location marks the southern limit of extensive rocky habitat and coastal upwelling along the Pacific coast of North America. However, the southern limit of distribution probably varied with the northward intrusion of anomalously warm, nutrient-poor waters during particularly strong ENSO (El Niño) events, or with the southward extension of cold, nutrient-rich water during periods when the California current was especially strong.

Before commercial exploitation, the worldwide population of sea otters was estimated to be 150,000 (Kenyon 1969) to 300,000 (Johnson 1982) animals. At that time, the population in California was estimated to be 16,000-20,000 (California Department of Fish and Game 1976; U.S. Fish and Wildlife Service 1982) and 20,000 (Johnson, personal communication, cited in Ralls et al. 1983). According to Evermann (1923), the estimated total number of otters killed in California and Baja California between 1786 and 1868 was 200,000, an average of 2,400 per year. Ogden (1941) estimated that 100,000 pelts were taken in California between 1776 and 1911, an average of 800 per year. Historical records suggest that the population may have been especially abundant in the central and northern portions of the State and in the Channel Islands of southern California (Ogden 1941; Kenyon 1969).

Aboriginal hunting of sea otters took place throughout the range. In some areas, localized overexploitation and substantial reduction of sea otter populations by indigenous people apparently occurred (Simenstad et al. 1978). Evidence for this conclusion comes from faunal remains in the Aleut kitchen middens at Amchitka Island. The calcareous remains of sea urchins, from which size of living urchins can be estimated, are abundant throughout the middens. Ecological studies of this area have shown that sea urchin size varies predictably with the presence or absence of sea otter predation. Habitats without sea otters contain sea urchins ranging from 60 to 80 mm in test diameter, whereas sea urchins >35 mm test diameter are almost never found where sea otters are present, regardless of how long the otter population has been present. Thus, the presence of 60–80 mm test diameter sea urchins throughout the kitchen middens indicates that sea otters were absent from at least certain areas during the era of Aleut prehistory. However, it is unlikely that any such effect was widespread because abundant populations were encountered by the Russians and other early fur hunters.

Extensive exploitation of sea otters began in 1741, following the discovery of Alaska, the Aleutian Islands, and the Commander Islands by the Bering expedition. Subsequent exploitation in the eighteenth and nineteenth centuries reduced the species throughout its range. By 1911, when protection for sea otters was established under the International Fur Seal Treaty, only 13 small remnant populations are thought to have persisted. These occurred in the Kuril Islands and along the Kamchatka Peninsula, the Commander and Aleutian islands, southwestern Alaska, the Alaska Peninsula and northern Gulf of Alaska, the Queen Charlotte Islands in British Columbia, the Point Sur area in California, and Islas San Benitos in Mexico (Fig. 7). The total population at this time may have contained as few as 1,000–2,000 animals (Ogden 1941; Kenyon 1969). Several of the remnant populations declined to extinction, including those in Mexico and British Columbia (Kenyon 1969; Estes 1980).

Sea otter populations from the Kuril Islands northeast to Prince William Sound have subsequently recovered and presently occupy most of their historical range. However, sea otters became extinct along the Pacific coast of North America from Prince William Sound to central Baja California, except for the remnant population in central California and, more recently, translocated populations in southeastern Alaska, British Columbia, Washington, and Oregon. Legal protection of sea otters began in 1911; recovery patterns following this action are poorly known. Kenyon (1969: 192–193) concluded that "... an isolated population having ample unused habitat may grow through local reproduction (no immigration) at a rate of about 10 to 12 percent per year." However, an analysis of survey data from several recently reestablished sea otter populations (the naturally recolonized population at Attu Island and the populations translocated to southeastern Alaska, British Columbia, and Washington State) indicates that these populations all have increased at rates of 17–20% per year (Estes 1990a). In contrast, the population in California has increased at a rate of 4–5% per year (Estes 1990a). Chapman's (1981) analysis of Kenyon's data indicates that the population at Amchitka Island grew 19% per year, an estimate consistent with Estes's

Table 6. *Size and probable status of sea otter* (Enhydra lutris) *population in the North Pacific Ocean. Data from International Union for the Conservation of Nature, Otter Action Plan, and Estes, 1990b.*

Location	Date surveyed	Count or estimate[a]	Population status[b]	Comments	Source
Soviet Union					
Kuril Islands	1984	6,000–7,000[a]	1	Survey methods and estimation technique unknown	Marinov 1984*
Kamchatka Peninsula	1984	2,132	3	Survey methods unknown; population may be limited by winter sea ice	Khromovskikh 1984*
Commander Islands	1988	4,714	2	Survey methods unknown; Medny Island at or near equilibrium density; Bering Island below equilibrium density	A. Zorin and A. Burdin (personal communication)
Alaska					
Near Islands	1986	1,599	2	Skiff and shore survey. Attu Island only; Agattu Island unsurveyed	Estes 1990a
Rat Islands	1965	3,145	1	Aerial survey; presently may support 14,420–20,650 otters (see text)	Kenyon 1969
Andreanof Islands	1969	2,393	1	Aerial survey; population probably much larger	Schneider and Faro 1969*
Islands of Four Mountain	1982	69	2	Skiff survey; small colony established recently	Bailey and Trapp 1986*
Fox Islands	1986	858	3	Aerial survey	Brueggeman et al. 1987*
Alaska Peninsula	1986	15,244	3	Aerial survey	Brueggeman et al. 1987
Pribilof Islands	1988	7	2	Occasional sightings; may be wanderers from Bristol Bay	A. L. Sowls (personal communication to A. DeGange)
Kodiak archipelago	1985	2,811	2	Aerial survey	Simon-Jackson et al. 1986*
Kenai Peninsula	1982	880	3	Aerial survey	Schmidt 1983*
Prince William Sound	1984–85	4,747	3	Skiff survey within 200 m of shore; occasional offshore areas surveyed	Irons et al. 1988
Northern Gulf of Alaska	1986	1,432	2	Aerial survey; all sightings between Orca Inlet and Cape Suckling	Simon-Jackson 1986* Simon-Jackson and Hodges 1986*
Southeast Alaska	1988	4,520	2	Skiff and shore surveys	Pitcher 1987* and unpublished data
British Columbia	1987	380	2	Aerial survey	MacAskie 1987
Washington (State)	1989	211	2	Aerial, skiff, and shore surveys	R. Jameson (personal communication)
Central California	1989	1,864	3	Shore and aerial surveys	R. Jameson and J. Estes (unpublished data)
San Nicolas Island	1989	15–20	2	Shore surveys	U.S. Fish and Wildlife Service (unpublished data)

[a] Estimate.
[b] 1 = at or near equilibrium; 2 = below equilibrium; 3 = unknown or uncertain population status.

calculation of r_{max} for sea otters.

Sea otters occur throughout most of their historical range from Prince William Sound west (Table 6). Although the size of these populations is not precisely known, they may total more than 150,000 (Estes 1980; Johnson 1982; Calkins and Schneider 1985*; Rotterman and Simon-Jackson 1988). Populations in the Kuril Islands presently number an estimated 6,000–7,000 (Maminov, personal communication). Most of the available habitat along the Kamchatka Peninsula also is occupied and contains an estimated 2,500 otters (Khromovskikh, personal communication). In the Commander Islands, Medny Island contains 900–1,200 individuals, which are probably resource-limited, whereas Bering Island has an estimated population of 1,500–1,800 and is still increasing. Alaska populations are less well known, although all available data are summarized by Rotterman and Simon-Jackson (1988) and in Table 6. Sea otters probably are at or near equilibrium density throughout the Aleutian archipelago, except for the western end (Near Islands) and from the eastern Andreanof Islands through part of the Fox Islands. It is likely that the most recent survey data from the Rat and Andreanof islands (Fig. 24) grossly underrepresented the size of these populations. For example, 3,145 otters were counted in a 1965 survey of the Rat Islands even though Estes (1990a) estimated that Amchitka Island alone supports a population of 5,500–8,500 otters. Recent surveys of the Alaska Peninsula, Kodiak archipelago, Kenai Peninsula, northern Gulf of Alaska, southeastern Alaska, and Prince William Sound provided respective counts of 15,244, 2,811, 880, 4,747, 1,432, and 4,520 sea otters (Table 6).

Fig. 31. Large group of sea otters discovered at Bixby Creek cove in Big Sur, California, on 15 April 1938 (W. L. Morgan).

Status of the California Sea Otter Population

Population Growth and Abundance (1914–1984)

In 1914, the total California population was estimated to be about 50 animals (California Department of Fish and Game 1976*), after Bryant (1915) reported at least 32 otters observed near Point Sur. In 1938, a group of about 50 otters was observed off Bixby Creek (Bolin 1938: Fig. 31), at which time the population size was estimated at 100–150 (Fisher 1939) to 300 animals (Boolootian 1961; California Department of Fish and Game 1976*). The population was estimated to be approximately 1,000 animals by 1960 (California Department of Fish and Game 1976*).

Periodic surveys of the California sea otter population were conducted from 1958 to 1979, primarily by the California Department of Fish and Game (Miller 1958*, 1976*; Carlisle 1965*; Wilson 1968a*, 1968b*; Odemar 1969*; Wild 1973*). Most were aerial surveys of part or all of the range, and some were supplemented with various types of shore-based counts. Results of these surveys are summarized in Boolootian (1961), Carlisle (1966), Wild and Ames (1974), California Department of Fish and Game (1976*), and Geibel and Miller (1984). From 1980 to 1983, 16 aerial surveys of the entire range were conducted (Bonnell 1982; Bonnell et al. 1983*). Estes (1982*) also conducted aerial surveys in 1981 and 1982. Since different methods were used in these various surveys, it is not possible to determine population changes from the data, except for general trends. Quality of the early data is particularly difficult to evaluate—to some extent, apparent population increases have probably resulted from improved methodology. In 1982, standardized survey methods, primarily involving shore-based counts, were adopted to eliminate this source of variation from future counts.

Table 7. *Results of 1982–89 shore-based California sea otter (*Enhydra lutris*) censuses of the entire range. These data were cooperatively collected by the Fish and Wildlife Service and California Department of Fish and Game. Small pups are <3 months, and large pups are ≥3 months (Payne and Jameson 1984).*

Census		Number of independent otters	Number of small pups	Number of large pups	Total pups	Total otters
1982	Spring	1,124	[a]	[a]	222	1,346
	Fall	1,194	72	72	144	1,338
1983	Spring	1,153	56	66	122	1,275
	Fall	1,062	94	70	164	1,226
1984	Spring	1,181	84	39	123	1,304
	Fall	[b]	[b]	[b]	[b]	[b]
1985	Spring	1,124	144	92	236	1,360
	Fall	1,066	74	81	155	1,221
1986	Spring	1,345	128	97	225	1,570
	Fall	1,088	59	54	113	1,201
1987	Spring	1,430	81	139	220	1,650
	Fall	1,261	47	61	108	1,369
1988	Spring	1,505	136	83	219	1,724
	Fall	[b]	[b]	[b]	[b]	[b]
1989	Spring	1,574	142	148	290	1,864
	Fall	1,484	52	63	115	1,599
1990	Spring	1,464	130	84	214	1,678

[a] Not separated.
[b] Not surveyed.

The most recent method involves shore-based censuses of approximately 80% of the population, supplemented with aerial surveys of the remaining 20%. These surveys have been conducted twice each year (in spring and fall) since 1982. Results to date (spring 1990) are summarized in Table 7. These data indicate a stable population through about 1983–84 and then an increasing population from the mid-1980's to the present, with the exception of a 10% decline in the total number of otters counted in the 1990 spring census compared to the 1989 spring census. The reason for this decline is unknown: most of it occurred in the center of the range between Malpaso Creek and Dolan Rock (just south of Esalen).

To estimate the number of sea otters not seen during these surveys, a calibration study was begun in 1984. The calibration was done by a double-counting technique in which two teams of observers simultaneously counted sea otters in predetermined areas, otherwise using the same methods employed during the rangewide surveys. These counts were replicated five times in each of six areas, and the probability of sighting individual otters was estimated as $P = 2A/2A + B$, where A = the number of otters seen by both teams and B = the number of otters seen only by either one of the teams. Data from this study indicate an average probability of 0.945 that otters counted from shore will be sighted by a single team (Estes and Jameson 1988).

During the most recent survey (spring 1990), 1,464 independent sea otters (that is, all but dependent pups) were counted. When the correction factor of 0.945 is applied to this count, it provides an estimate of 1,549 independent otters. However, this is probably conservative since aerial counts—which detect a lower proportion of sea otters than do shore-based counts—were included in the survey total.

The number of pups in the population varies seasonally and possibly among years, with actual pup counts ranging from 122 to 290. Pup abundance usually is highest in spring, which reflects the peak pupping period of January to March (Estes and Jameson 1983a*, 1983b*). The ratio of dependent pups to independent animals from 1982 to 1990 during spring surveys varied form 10.4 to 21.0 pups per 100 independent otters, averaging about 16:100.

Population changes can be estimated from the data in Table 8. We based these calculations on estimated numbers and lineal extent of range. For each of these data sets, we made two series of calculations for average annual rate of population change. The calculations in one series were based on changes in estimated population size and range from 1914 through each succeeding year for which estimates were made. The other series of calculations was based on each sequential pair of years for which data were available—for example, 1914 and 1938, 1938 and 1947, and so forth.

From 1914 to 1984, the annual rate of increase in population size and range was about 5% (Fig. 32). Average rates of range increase, calculated from 1914 onward, seem to have declined slightly. The same pattern is evident in changes in rate of increase in the number of otters counted, although the magnitude of change is somewhat higher, indicating that density has declined within the established range. Patterns of change in rate of increase between sequential estimates are more variable, but they indicate a distinct reduction of growth during the last several decades and a modest decline in numbers from the mid-1970's. These data indicate that the California sea otter population has never increased more than about 6–7% each year, at least during this century. At best, the California population has increased at an average rate of about half to one-third the 17–20% per year growth rate of populations in Alaska (Estes, 1990a).

Range Expansion (1914–84) and Present Distribution

The range of the California population encompasses approximately 353 km of coastline extending from near Año Nuevo Point in San Mateo County to the Santa Maria River in San Luis Obispo County. Most of the established population—which includes the consistent presence of female and pup pairs or groups of three or more animals—is centered between Año Nuevo Point and the Santa Maria River. However, widely scattered individuals or pairs of otters occur north and south of these limits (Leatherwood et al. 1978). Temporal changes in distribution that have occurred from 1914 to 1984 (Fig. 33; Table 8) indicate that the rate of range expansion to the south has been more rapid than that to the north (Lubina and Levin 1988). Lubina and Levin (1988) analyzed the historical data on range expansion with a mathematical model incorporating population growth, diffusion, and advection. They concluded that growth and diffusion largely account for the observed patterns. Ames et al. (1983*) suggested that the rate of range expansion may be limited in part by mortality from entanglement in shallow water set-net fisheries, white shark attacks, and shooting.

The northern peripheral group of males moved northward from Seaside (near Monterey) to Soquel Point (near Santa Cruz) in February 1977 (Estes and Jameson 1983a*, 1983b*). Before then, the male peripheral group at the northern end of the range was located along Cannery Row off Hovden Cannery in Monterey (Loughlin 1977). In the 1970's, sea otters were occasionally observed singly or in pairs along the north coast between Santa Cruz and Año Nuevo Island; most sightings probably were of males, although in one case, a female and pup were seen crossing the channel between Año Nuevo Island and the mainland (Wilson et al. 1970–1976*; Yellin et al. 1977*; Riedman, unpublished data; F. Wendell, California Department of Fish and Game, Morro Bay, personal communication). From 1980 to 1983, the abundance of otters between Año Nuevo Island and Santa Cruz increased slightly. Most of these animals were centered at Sand Hill Bluff, where at

Table 8. *California sea otter* (Enhydra lutris) *population growth and range expansion, 1914–88 (updated from California Department of Fish and Game 1976*[a]*, U.S. Fish and Wildlife Service 1982).*

Year	Limit of range: Northern	Limit of range: Southern	Increase in range (km): North	Increase in range (km): South	Increase in range (km): Total	Average annual increase (in km): North	Average annual increase (in km): South	Average annual increase (in km): Total	Linear km of range	Total estimated population	Total[a] counted	Years between estimates
1914	Point Sur	Pfeiffer Point	—	—	—	—	—	—	(11)[b]	(50)[b]	—	—
1938	Rocky Point	Slate Hot Springs	11	21	32	0.46	0.88	1.34	43	310	—	24
1947	Malpaso Creek	Mill Creek	8	23	31	0.89	2.56	3.45	74	530	—	9
1950	Yankee Point (1951)	Gorda	2	13	15	0.67	4.33	5.00	89	660	—	3
1955	Point Lobos south shore	Ragged Point	3	16	19	0.60	3.20	3.80	100	800	—	5
1957	Pescadero Point	Point Sierra Nevada	11	6	17	5.50	3.00	8.50	125	880	—	2
1959	Point Joe	Point Piedras Blancas	6	6	12	3.00	3.00	6.00	137	1,050	—	2
1963	Outer Point	San Simeon	5	10	15	1.25	2.50	3.75	152	1,190	—	4
1966	Lover's Point	Pico Creek	0	6	6	0.00	2.00	2.00	158	1,260	—	3
1969	Seaside	Point Estero	6	13	19	2.00	4.33	6.33	177	1,390	—	3
1972	Seaside	Cayucos Point	0	15	15	0.00	5.00	5.00	192	1,530	—	3
1973	Moss Landing	Point Buchon	23	29	52	23.00	29.00	52.00	244	1,720		1
1974	Pajaro River	Diablo Cove	6	5	11	6.00	5.00	11.00	255	1,730	—	1
1975	Sunset State Beach	Diablo Cove	8	0	8	8.00	0.00	8.00	263	[e]	—	1
1976	Rio Del Mar	Pecho Rock	10	6	16	10.00	6.00	16.00	279	1,789[c]	—	1
1977	Soquel Point	Point San Luis	8	6	14	8.00	6.00	14.00	293	[e]	—	1
1978	Soquel Point	Point San Luis	0	0	0	0	0	0	293	[e]	—	1
1979	Soquel Point	Sunset Palisades	0	6	6	0.00	6.00	6.00	299	1,443[d]	—	1
1980	Soquel Point	Oceano	0	13	13	0.00	13.00	13.00	312	[e]	—	1
1982	Soquel Point	Oceano	0	0	0	0	0	0	312	[e]	1,338	2
1983	Sand Hill Bluff	Santa Maria River	10	15	25	10	15	25	337	[e]	1,216	1
1984	Sand Hill Bluff	Santa Maria River	0	0	0	0	0	0	337	1,372	1,304 (USFWS) 1,203 (CDFG)	1
1985	Sand Hill Bluff	Santa Maria River	0	0	0	0	0	0	337	[e]	1,360	1
1986	Sand Hill Bluff	Santa Maria River	0	0	0	0	0	0	337	[e]	1,570	1
1987	Año Nuevo	Santa Maria River	16	0	16	16	0	16	353	[e]	1,650	1
1988	Año Nuevo	Santa Maria River	0	0	0	0	0	0	353	[e]	1,724	1
Totals			133	209	342	1.38	1.61	2.99	353			74

[a] Ground count initiated 1982.
[b] No records, rough assumptions made (see text).
[c] Some small pups included.
[d] Poor weather conditions during survey led to lack of confidence in final figure; also some large pups included.
[e] No estimates calculated.

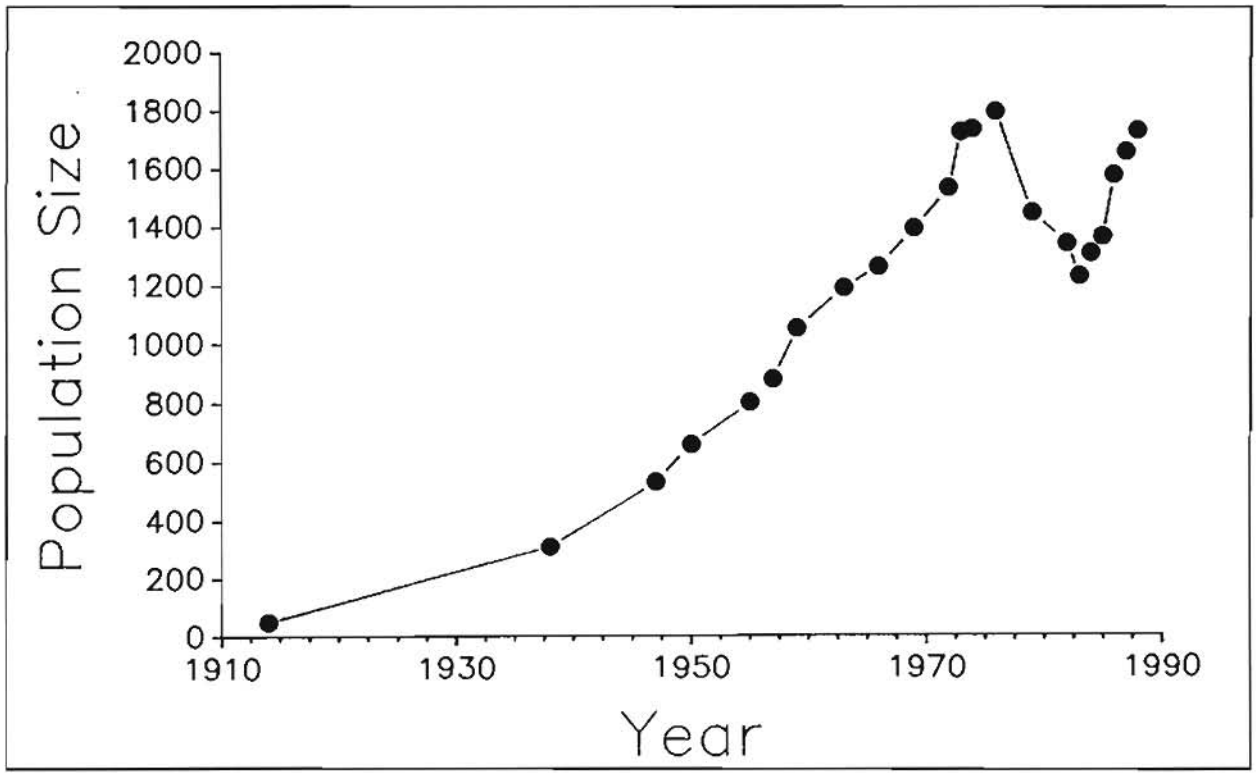


Fig. 32. Trends in the California sea otter population, 1914–88.

least one mother and pup pair was consistently observed (Bonnell et al. 1983*). In February 1984, a group of 19 otters containing 5 female and pup pairs was observed near Sandhill Bluff (Ames and Hardy, unpublished data). During 1980–83, the size of the large male raft at Soquel Point decreased (Bonnell et al. 1983*; Estes, unpublished data), and the abundance of otters occupying the eastern Monterey Bay from La Selva Beach to Marina correspondingly increased (Bonnell et al. 1983*). A group of otters, presumably males, inhabited lower Elkhorn Slough and Moss Landing in winter of 1984. The size of this group seems to fluctuate seasonally (Kvitek and Oliver 1988; Kvitek et al. 1988), as does the male group near Soquel Point (Estes, unpublished data), both reaching highest numbers in winter and spring.

From 1977 to 1982, southward range expansion occurred from Pecho Rock to Oceano (about 25 km); in 1983–84, it expanded an additional 15 km from Oceano south to the Santa Maria River (Figs. 33 and 34; Estes and Jameson 1983b*). From 1973 to 1979, southern peripheral groups of males occurred at Point Buchon and Diablo Cove. In 1979, females began to occur in this area, which at latest observations contained a low-density population of females, pups, and territorial males (Benech 1981*; Estes and Jameson 1983a*; California Department of Fish and Game and U.S. Fish and Wildlife Service, unpublished data). Estes and Jameson (1983b*) reported a population decline of 79 otters from 1976 to 1982 in the area between Diablo Canyon and Point San Luis, while there was a net increase of 16 otters south of Point San Luis.

The southernmost established group of otters, centered in the Shell Beach to Oceano area, appears to be predominantly composed of males. Female and pup pairs have not been observed south of Shell Beach. A number of otters, presumably males, were seen south of Oceano to the Santa Maria River. Several otters, mostly single animals, have been sighted between the Santa Maria River and Point Conception from 1983 to the present (February 1989; Bonnell et al. 1983*; California Department of Fish and Game, unpublished data).

There have been recent changes in abundance throughout the center of the range. From 1981 to 1983 the density of otters declined in the Monterey Bay area and along the Big Sur coast from Pfeiffer Point to Gamboa Point; correspondingly, density increased from Cypress Point to Point Sur (Bonnell et al. 1983*; Estes and Jameson 1983b*). Estes and Jameson (1983b*) reported an overall decline in numbers from Monterey Harbor to Diablo Canyon between 1976 and 1982.

Environmental Variables Affecting Distribution Patterns

Small-scale, local distribution patterns throughout most of the range seem to be affected by weather and sea conditions, and especially by the abundance and distribu-

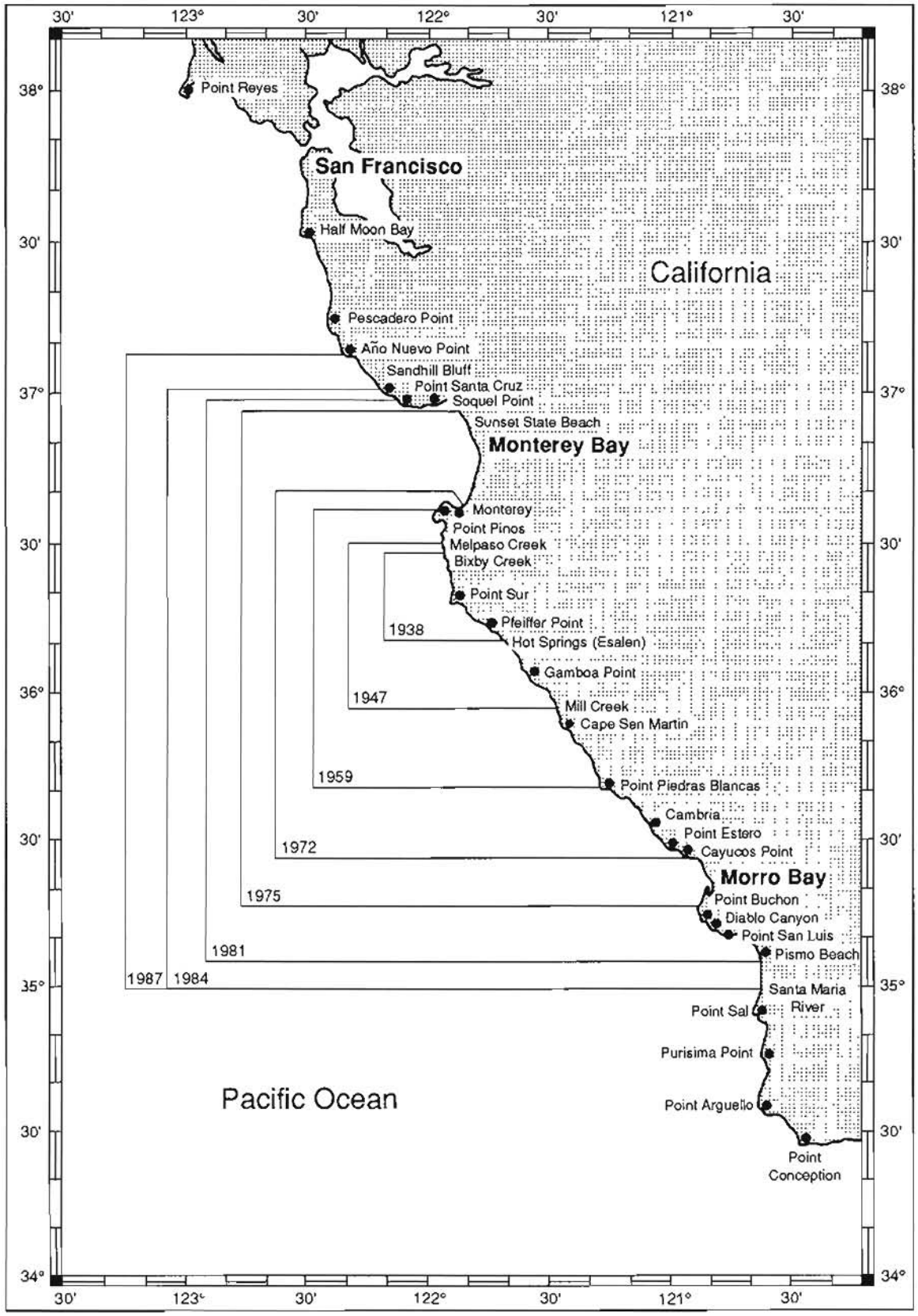


Fig. 33. Sea otter range expansion in California, 1938–89.

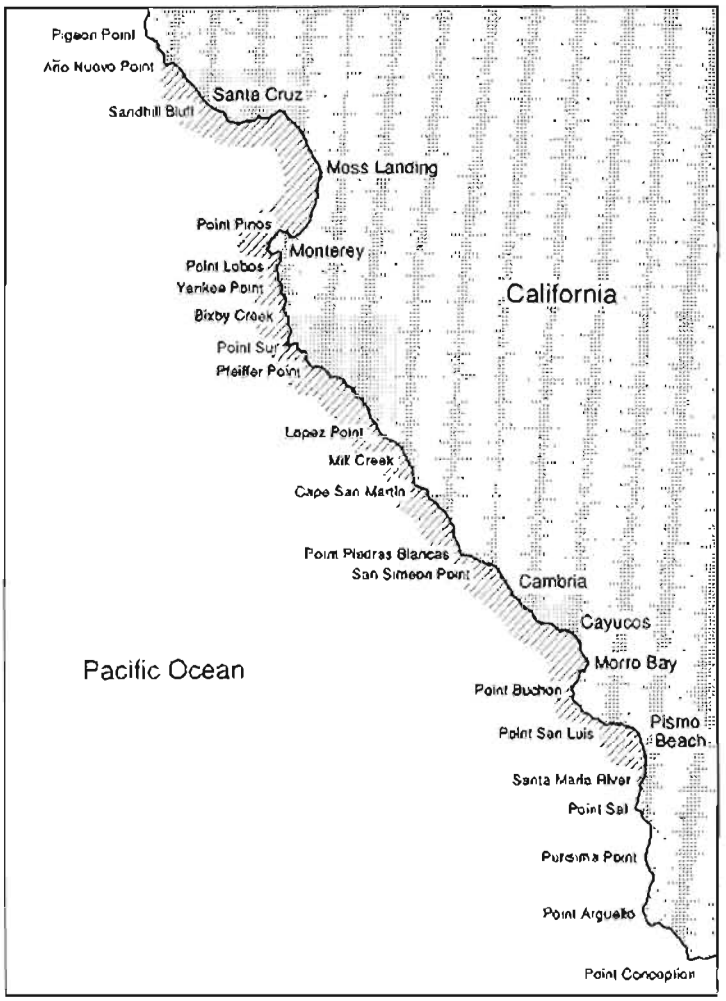


Fig. 34. Central California coastline, indicating range of sea otter (*hatched areas*) and areas referred to in text.

tion of the kelp canopy, all of which vary seasonally. The location of protected rafting areas also influences sea otter distribution, especially during winter–spring periods of high winds and rough seas (Sandegren et al. 1973; Riedman 1984a*, 1984b**; Jameson, unpublished data). Sandegren et al. (1973) found that during prolonged periods of inclement weather or rough seas, mothers with pups moved to calmer, protected coves. In addition, preliminary information suggests that rough seas, high winds, and heavy rain may cause a more dispersed distribution pattern by disrupting groups of resting otters in California (Sandegren et al. 1973; Estes et al. 1986; Riedman, unpublished data) and in Alaska (Garshelis 1983).

Local distribution patterns of sea otters are correlated with seasonal changes that occur in the surface kelp canopy (Estes and Jameson 1983a*; Riedman 1984a*, 1984b**; Jameson 1989; VanBlaricom and Jameson, unpublished data). In winter and early spring, the kelp canopy typically is substantially reduced; kelp that remains is usually in areas protected from heavy seas and ocean swell, at which time sea otter distribution becomes more dense as the animals aggregate in the few available kelp beds. The winter–spring reduction in kelp canopy may also increase male–male competition for suitable territories, in part affecting the seasonal movement of adult males from the center of the range (Jameson 1989). In summer and fall, distribution becomes more dispersed, and otters may rest farther offshore, reflecting the seasonal increase in kelp canopy abundance and offshore kelp distribution (Jameson 1989; VanBlaricom and Jameson, unpublished data).

Demographic Variables Affecting Dynamics of the California Population

Population changes could be affected by three general factors: emigration, natality, and mortality. Each factor may vary with age and sex, and each may be affected by density-dependent and density-independent processes

(Estes 1981; U.S. Fish and Wildlife Service 1982; Ralls et al. 1983).

Extralimital occurrences of sea otters are relatively rare and do not seem to constitute a significant level of emigration. Over the past 30 years, extralimital sightings of sea otters have been made north of the established range as far as Tillamook Bay, Oregon (Pederson and Stout 1963), and Cape Mendocino, California (Orr and Poulter 1964; Bonnell et al. 1983*; Wendell, personal communication), and as far south as central Baja California, Mexico (Leatherwood et al. 1978; Estes, unpublished data; Wendell, personal communication). Because extralimital sightings are infrequent (and in some cases probably represent consecutive sightings of the same individual), and since large numbers of otters are not seen concentrating outside of the established range, it seems unlikely that substantial losses to the population have occurred through emigration (Estes 1981; U.S. Fish and Wildlife Service 1982).

Annual recruitment to the California population seems to be comparable to that observed in Alaskan populations (but see Estes 1990a). In both California and Alaska, average proportions of 20–30 pups per 100 independent otters are found during censuses taken near the end of the pupping season; average proportions of 15–16 per 100 are observed throughout the year, although rangewide censuses conducted in California indicate that this ratio may vary from year to year. Overall birth rates appear similar in both populations (Estes 1981; Estes and Jameson 1983a*); therefore, the recent lack of growth (even possible decline in numbers) shown by the California population probably is due to elevated mortality (Estes 1981).

Growth-limiting mortality of the California sea otter population may result from density-independent or density-dependent factors. Miller (1980) believed that the California population was at equilibrium density and that starvation was the principal (density-dependent) limiting factor. However, Estes et al. (1986) found that the proportion of time allocated to foraging was indicative of populations below equilibrium density in Alaska and Oregon. Estes et al. (1986) believed this conclusion to be further supported by the facts that (1) unoccupied habitat into which the population presumably could grow exists at both ends of the present range, and (2) recent estimates of sea otter entanglement mortality in the coastal set-net fishery are 7–8% of the total population each year (Wendell et al. 1985*). However, by using radiotelemetry, Ralls and Siniff (1988*) found that juvenile females in the central part of the range spent more time foraging and experienced higher mortality than other age and sex classes (except adult males, which had the lowest survival rates). They believed these data were inconsistent with the conclusion of Estes et al. (1986), thus implying that further growth in the California sea otter population was limited by food availability. Ralls and Siniff (1988*) reasoned that juvenile females were at a competitive disadvantage with other age and sex classes in foraging, so they experienced a resulting higher rate of mortality. Consequently, food availability was probably limiting further population growth because of the high reproductive value of juvenile females. The possibility also exists that density-dependent processes may be operating in the center of the range, where the population has been established for the longest time, while density-independent factors may be affecting population growth at either end of the range, where the frequency of mortality due to set-net fishing, shark attacks (northern periphery), and shooting incidents (southern periphery) is highest (Ames et al. 1983*).

Siniff and Ralls (1988b) found that half (8) of 19 sea otter pups born to radio-instrumented adult females in California survived to weaning. Similar data obtained by Garshelis (1983) in Prince William Sound led Siniff and Ralls to suggest that early pup survival rate is lower in central California than in Alaska. This conclusion is further supported by the work of Monnett and Rotterman (1988b*), who found that, excluding human-caused deaths, nearly 100% of the pups they studied in Prince William Sound survived from the time they were instrumented to the time they were weaned. These differences could account for the lower growth rate of the California sea otter population compared with that in the Aleutian Islands, Washington State, British Columbia, and southeastern Alaska (Estes 1990a). It should be noted, however, that Monnett and Rotterman (1988b*) found pups to survive in Prince William Sound that were weaned only an estimated 2.5 months after birth. Heisey and Fuller (1985) developed methods for estimating annual survival from telemetry data; with these methods, Siniff and Ralls (1988*) estimated the following survival rates for sea otters in California: adult females, 0.91; adult males, 0.67–0.71; juvenile females, 0.77–0.85; and juvenile males, 0.86–0.88. Because these radio-tagged sea otters were also flipper-tagged, Siniff and Ralls (1988*) were able to estimate annual flipper tag survival to be 0.74. They found, in addition, that significantly more of the radio-tagged otters lost both flipper tags than expected from the single tag loss rate, indicating that individual sea otters have different tendencies to lose tags. Riedman, Staedler, and Estes (unpublished data) have also found individual variation in rate of tag loss among otters in the Monterey Bay area.

Sea otter natural mortality outside California is known mainly from studies done in Prince William Sound (Garshelis 1983; Monnett and Rotterman 1988b*) and the western Aleutian Islands (Kenyon 1969). Kenyon (1969) reported that as the sea otter population at Amchitka grew toward food limitation, starvation-related mortality increased substantially. From carcasses found on the beach, he determined that about 70% of these animals were

juveniles, and that the sex ratio was biased toward males. Few data are available from other populations because those that are probably food limited have not been studied, and carcasses from those that are below food limitation are seldom found on the shore. This is probably because individuals in populations that are not food limited rarely haul out, and because the mortality rate, especially among juveniles, is low. In their study of radio-tagged weanling sea otters, Monnett and Rotterman (1988b*) showed that males and females died or disappeared in nearly equal proportions. However, female losses were concentrated in January–April whereas male losses were more evenly distributed among the seasons. This pattern is different from the one reported by Kenyon (1969) at Amchitka Island. Unfortunately, whether food is an important limiting resource to sea otters in Prince William Sound is unclear. Since the habitat there is very different from that at Amchitka Island (Prince William Sound consists mainly of soft-sediment benthos and is protected from ocean swells, whereas Amchitka Island is a highly exposed, rocky benthos system), these apparent differences in juvenile mortality patterns are hard to interpret.

Sources of Documented and Potential Mortality

Documented Mortality

Introduction and Summary

The California Department of Fish and Game has investigated sea otter mortality in California since 1968. Ames et al. (1983*) and Ames (unpublished data) summarized information on 1,733 sea otters that died or were otherwise removed from the population from 1968 to 1989. Percentage of the total mortality that is recovered is unknown, and recovered animals undoubtedly represent only a portion of the total sea otter mortality.

Ames et al. (1983*) pointed out that a number of variables relating to temporal and spatial differences in carcass recoverability and search effort must be considered when interpreting trends in these data. The following factors may influence the likelihood that a dead otter will wash ashore and be recovered: cause of death, wind and current patterns, the presence and density of kelp canopies, location, age of the otter (pup versus independent animal), search effort, and public awareness of the salvage program. Recoverability may be influenced by cause of death (e.g., sea otters drowned at depth in gill nets tend to sink, but otters that are shot tend to float on the surface). This is because normal air volume in the lungs is the principal source of buoyancy (Kooyman 1973). In addition, some sea otter carcasses have been known to drift considerable distances; therefore, the area of recovery along the coast does not necessarily indicate the area of death.

The proportion of dependent pups recorded is probably especially low relative to actual mortality, due to difficulties associated with recovering small pup carcasses. Because of the rapid rate of decomposition and the likelihood of sand and other debris obscuring them, dead pups are less conspicuous than adults when floating in kelp beds or lying on the beach. In addition, females sometimes care for dead pups for several days, further reducing the likelihood of recovery (Ames et al. 1983).

Sea otter carcasses are recovered most frequently at the ends of the range (Fig. 35). Some possible explanations for this pattern include (1) systematic salvage efforts were not conducted in much of the center of the range until 1983; (2) the remoteness and low human population density in the center of the range result in few public reports of otter mortality; and (3) mortality may be comparatively low in the center of the range.

Monthly salvage efforts in the relatively isolated central and southern portions of the range have resulted in increased carcass recoveries in these areas (Jameson 1983*, 1984*, Bodkin, personal communication) Information collected during a study in the northern part of the range from March to August of 1984 showed that monthly salvage efforts increased the number of carcasses retrieved in isolated areas but not in areas of high accessibility or human population density (Riedman 1984c*).

Weekly salvage efforts conducted by the Fish and Wildlife Service near Point Piedras Blancas have shown that a sea otter carcass remains on the beach for an average of 18 days, although there is considerable variation (maximum = 100 days; Bodkin, personal communication).

From 1968 to 1984, the number of sea otter carcasses recovered generally increased (Table 9). However, the number of dead sea otters reported each year has also increased over this period, along with an increase in public awareness of the California Department of Fish and Game salvage program. After 1984, sea otter mortality declined, probably because fewer otters were being drowned in gill and trammel nets. Gerrodette (1983*) reviewed sea otter salvage efforts conducted from 1968 to 1983 and discussed inadequacies in the available data.

The causes of death classified by California Department of Fish and Game (CDFG) and the number and proportion of otters within each mortality category are presented in Table 9. Ames et al. (1983*) and Ames (unpublished data) provided a description of each mortality category. Of the 1,733 sea otters that died or were otherwise removed from the California population from 1968 to 1989, 53 were animals either accidentally killed or captured for public display or research purposes. Of the

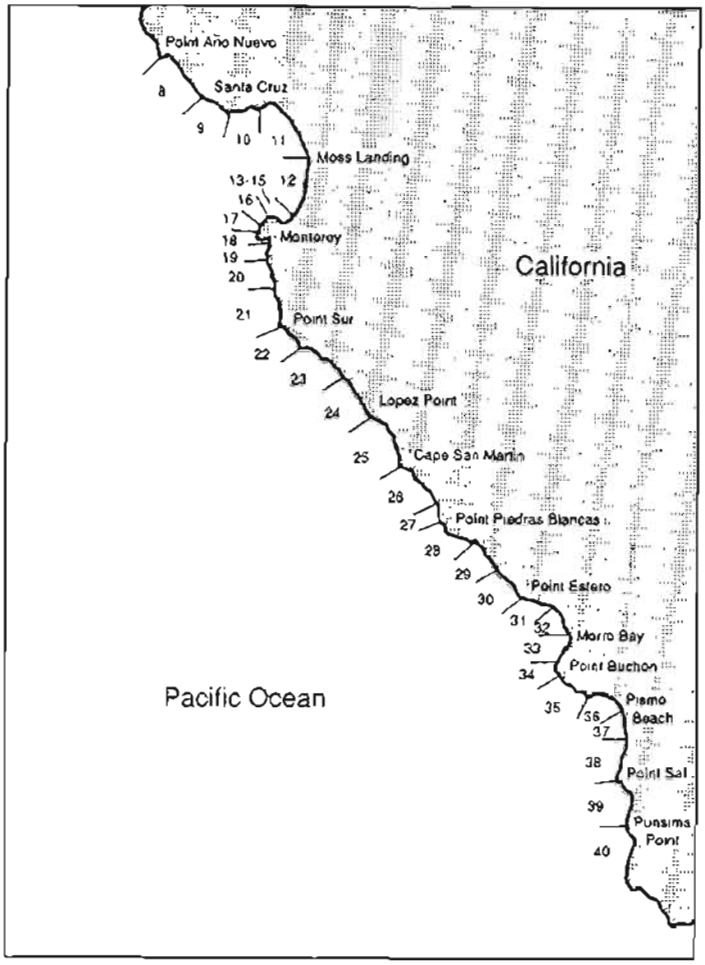


Fig. 35. California Department of Fish and Game mortality recovery areas in central California.

remaining 1,680 recorded deaths, 933 (56%) died of unknown causes (CDFG mortality categories 1, 2, and 3). Many of these carcasses were badly decomposed. The cause of death was conclusively or probably determined in 402 (24%) of the cases (CDFG categories 4, 5, 7, 8, 10, 11, 14, and 16). Mortality involving dependent pups (categories 12, 13, and 15) represented 301 cases, or 18% of the total mortality.

Information on 1,027 dead sea otters collected from 1968 to 1982 showed that when sex, age, and state of decomposition were recorded, 525 (58%) were males and 386 (42%) were females; 525 (52%) were adults, 183 (18%) were subadults, and 293 (29%) were pups; 607 (60%) were decomposed, and 402 (40%) were relatively fresh or in fair condition (Ames et al. 1983*).

Ames et al. (1983*) documented the following trends with respect to sea otter mortality. Monthly mortality data were characterized by a bimodal frequency distribution, with mortality peaking in early spring (March–April) and summer (June–August). The frequency of pup mortality almost always peaked in winter–spring, while the frequency of adult mortality often peaked in summer–fall. The winter–spring peak in pup mortality, which occurs during the peak pupping season, suggests that many females may lose their pups at a young age. Males predominated in the sample of small dead pups (<75 cm total length). Mortality of females and pups was generally higher in the center of the range (Point Pinos to Cambria), while the proportion of male carcasses recovered was highest at either end of the range.

The most significant sources of sea otter mortality in California seem to be (1) incidental drowning in commercial set nets, (2) white shark attacks, (3) a combination of conditions related to pathological disorders, starvation, and adverse winter weather, and (4) possible shooting incidents occurring primarily in the southern part of the range.

Mortality Caused Directly by Humans

Net Entanglement. Several kinds of evidence indicate that incidental drowning of sea otters in gill and trammel nets may represent a significant source of mortality. From June 1982 to January 1985, 29 otters were observed

Table 9. *Causes of sea otter* (Enhydra lutris) *mortality, and the number and proportion of otters within each category, 1968–89. Modified from Ames et al. 1983*[a] *and Ames, unpublished data.*

Mortality category	Year																						Total	Percent[a]
	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989		
1. Unknown	3	11	16	4	9	20	11	23	38	32	43	28	57	42	22	3	21	14	13	11	9	12	452	26.9%
2. Uncertain with trauma	1	4	7	2	6	7	1	2	4	5	4	8	13	5	4	7	11	4	9	9	4	10	127	7.6%
3. Uncertain with no trauma	2	1	8	2	5	10	3	1	2	18	11	6	28	46	32	48	29	12	28	1	23	25	354	21.1%
4. Shark-bitten	0	0	0	0	1	2	0	3	2	5	2	3	6	7	1	10	4	1	2	7	3	2	61	3.6%
5. Probably shark-bitten	3	4	4	7	6	4	6	3	1	2	4	2	3	6	3	2	7	4	2	6	4	3	86	5.1%
6. Lacerated	1	1	2	2	6	6	6	6	1	1	1	0	2	3	1	0	2	1	0	2	1	3	48	2.9%
7. Shot	1	1	5	2	0	3	1	0	2	4	1	1	3	5	5	3	6	6	3	9	1	3	69	4.1%
8. Probably shot	0	3	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	8	0.5%
9. Research and display	0	6	1	0	5	0	0	4	6	7	1	3	0	0	0	0	1	1	1	8	3	6	53	—
10. Other man-causes (entanglement in fishing line)	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	2	4	2	0	11	0.7%
11. Other natural causes (pathological disorders)	0	0	2	0	2	4	0	1	1	2	0	7	1	2	3	6	2	7	2	4	8	9	63	3.7%
12. Dependent animal	4	3	3	0	3	13	11	7	7	17	9	8	26	30	16	20	24	5	11	1	17	4	249	14.8%
13. Dependent animal with trauma	0	2	1	0	4	6	3	0	0	2	1	0	4	2	1	0	2	0	0	0	0	0	28	1.7%
14. Mating wounds in females	1	0	0	2	2	5	2	2	0	2	3	2	1	2	0	1	6	1	1	0	3	2	38	2.3%
15. Dead pups with mother	0	0	1	0	0	0	0	0	0	1	0	1	2	3	4	2	0	2	3	1	2	2	24	1.4%
16. Net-drowned[b]	0	0	1	0	0	0	0	0	0	0	1	0	0	0	6	6	16	12	3	5	5	11	66	3.9%
Total	16	36	52	21	49	82	44	52	64	99	81	69	147	153	99	118	132	70	80	91	86	92	1733	
Total (without research category 9)	16	30	51	21	44	82	44	48	58	92	80	66	147	153	99	118	131	69	79	83	83	86	1680	

[a] Using total without research category 9.
[b] Category 16, previously "immature females with bite wounds," was discontinued; these animals are included in Category 14. Category 16 now comprises net-drowned otters.

Table 10. *Estimates of incidental drowning of sea otters (*Enhydra lutris*) in gill and trammel nets, calculated from estimates of set-net effort 1973–83. (From Wendell et al. 1985*).*

Year	Number of landings	Estimated number of dead sea otters[a]
1973	457	49
1974	645	69
1975	[b]	69
1976	980	105
1977	663	71
1978	874	93
1979	1,449	154
1980	1,407	150
1981	1,578	168
1982	1,057	113
1983	696	73

[a] Estimate of effort is based on the number of landings of set-net boats within the sea otter range. Estimated take is based only on the rate of take observed in 1983 and part of 1982. Therefore, the estimated number of dead sea otters is only a rough approximation in years before 1982.
[b] No data.

drowned (or otherwise known to have drowned) in commercial fishing nets: 6 in 1982, 6 in 1983, 16 in 1984, and 1 in 1985 (to January 5; Ames et al. 1983*; Bishop 1983*, 1984*; Croll and Keating 1983*; Wendell et al. 1985*). However, only a small proportion of the set-net fishing effort within the sea otter's range was sampled for sea otter mortality. For example, 3% of the halibut set-net effort in 1982 was sampled for recovery of dead otters (Ames et al. 1983*), 10% was sampled in 1983, and 15% was sampled in 1984 (California Department of Fish and Game, unpublished data). Therefore, the actual frequency of net-entanglement mortality for the California population was presumed to be substantially higher than indicated by the confirmed observations of drownings. Extrapolations from the number of otters observed drowned and the proportion of the set-net fishery sampled indicated that from June 1982 to June 1984, an average of 80 sea otters drowned in gill and trammel nets each year (Wendell et al. 1985*). Wendell et al. (1985*) attempted to estimate annual entanglement mortalities between 1973 and 1983 and found that they may have ranged from 49 to 168 otters per year (Table 10). However, the estimates before 1982 were based on a rough approximation of set-net fishing effort as well as uncertain changes in the distribution of otters and fishing activity that varied from year to year (Hardy, personal communication).

An analysis of set-net effort and temporal and spatial aspects of sea otter mortality also supports the idea that a significant proportion of otter mortality is associated with commercial set-net fishing. Ames et al. (1983) compared the monthly fishing effort (defined as the landing and sale of starry flounder [*Platichthys stellatus*] or California halibut [*Paralichthys californicus*] by fishermen using entangling nets) with monthly fluctuations in numbers of decomposed, independent otters that died of unknown causes and were recovered from areas close to intensive set-net fishing. From 1979 to 1982, there was a high correlation ($r = 0.88$; $P < 0.1$) between the two variables; that is, summer was the peak for both halibut set-net effort and mortality involving independent, decomposed otter carcasses near intensive fishery areas. There was also a correlation in previous years, although the sample size of dead otters was low in some areas during certain years.

Decomposed beach-cast sea otters were used in the analysis because evidence suggests that net-drowned otters sink and remain underwater until decomposition gases accumulate (Ames, personal communication). Ames et al. (1983) found that the frequency of beach-cast otter carcasses in fresh condition peaked in late winter, while the number of decomposed otter carcasses tended to peak in summer, when set-net fishing operations were most intensive.

Although gill and trammel net fishing occurs throughout the sea otter's range, the principal set-net commercial fisheries—starry flounder and California halibut—are situated in sandy-bottom areas at both ends of the sea otter's range: in Monterey Bay and in the Morro Bay and Avila Beach areas (Fig. 34). Monofilament and multifilament nylon set nets have incidentally caught and drowned thousands of diving marine birds and numerous marine mammals, especially in the early 1980's in the Monterey Bay area (Croll and Keating 1983*). Before 1979, the gill net fishery in Monterey operated at a fairly low level, with about five boats fishing in the bay each year. In the early 1980's, set-net fishing operations increased to include about 18–26 commercial fishing boats per year (Croll and Keating 1983*; Wendell et al. 1985*); set-net fishing activity subsequently declined to about 8–10 commercial fishing boats per year (Hardy, personal communication).

Because many sea otters were suspected of being drowned in gill nets—and since it is difficult to positively determine that drowning was the cause of death, even in fresh carcasses (e.g., Yagil et al. 1983)—a number of observer programs were implemented to monitor incidental take of sea otters in set nets. In the Monterey Bay, observations of gill and trammel net fishing operations were conducted by the California Department of Fish and Game (CDFG) in 1980 and by students of both CDFG and Moss Landing Marine Laboratories in 1981 and 1982 (Croll and Keating 1983). CDFG has maintained an observer program in Monterey since 1983 (C. Haugen, California Department of Fish and Game, Monterey, Calif., personal communication). The Morro Bay and Port San Luis set-net fisheries have been monitored since 1982

(Bishop 1983*, 1984*; California Department of Fish and Game, unpublished data). Direct observations of entanglement mortality are made from shore through telescopes or at sea from small boats stationed close to the fishing boats. Observers record the number of sea otters caught during each occurrence of net pulling: they also record the number of birds, fish, and other marine mammals and the depth, location, and estimated net length.

The use of large mesh set nets in Monterey Bay was prohibited within the 10-fathom (18-m) isobath (depth contour) by California law in 1982; use was restricted from water <15 fathoms (27 m) in spring 1984. Since the 15-fathom closure, fewer sea otters have been drowned in gill or trammel nets in the Monterey Bay area. In late January 1985, a temporary emergency closure prohibited the use of entangling fishing nets (with mesh >3 inches) within the 15-fathom isobath from Monterey to the mouth of the Santa Maria River. On 24 May 1985, the governor of California signed into law a similar closure to gill and trammel net fishing (with net mesh ≥3.5 inches).

Hardy (personal communication) estimated that the effect of the 1985 closure was to reduce net entanglement by about 50%; in 1982–84, an estimated 80 otters drowned each year in gill and trammel nets, but since 1985, the yearly number of net-drowned otters declined to an estimated 30–40. Ten otters were observed drowned in gill nets throughout the range between 1 February 1985 and 1 April 1986. All but one of the net drownings occurred in the southern and central parts of the range (south of Point Sur), especially in the area between Cape San Martin and San Simeon Point; this area was subsequently closed to 20 fathoms. In addition, only 69 otter mortalities were recorded in 1985: this represents a decline from the 131 otters recorded in 1984 (Ames, unpublished data).

The importance of entanglement mortality to other sea otter populations is largely unknown, although various nets and traps that are probably capable of entangling and killing sea otters are used throughout much of the species' range. Significant numbers of sea otters seem to be lost to fishing gear in Prince William Sound and the nearby Copper River Delta (Simon-Jackson and Rotterman 1987; Monnett and Rotterman 1988b*).

Shooting. About 4.6% (77 of 1,680) of the recorded sea otter mortalities from 1968 to 1989 was attributed to known or probable instances of shooting (Mattison and Hubbard 1969*; Wild and Ames 1974; Morejohn et al. 1975; Ames et al. 1983*; Ames, unpublished data). Cases of shooting can be conclusively determined by the presence of visible bullet wounds or by X-ray photography, which allows the detection of bullets, shotgun pellets, or fragments of bullets.

Each year the recorded number of sea otters that died from being shot ranged from 0 to 9 animals and showed no clear pattern of increase or decrease. However, shooting was responsible for a greater proportion of mortality in the southern part of the range. From 1968 to 1983, about 9% of the sea otter carcasses found south of Cambria had been shot, while 2% of those recorded north of Cambria had been shot (Ames et al. 1983*). Ames et al. (1983*) suggest that shooting incidents occurring near the southern edge of the range may tend to curb southward emigration of sea otters.

Collisions with Boats and Propeller Injuries. Mortality associated with laceration and trauma resulting from collision with boats and contact with propeller blades seems to be negligible. Propeller injuries have been suspected of causing significant mortality associated with lacerated carcasses (e.g., Wild and Ames 1974; Morejohn et al. 1975). However, subsequent reexamination of mortality records revealed that most cases thought to be propeller injuries were actually attributable to white shark bites, and that boat collisions and propeller injuries were rare (Morejohn et al. 1975; Ames and Morejohn 1980; Ames et al. 1983*).

Only one incident has been documented in which a sea otter was known to have been injured by a boat propeller: In 1970, a small salmon boat (powered by a 65-hp outboard engine) traveling at full speed struck an otter just beyond Monterey Harbor. Although the otter was not retrieved, a considerable amount of blood was observed in the water. A beached, lacerated otter was found two days later in the vicinity of the incident and died a week later (Ames and Morejohn 1980).

The definitive criteria for diagnosing boat propeller lacerations are unclear, but preliminary information (derived from a California Department of Fish and Game experiment in which two sea otter carcasses were intentionally struck by a vessel traveling at full speed) indicated that one carcass sustained two parallel lacerations preceded by a distinctive shaved area, while the other carcass was evidently destroyed (Ames and Morejohn 1980).

Entanglement in Fishing Lines. Sea otter mortality from entanglement in fishing lines with and without fishing hooks is extremely rare. From 1968 to 1989, only 11 (0.7%) of 1,680 otters died after becoming entangled in fishing lines (Ames, unpublished data).

Accidental Mortality Associated with Field Research Operations and Capture for Public Displays. This California Department of Fish and Game mortality category (9) includes all sea otters that incidentally died as a result of field research and capture operations, as well as those removed from the population for actual public display or research purposes (some of which are still alive). Two otters that drowned in entangling nets set by researchers to sample fish (near Point Piedras Blancas and Moss Landing) were included within another mortality category (16), encompassing all sea otters drowned in commercial fishing nets (Ames et al. 1983*). A total of 53 of

1,680 otters (3% of the total otters lost) either died or were placed in captivity for research, rehabilitation, or public display (Ames et al. 1983*; Ames, unpublished data).

Natural Mortality

Predation by White Sharks. White sharks occur in temperate coastal waters worldwide. On the west coast of North America, the species is known from Washington to Baja California, with large individuals in nearshore waters seeming to be most abundant in central and northern California (Klimley 1985). Large white sharks (>3 m total length) attack and feed on marine mammals (Tricas and McCosker 1984; Klimley 1985). Recent increases in white shark attacks on pinnipeds (Ainley et al. 1985) and humans (Lea and Miller 1985) in California and Oregon have caused some people to speculate that shark populations also have increased, probably in response to growing pinniped populations. However, Lea and Miller (1985) and Klimley (1985) pointed out that these patterns may well have been caused by increasing numbers of people and pinnipeds in coastal waters, regardless of any change in size of the shark population.

Attacks on sea otters by white sharks may represent a significant source of natural mortality in the California population. Sea otter carcasses with definitive white shark bites have been documented since 1959 (Orr 1959; Wild and Ames 1974; Morejohn et al. 1975; Ames and Morejohn 1980; Ames et al. 1983*) and probably have occurred throughout the historical association of the two species. Ames (unpublished data) attributed about 12% (195 of 1,680 otter deaths) of the recorded mortality from 1968 to 1989 to white shark attacks; 61 of the carcasses were definitely shark-bitten, 86 were probably shark-bitten, and 48 were lacerated. Ames and Morejohn (1980) determined that white shark bites seemed to be responsible for 9–15% of all recorded mortalities in California from 1968 to 1979.

The frequency of white shark attacks on sea otters could be higher than the number of definite or probable shark-bitten, beach-cast otter carcasses if many of the badly decomposed carcasses that were not examined were shark-bitten. Moreover, it is unknown if white sharks regularly prey on sea otters, nor is it known whether they actually consume many otters following an attack. If so, the proportion of otter mortality from shark attack would be still higher. Because of the relative size of the two species, and the fact that surface shark attacks typically involve jaw protrusions that produce a large mouth gape (Tricas 1985), sea otters could easily be consumed without leaving any remains.

Several lines of evidence, however, suggest that white sharks prefer to prey on pinnipeds, such as northern elephant seals and harbor seals, and that the apparent increase in white shark attacks along the California coast is related to increases in abundance of these pinniped species (particularly elephant seals) over the past 20–30 years (Ainley et al. 1981, 1985; McCosker 1981; Le Boeuf et al. 1982). Sea otter remains have not been discovered in white shark stomachs, although few sharks have been caught or examined from within the sea otter's range (Klimley 1985). Furthermore, it seems unlikely that sea otters have the agility or speed necessary to escape an attacking white shark, as some pinnipeds might (Ainley et al. 1985). Therefore, the large number of otter carcasses sustaining shark bites may represent animals that the shark mistook for another prey species, such as harbor seals, and chose not to consume after the initial attack. According to McCosker (1981, 1985) and Tricas and McCosker (1984), the attack strategy of white sharks is to severely lacerate their prey during a single, initial hit, then to return and eat it after the prey has bled to death. Based on the wounding patterns of humans (Miller and Collier 1980), pinnipeds (Ainley et al. 1985), and small cetaceans (Arnold 1972), white sharks usually attack marine mammals from beneath their posteriors. This strategy seems to minimize risk of injury to the shark, that might be incurred in a struggle with the large, powerful animals on which they typically prey. In view of the extensive tissue damage often inflicted on large-sized pinnipeds (Le Boeuf et al. 1982), it is peculiar that shark-bite injuries on sea otter carcasses are comparatively mild, which also suggests that white sharks often do not follow through after initial attacks on sea otters. It may also be that the comparatively small mass of a sea otter has insufficient static inertia for a shark to work against, in effect causing an attacked otter to be knocked aside rather than sliced apart.

Although shark-bitten sea otters in California have been found throughout their range, the highest proportion of shark-bitten carcasses are recovered north of Point Sur, especially in the Monterey peninsula area. Between Cypress Point and Point Pinos, for instance (Fig. 35), 36% of the otter mortality from 1968 to 1983 (including all undiagnosed, lacerated carcasses) may have been due to white shark attack (Ames and Morejohn 1980; Ames et al. 1983*). This pattern is consistent with the distribution of white shark attacks on humans (Lea and Miller 1985) and pinnipeds (Klimley 1985), most of which have been reported north of Point Sur. Klimley (1985) speculated that the number of pinnipeds in this area attracts large white sharks to the nearshore environment.

Shark-bitten and lacerated sea otter carcasses have been observed throughout the year, although they have been recovered most frequently in late winter and spring and least frequently in fall (Ames and Morejohn 1980; Ames et al. 1983*). In comparison, at Año Nuevo (Le Boeuf et al. 1982) and the Farallon Islands (Ainley et al. 1985), most shark-bitten northern elephant seals were observed in late fall and winter. Ainley et al. (1985) further reported that white shark attacks on harbor seals at a coastal site in

the Gulf of the Farallones were most frequent during spring and summer, from which they speculated that sharks may make inshore–offshore movements in response to seasonal availabilities of the relatively vulnerable pups of the pinnipeds. These observations suggested that the increased occurrence of shark-bitten sea otters in late winter and spring may be caused by the seasonal movement of sharks towards shore in search of young phocid seals, for which the sea otters are perhaps mistaken. Although the annual number of shark-bitten sea otter carcasses observed from 1968 to 1982 has varied from year to year (Ames et al. 1983), shark attacks on elephant seals north of the sea otter's range near Año Nuevo and the Farallon Islands have increased since the mid-1970's along with the increasing abundance of pinniped populations in these areas (Ainley et al. 1981, 1985; Le Boeuf et al. 1982).

Predation by Other Predators. There have been other documented cases of predation on sea otters, although such interactions may often go unnoticed because most of the species' range is remote and poorly studied. Although a Soviet biologist (Nikolaev 1965) observed a killer whale (*Orcinus orca*) capture one sea otter in the Soviet Union, this type of predation is probably very rare (Kenyo 1969, 1982). On several occasions, Kenyon (1969) observed killer whales swimming within a few meters of resting or feeding sea otters; the whales never attacked an otter, although active or foraging otters sometimes became inactive or lay still on the surface until the whale passed. Sherrod et al. (1975) found that bald eagles captured and consumed newly born sea otter pups at Amchitka Island, Alaska (also discussed in Maternal Care and Pup Development). Amchitka Island supports high-density populations of sea otters and bald eagles, both of which probably were food-limited at the time of the Sherrod et al. (1975) study. Prey captures were determined by examining food remains in eagle nests during the birds' breeding season, which coincides with the seasonal peak in sea otter pupping. Apparently, only certain breeding pairs or individual eagles prey on sea otter pups, as the distribution of otter remains among nest sites was strongly skewed toward some of the nests, and pup remains were never found in about half of the nests. The consumption of otter pups by bald eagles was known to occur from earlier studies, although Kenyon (1969) presumed that the otter pups had been scavenged by eagles following some other cause of death. In fact, this may have been true in some cases; however, hemorrhagic tissue around talon puncture wounds in several closely examined fresh otter carcasses demonstrated that these individuals were killed by the eagles. In addition, since newborn dead pups were rarely found during beach surveys, Sherrod et al. (1975) concluded that most of the otter pups found in eagle nests probably were not scavenged. It is also possible that eagles captured pups abandoned by their mothers—however, this is unlikely, since adult female sea otters are highly attentive to, and rarely become separated from, their newborn pups. Furthermore, several pup captures have been observed, and in each instance the pup was taken while its mother was diving for food. Often the pups vocalize loudly while their mothers are diving, and bald eagles that prey on sea otter pups may cue on this stimulus.

Monnett and Rotterman (1988b*), working in northeastern Prince William Sound, reported that newly weaned sea otters were killed and eaten by coyotes. The presence of fresh blood at the kill site suggests that (as with the bald eagle) these otters were killed rather than scavenged. The tidal range in Prince William Sound is extreme, and Monnett and Rotterman (1988b) speculated that after hauling out at high tide, the otters became separated from the water as the tide receded, so that their awkwardness on land made them easy prey for the coyotes.

A final example of predation on sea otters is by brown bears on the Kamchatka Peninsula (A. Zorin, personal communication). Zorin reported that numerous otters are captured and eaten by the bears in late winter to early spring, when many otters appear to haul out in a weakened condition from winter storms, and when hungry bears are emerging from hibernation.

Pathological Disorders. About 4% (63 of 1,680 otter deaths) of the total recorded in California mortality was directly related to disease conditions, particularly enteritis and pneumonia. Enteritis, or inflammation of the intestinal tract, is common in necropsied sea otters in California (Mattison and Hubbard 1969; Morejohn et al. 1975; Ames et al. 1983*), as well as in Alaska (Kenyon 1969). The presence of enteritis is associated with other diseases, poisoning, and various types of stress (Stulken and Kirkpatrick 1955).

Other fairly uncommon direct or contributing causes of death include perforated intestine, twisted intestine, intussusception (an unfolding of one part of the intestine into another), intestinal infection, stomach ulcers, prolapsed uterus, prolapsed vagina, prolapsed rectum, acute hepatitis, diaphragmatic hernia, valley fever, aspergillosis in the liver, severe peritonitis (inflammation of the membrane lining the abdominal cavity and enclosing the viscera), and one case of twin fetuses lodged in the birth canal (Morejohn et al. 1975; Williams et al. 1980; Ames et al. 1983*).

Heavy infestations of acanthocephalan parasites (such as *Polymorphus*) in the gastrointestinal tract are rare, but may occasionally contribute to mortality from resulting intestinal perforations. However, nonlethal cases of gastrointestinal tract parasites are common among sea otters in California (Mattison and Hubbard 1969*; Hennessey 1972; Wild and Ames 1974; Morejohn et al. 1975; Hennessey and Morejohn 1977; Hennessey et al. 1979*;

Ames et al. 1983*) and in Alaska (Rausch 1953; Kenyon 1969; Dailey and Brownell 1972; Margolis and Dailey 1972*). Nasal mite (Halarachnidae) infections occur infrequently in Alaskan otters; the few observed infestations were mild and did not affect the health of wild otters, although severe nasal mite infestations may have contributed to the death of captive sea otters (Kenyon et. al. 1965, Kenyon 1969).

One case of systemic coccidioidomycosis (a respiratory disease) has been reported as a cause of death in one sea otter near Morro Bay (Cornell et al. 1979). Williams and Pulley (1981) found uterine leiomyomas (a rare, benign, smooth muscle tumor) in 2 of 112 female sea otters necropsied in California.

Starvation. Many of the pathological disorders or unknown causes of death included in CDFG mortality categories 1 (case of death unknown), 3 (uncertain with no trauma), and 11 (other natural causes)—which collectively account for 52% (869 of 1,680) of the total recorded mortality—are observed in conjunction with an emaciated condition indicative of starvation. However, it is difficult to determine if the emaciated condition of the carcass resulted from (1) insufficient availability of food resources, (2) the inability of a diseased otter to forage adequately, (3) the inability of mother and pup pairs, juveniles, or aged animals to forage successfully (especially during harsh weather conditions); or (4) whether diseases such as enteritis and pneumonia partially resulted from a previously weakened condition caused by starvation (Ames et al. 1983*).

From the evidence, many small and large dependent pups (included under CDFG mortality category 12: dependent animals with no trauma) died of starvation. About 15% (249 of 1,680 otter deaths) of the total recorded mortality from 1968 to 1989 was composed of pup carcasses showing no signs of trauma (Ames et al. 1983*; Ames, unpublished data). Starvation might occur if the pup became separated from its mother or if the mother did not provide sufficient nourishment in terms of milk or solid food obtained while foraging. According to Ames et al. (1983*) harsh weather conditions are likely to promote instances of mortality involving starvation.

Adverse Weather Conditions. Ames et al. (1983*) found that the number of emaciated carcasses recovered showing increased indications that starvation contributed to death (whether the primary cause or secondary effect) increased during the winter period of severe storms. There was a positive correlation between rough sea conditions, the winter peak in mortality (other than human-caused), and the proportion of recovered emaciated carcasses and otters that died from unknown causes.

Thus, rather than chronically occurring throughout the year, starvation appears to be associated with inclement winter weather. Morejohn et al. (1975) also found that sea otter mortality (not caused by humans) increased during periods of winter storms, and that human-caused mortality peaked during summer when human activity, including gill-net fishing, was greatest along the coast.

Mating Wounds in Adult Females. During copulation, the male grasps the female's nose between his teeth, causing nasal and facial injuries and scars that are frequently observed in live adult female otters (Vandevere 1970*; Foott 1971, Brosseau et al. 1975). Severe or infected nose wounds have been reported in carcasses of adult females (Mattison and Hubbard 1969*; Wild and Ames 1974; Ames et al. 1983*). Although records of nose injuries in female carcasses are incomplete, mating wounds do not seem to represent a significant source of mortality. Severe nasal damage was recorded from 1968 to 1989 for at least 38 dead females (2.3% of the total mortality); of these, about half appear to have died as a direct result of injuries incurred during mating. Ames et al. (1983*) and Jameson (personal communication) suggested that complications and infections stemming from mating bite trauma may be a contributing cause of death in a some females, and they speculate that very young, very old, and unhealthy females may be especially susceptible, not only to severe nose damage but also to drowning resulting from vigorous breeding activity. On two occasions, the same territorial male was observed mating with the carcass of an adult female; it was known that he killed one of the females during mating activity, and he may have killed the other female as well (Riedman, Staedler, and Estes, unpublished data).

At least 10 immature female carcasses (about 1% of the total recorded mortality from 1968 to 1983), measuring 90–105 cm total length, sustained severe bite injuries, particularly on the nose and feet. Similar sorts of wounds were found on some juvenile female carcasses measuring <90 cm, but these females were placed in CDFG mortality category 13 (dependent animal with trauma; Ames et al. 1983*). It is possible that most of the severe bite injuries on young females resulted from males attempting copulation. Jameson (personal communication) suggested that it may be the younger, sexually immature males that inflict most of the injuries.

Fight Injuries in Males. Potential mortality resulting from injuries incurred during male–male aggression seems to be negligible. Although overt fights between males are rarely observed (Loughlin 1977, 1980), at least 20 male carcasses examined from 1968 to 1982 sustained severe fresh or old fight injuries. Most of the injuries were found on the hind feet, but occasionally wounds were on the nose, face, and penis. Fighting injuries were observed more frequently in older males (Ames et al. 1983*). Ames et al. (1983*) suspected that complications from fight trauma (included within category 11) were the probable cause of death for some of the males that sustained injuries during aggressive interactions.

Potential or Undocumented Sources of Mortality or Pathological Disorders

Potential Reduction of Genetic Diversity in the California Sea Otter Population

Any population that has been reduced to a small size may lose some of its natural genetic variability and thus, some adaptability (e.g., Denniston 1978). The sea otter population along the Pacific coast of the United States was reduced to an estimated 50 animals in 1914 (Bryant 1915; California Department of Fish and Game 1976*); this created a potential "genetic bottleneck." However, theoretical analysis indicated that significant loss of genetic variation in the California sea otter population is unlikely (Ralls et al. 1983), and the population has subsequently increased to about 1,700 independent animals (Estes and Jameson 1983a*, 1983b*; California Department of Fish and Game and U.S. Fish and Wildlife Service, unpublished data). A reduction in genetic diversity may occur in small populations by inbreeding and genetic drift, frequently leading to increased homozygosity, which in turn may result in reduced fertility, higher mortality of young, and a decreased ability of offspring to adapt to changing environmental conditions (Kimura and Crow 1963; Crow and Kimura 1970; Cavalli-Sforza and Bodmer 1971; Packer 1979).

Ralls et al. (1983) calculated that the current California sea otter population should theoretically retain a significant proportion (minimum of 77%) of the genetic diversity that occurred in the original population. Lidicker and McCollum (1981*) investigated genetic biochemical variation in sea otters from California, as well as Alaska, and found 16.7% polymorphisms among 30 loci and a mean heterozygosity of 6.0%. No rare alleles were detected. No fixed differences were found between the Alaska and California specimens, although the sample size from Alaska was too small to conclusively establish differences between the two populations. Lidicker and McCollum (1981*) concluded that the only effect of the genetic bottleneck in the California population was the loss of rare alleles at variable loci.

Environmental Contaminants

Adverse effects on sea otters from environmental toxicants have not yet been documented, although variable residue levels of a number of polychlorinated biphenyls (PCB's), chlorinated hydrocarbons (DDT and its derivatives), and heavy metals have been found in sea otter tissue samples. Because environmental contaminants (e.g., organochlorine pesticides and some heavy metals) exhibit biomagnification as they progress through the food chain (Keith 1966; Meeks 1968), top-level predators such as sea otters may accumulate high and potentially toxic residue levels of such contaminants.

From 1968 to 1980, California sea otter tissue samples were analyzed for residues of chlorinated hydrocarbons, heavy metals, and other elements by Shaw (1971), Rote (1976), Martin (1979*), and the California Department of Fish and Game's Fish and Wildlife Water Pollution Control Laboratory. There was no evidence of a detrimental cause-and-effect relation between any environmental toxicant and mortality or pathological condition in sea otters, with the possible exception of potentially harmful levels of naturally occurring cadmium found in tissues of several old females (Ames et al. 1983*; Risebrough 1984*). The residue levels of heavy metals, polychlorinated biphenyls, and organochlorine pesticides in sea otter tissues generally appeared to be below levels known to be the principal cause of debilitation or mortality, although PCB residues in a number of liver samples were higher than levels known to cause reproductive failure in mink (Ames et al. 1983*; Risebrough 1984*). However, few tissue samples of sea otters that died after 1980 have been analyzed to determine levels of environmental contaminants, because such contaminants in mussels within the sea otter range have been routinely monitored since then by the California Department of Fish and Game's (CDFG) State Mussel Watch Program.

Based on data collected by Shaw (1971), Rote (1976), Martin (1979*), and the CDFG Fish and Wildlife Water Pollution Control Laboratory, Ames et al. (1983*) concluded that there were some significant relations between sea otters and residue levels of environmental contaminants in their tissues. Temporal variation in the levels of pesticide residues (DDT, DDD, and DDE), which accumulates primarily in fat tissues, indicated that residues were lowest among otters that died between May and August and highest in otters that died between January and April. The higher levels of pesticide residues found in otters that died in winter may be caused by agricultural runoff, which is heaviest during rainy winter months. No significant differences in pesticide accumulation patterns were found in relation to sex or size of the otters.

However, variation in accumulation patterns of heavy metals and trace elements in the liver and kidneys were found in relation to sex and size of the otter. The amount of cadmium, copper, iron, mercury, and zinc residues in the liver or kidneys increased with sea otter size or were higher in animals >100 cm total length, while the level of magnesium and silver residues in the liver were higher in otters measuring <100 cm. The levels of cadmium, manganese, and silver in the liver or kidneys were highest in females, and levels of iron and mercury in the kidneys were highest in males. Silver and calcium residues in the liver were higher in otters that died before 1974. Mean levels of calcium residues in the liver consistently decreased over time. Ames et al. (1983*) and Risebrough (1984*) noted that different methodologies employed by the various laboratories in analyzing sea otter tissue sam-

ples may have affected some of the resultant conclusions suggested by the collective data between residue levels and sea otter size, sex, and time of year.

Smith et al. (1990) evaluated postindustrial lead accumulation in sea otters at Amchitka Island by comparing lead concentrations and isotopic compositions in teeth collected from the modern population and preindustrial middens. Although lead concentrations in the North Pacific Ocean have increased 5- to 15-fold since preindustrial times, there was no detectable difference in lead concentration between preindustrial and modern sea otter teeth, perhaps because of lead biodepletion with increased trophic status in marine food webs. However, lead isotope analysis indicated that preindustrial animals contained lead derived from natural deposits in the Aleutian arc, whereas contemporary animals contained primarily industrial lead from Asia and western Canada.

The level of cadmium residues found in sea otter tissues were high compared to other marine mammals. Cadmium accumulated with age, especially in the kidneys. Old females were found to possess the highest levels of cadmium (Martin 1979*; Ames et al. 1983*). Because similarly elevated levels of cadmium may be toxic in other species, the high cadmium residue levels found in aged female sea otters may present potential health risks from cadmium toxicity (Martin 1979; Risebrough 1984). The cadmium found in coastal waters of central California occurs naturally in many of the molluscs used for food by sea otters. Risebrough (1984) speculated that sea otters may have evolved a biochemical mechanism of cadmium detoxification, as piscivorous marine mammals have, to reduce the toxic effects of mercury and possibly selenium, which are present in fish.

Information collected by Rote (1976), Martin (1979), Martin and Castle (1984), and the CDFG State Mussel Watch Program (which monitors the marine environment for pollutants; Stephenson et al. 1979) indicates an increase in the following environmental toxicants within certain areas of the sea otter's range: synthetic organic compounds, such as chlorinated hydrocarbons, Endosulfan I, and Dieldrin; petroleum hydrocarbons; and trace and heavy metals, including cadmium, copper, lead, mercury, silver, and zinc.

The U.S. Fish and Wildlife Service (1982) noted that the high degree of pesticide use associated with Salinas Valley agricultural development, maritime traffic, and discharge of industrial and municipal wastes seemed to be the primary sources of environmental contaminants within the sea otter's range. High concentrations of pesticides entered Monterey Bay from agricultural runoff in the Salinas River and Elkhorn Slough; the most common were Endosulfan I, toxaphene, and DDT and its metabolites (Martin and Stephenson 1984).

In general, the sea otter's range has low concentrations of most environmental pollutants. Along the open coast, concentrations of complex hydrocarbon mixtures (principally petroleum) in mussels were the lowest in the State and were equaled only by locations on the open coast of northern California; concentrations in San Francisco Bay and Los Angeles Harbor averaged 20–30 times greater (Martin and Stephenson 1984). However, in Monterey Bay very high concentrations of some metals and pesticides have been detected. Unusually elevated concentrations of lead and zinc, for example, have been found between Point Piños and Monterey Harbor—lead concentrations were 22 times those of ambient levels elsewhere in the range (Martin and Castle 1984). While the source of the contaminants has not been identified, it is believed to be leachate from waste dumps associated with historical cannery activity (Loehr and Collias 1983). In addition, very high levels (about one part per million) of tributyltin (a toxic marine paint used on the bottom of vessels) were found in the livers of two sea otters that were found dead in Monterey Harbor (M. Martin, California Department of Fish and Game, Monterey, Calif., personal communication).

Rote (1976) found that PCB levels in sea otter tissues throughout the range were highest in the Monterey area and speculated that industrial activity and vessel leakage may have been responsible. However, data collected by the State Mussel Watch Program indicated an overall decline in PCB levels in California coastal waters since the 1970's, corresponding to the prohibition of PCB use in the United States.

Municipal sewage outfalls are an additional source of marine pollution within the sea otter's range. Water quality has been degraded (containing increased coliform concentrations) in Monterey Bay and Morro Bay due to dairy operations and treated municipal sewage. A large outfall currently operates south of Moss Landing, about 1 mile from shore; it discharges secondary wastes into Monterey Bay from the communities of Monterey, Seaside, Pacific Grove, Salinas, and Castroville (L. Espinosa, California Department of Fish and Game, Monterey, personal communication). Other potential sources of marine pollution in the sea otter's range include the Pacific Gas and Electric power plant and magnesia refractory at Moss Landing, the Pacific Gas and Electric gas- and oil-fired power plant at Morro Bay, the nuclear power plant at Diablo Canyon (Point Buchon), tanker (and other ship) traffic, and outer Continental Shelf oil resource development.

The debilitating effects of PCB's and organochlorine pesticides, especially to the reproductive system, have been documented in mammals and birds: river otters (Halbrook et al. 1980; Henny et al. 1980), mink (Platonow and Karstad 1973; Aulerich and Ringer 1977; Jensen et al. 1977; Henny et al. 1980; O'Shea et al. 1980), rabbits (*Oryctolagus cuniculus*; Hart et al. 1972), California sea lions (Le Boeuf and Bonnell 1971; DeLong et al. 1973;

Buhler et al. 1975; Gilmartin et al. 1976), ringed seals (*Phoca hispida*; Helle et al. 1976a, 1976b), mallards (*Anas platyrhynchos*; Heath et al. 1969); brown pelicans (*Pelecanus occidentalis*; Anderson and Hickey 1970; Gress 1970*), double-crested cormorants (*Phalacrocorax auritus*; Gress et al. 1973), bald eagles (Wiemeyer et al. 1972), and ospreys (*Pandion haliaetus*; Wiemeyer et al. 1975). Deleterious effects of heavy metals, primarily methylmercury, have been found in mink (Wobeser and Swift 1976; Wobeser et al. 1976; O'Connor and Nielsen 1980), river otters (O'Connor and Nielson 1980), domestic cats (Davies and Nielsen 1977), domestic dogs (Davies et al. 1977), swine (*Sus scrofa*; Tryphonas and Nielsen 1973), and California sea lions (Braham 1973; Buhler et al. 1975; Martin et al. 1976).

Nearly complete reproductive failure has occurred in mink when experimentally allowed to eat food containing PCB's, even at levels as low as 0.6 ppm. The livers of female mink that exhibited reproductive failure sustained PCB levels of 1.2 ppm (Platonow and Karstad 1973; Aulerich and Ringer 1977; Jensen et al. 1977; O'Shea et al. 1980; Risebrough 1984), which is lower than PCB levels found to be in the liver of a number of California sea otters. Ames et al. (1983*) found PCB residues >1.2 ppm in about 20% (21) of the 102 sea otter liver samples. Because mink and sea otters are both mustelids, the reproductive system of otters might be similarly sensitive to the effects of PCB's (Risebrough 1984*). However, censuses conducted in California by the U.S. Fish and Wildlife Service and California Department of Fish and Game suggested that yearly pup-to-independent animal ratios (averaging 15–16 pups to 100 independents) and annual levels of recruitment to the population were similar to those observed in open-ended Alaskan populations (Estes 1981; Estes and Jameson 1983a; Estes 1990). Therefore, birth rates among California sea otters seem to be within the expected range and unaffected by accumulated levels of PCB's in liver tissues.

Potential and Documented Effects of Oil Contamination

Introduction and Summary

Sea otters are among the most sensitive marine mammals to the effects of oil contamination (Kooyman et al. 1977*; Geraci and St. Aubin 1980; Englehardt 1983). Unlike most other marine mammals, the sea otter has little subcutaneous fat, and therefore depends on an elevated rate of heat production and an entrapped air layer within its dense, water-resistant underfur, which provides insulation against the cold as well as buoyancy (Kenyon 1969; Iverson and Krog 1973; Morrison et al. 1974; Tarasoff 1974; Costa and Kooyman 1982).

The most harmful effect of direct exposure to oil involves fouling of the otter's fur, which causes the fur to lose its insulative properties. Loss of thermal insulation subsequently leads to thermoregulatory distress, along with an abnormally high rate of heat production, loss of buoyancy, hypothermia, pneumonia, and weight loss, any of which may cause death (Stulken and Kirkpatrick 1955; Kenyon 1969, 1975; Geraci and Smith 1977; Kooyman et al. 1977*; Williams 1978*; Kooyman and Costa 1979*; Costa and Kooyman 1979*, 1980*, 1982; Environment Canada 1982*; Siniff et al. 1982; Engelhardt 1983). Even partial oil contamination of the fur, equal to 30% of the total body surface, will result in death (Kooyman and Costa 1979*).

In addition to the documented loss of thermal insulation, another direct effect of oil contamination is the ingestion of oil, which is acutely or chronically toxic to sea otters. Substantial mortality associated with direct effects of oil contamination were documented in 1964, when over 100 sea otters died from a gasoline and diesel fuel spill that took place in the Kuril Islands (Barabash-Nikiforov et al. 1968), and during the 1989 *Exxon Valdez* oil spill in Prince William Sound.

Although little information is available on sea otters concerning the indirect effects of crude oil environmental contamination, effects may include (1) loss of habitat and (2) food reduction, due to mortality or unpalatability of prey organisms resulting from direct contact of oil with marine invertebrates and overall degradation of the nearshore marine ecosystem (e.g., Evans and Rice 1974; Moore and Dwyer 1974; Hodgins et al. 1977; Malins 1977; Atlas et al. 1978; Roesijadi et al. 1978; Cross and Thompson 1982*; National Research Council 1985).

The toxic or deleterious effects of oil contamination have been demonstrated in a number of sea otter prey species (or closely related forms), including the following macroinvertebrates: sea urchins (*Strongylocentrotus* and *Paracentrotus*; North et al. 1965; Allen 1971; Wells and Keizer 1975; Axiak and Saliba 1981; Hose and Puffer 1983), crabs (*Cancer* and *Uca*; Caldwell et al. 1977*; Krebs and Burns 1977; Johns and Pechenik 1980; Sanders et al. 1981), clams (*Protothaca*, *Mya*, *Mercinaria*, and *Donax*; Avolizi and Nuwayhid 1974; Dow 1975; Gilfillan and Vandermeulen 1978; Pearson et al. 1981; Hartwick et al. 1982; Olla et al. 1983), mussels (*Mytilus*; Dixon 1982), and possibly turban snails (Chan 1973*).

It is still unclear whether or not sea otters are able to detect an oil slick in natural surroundings. However, captive otters do not seem to avoid oil (e.g., Barabash-Nikiforov 1947; Barabash-Nikiforov et al. 1968; Kenyon 1969; Williams 1978* 1989; Siniff et al. 1982). The fact that many sea otters were killed by the 1989 *Exxon Valdez* spill in Prince William Sound established that free-ranging otters are unable to avoid large oil slicks in nature.

Direct Effects

Loss of Thermal Insulation. The contamination of a sea otter's fur with sufficient quantities of crude oil will result in loss of warmth, buoyancy, and thermoregulatory abilities due to the destruction of the insulative barrier of entrapped air maintained in the dense underfur (Kooyman et al. 1977*; Kooyman and Costa 1979*; Costa and Kooyman 1979*, 1982). Sea otters cope with the problem of thermal stress not only by means of their insulative fur, but also by maintaining an elevated rate of heat production, which is higher than that of similar-sized mammals (Kenyon 1969; Iverson and Krog 1973; Morrison et al. 1974; Costa 1978a; Costa and Kooyman 1982, 1984). A sea otter could not maintain the increase in heat production for the prolonged period that would be necessary to compensate for a reduction in thermal insulation resulting from oil fouling of the fur (Costa and Kooyman 1982).

Kooyman and Costa (1979*) found that the normal metabolic rate of captive sea otters immersed in water (15° C) increased by about 40% when 25% of the fur surface was contaminated with oil. Metabolic rate increased 110–130% above normal when the oil was removed with detergents. One of the experimental otters died and two contracted pneumonia. Kooyman and Costa (1979*) estimated that oil fouling of 30% or more of the sea otter's pelage surface will result in death from hypothermia or pneumonia. Subsequent studies have confirmed the loss of thermal insulation and resultant increase in metabolism associated with oil contamination of sea otter fur, especially following detergent washing, which appears to remove the natural fur oils and thus reduce the fur's water-repellent quality (Costa and Kooyman 1979*; Costa and Kooyman 1982; Siniff et al. 1982; Williams et al. 1986*; Davis et al. 1986*, 1988a, 1988b*; Williams et al. 1988). Crude oil applied to pelt samples caused a 2- to 4-fold increase in thermal conductance (Williams et al. 1988).

Davis et al. (1988a, 1988b*) contaminated 20% of the fur surface area of several captive Alaskan sea otters with fresh crude oil and found that average metabolic rate increased 1.9 times and whole body thermal conductance increased 1.8 times. After application of the oil, the otters exhibited several changes in behavior: time spent grooming increased from 35% to 61%, time spent swimming increased from 10% to 17%, and time spent resting decreased from 49% to 12%. Grooming attempts worsened the effects of the oil contamination by spreading oil to clean areas and pushing oil deeper into fur. All visible evidence of oil was removed after 40 min of washing with Dawn detergent (Proctor and Gamble; 1:16 in water) along with adequate rinsing. Within 3–6 days, core body temperature, average metabolic rate, and thermal conductance returned to normal control levels, although the metabolic response to cleaning showed individual variation, with the metabolic rate of some otters returning to normal levels much more slowly than others. Natural oils in pelt samples were removed by cleaning, although water repellency was retained (Williams et al. 1988); in live animals, the natural oils removed by cleaning had not been restored after 7 days. Davis et al. (1988a, 1988b*) concluded that oiled sea otters required 1–2 weeks to restore their fur and recover from the stress of cleaning. Following the *Exxon Valdez* spill, oiled sea otters that were properly captured, cleaned, and dried quickly recovered their thermal insulation (G. VanBlaricom, Fish and Wildlife Service, Santa Cruz, Calif., personal communication).

Additional experiments have shown that wild sea otters seem able to survive levels of oil contamination ≤10% of their total body surface for 4 days to 3 weeks, at least during summer months (Costa and Kooyman 1979*; Siniff et al. 1982). However, in a major oil spill, otters encountering oil slicks would probably contaminate more than 10% of their total body surface. The effects of oil contamination on otters may be accentuated during winter, when energy expenditure may be higher due to colder water temperatures, and ability to forage effectively is diminished because of rough seas. In all studies, an increase in grooming activity was documented, as otters attempted to remove the oil from their fur (Costa and Kooyman 1979*; Siniff et al. 1982).

Little is known concerning the effects of weathered oil on sea otters. Englehardt (1983) suggested that a heavy, viscous oil would be most likely to adhere to an animal's pelage or skin. However, studies on the effects of oil contamination on sea otter pelts showed that fresh crude oil and oil dispersant mixtures caused water to penetrate most of the pelt, while 5-day weathered crude oil caused the least change in thermal conductance. This was apparently due to higher oil viscosity, which tended to remain on the guard hair tips, reducing oil penetration into the fur, and maintaining insulating air pockets. The effect of weathered crude oil on living sea otters, however, may be comparable to that of fresh crude, since the otters would probably spread the oil and compress air pockets during grooming (Williams et al. 1988).

Controlled experiments have demonstrated that oil-contaminated fur also results in a loss of thermal insulation and increase in metabolism in polar bears (Hurst et al. 1982) and muskrats (*Ondatra zibethica*: McEwan et al. 1974). Kooyman et al. (1977*) measured thermal conductance in oil-fouled northern fur seal pelts and concluded that a light oiling would substantially impair a fur seal's thermoregulatory abilities.

Potential Toxicity of Ingested Oil. Sea otters may ingest petroleum compounds in an oil-contaminated area by grooming soiled fur or by feeding on oil-tainted prey. Resultant effects of oil ingestion could involve acute and immediate impairment to the otter's health or latent

pathological disorders, including gastrointestinal, renal, and hematological abnormalities (Baker et al. 1981; Engelhardt 1983; Oritsland et al. 1981). Pathological effects of oil were demonstrated conclusively following the 1989 *Exxon Valdez* spill in Prince William Sound: pulmonary emphysema, subcutaneous emphysema, hemmorrhagic enteritis, and liver and kidney dysfunction (DeGange 1990*) resulted from the ingestion, inhalation, and external exposure to oil. A number of petroleum hydrocarbons are known to be highly carcinogenic.

Potentially toxic effects of ingested oil may especially be of importance in cases of lightly oiled otters that do not die of thermoregulatory failure, hypothermia, or pneumonia, since free-ranging sea otters are evidently able to survive crude oil covering ≤10% of the fur surface (Costa and Kooyman 1979*; Siniff et al. 1982). Costa and Kooyman (1982) did not find any evidence of oil toxicity in captive, oil-contaminated sea otters, although the oil was cleaned from the fur within 12 h in all but one case (in which it was removed after 6 days). According to Siniff et al. (1982), it was possible that oil toxicity contributed to the death of one captive otter that had remained in an oil-contaminated pool for 12 h. Wild sea otters that were partially oiled (on about 10% of the total fur surface) and monitored for 2–3 weeks did not have any visible toxic reactions, although it was possible that oil toxicity could have occurred after the relatively short observation period (Costa and Kooyman 1979*; Williams et al. 1981; Siniff et al. 1982).

Other marine or aquatic mammals have exhibited variable sensitivities to ingested oil. Acute toxicity resulted when three captive polar bears ingested oil while grooming their oil-contaminated fur. A number of serious pathological disorders developed 5–6 weeks after oil ingestion in all three bears, resulting in the deaths of two (Oritsland et al. 1981*). Baker et al. (1981) found that at least 13 European otters (*Lutra lutra*) died following an oil spill—hemorrhagic gastroenteropathy from ingestion of oil during grooming seemed to be responsible for the deaths, although hypothermia may also have been a contributing factor.

Phocid pinnipeds have shown varied tolerance to the presence and ingestion of crude oil. Duguy and Babin (1976) reported that a harbor seal died of oil toxicity from ingested oil. Geraci and Smith (1976) found that ringed seals immersed in a simulated crude oil slick for 24 h did not exhibit any lasting toxic or pathological reactions, although eye irritation and lesions temporarily occurred. Engelhardt et al. (1977) reported low levels of hydrocarbons in ringed seal tissue samples. Ringed seals fed 5 mL of crude oil daily for 5 days accumulated hydrocarbons in the blubber and liver; however, the seals were able to clear tissues and blood of the accumulated residues within 7 days by excreting hydrocarbons in the urine and bile (Engelhardt 1978).

Behavioral Avoidance of Oil Slicks

It is unclear if sea otters are able to detect and effectively avoid an oil slick in natural surroundings. The large number of sea otters that died from oil contamination following the *Exxon Valdez* spill in Prince William Sound demonstrated that, even if sea otters attempted to avoid the oil, many of them were unable to do so. Williams (1978*) and Siniff et al. (1982) found that sea otters did not avoid oil in a captive situation. Two otters were placed in a small pool (5-m diameter), half of which was covered with crude oil. Although both otters spent comparatively little time in the oiled side of the pool, each otter repeatedly entered the oil-contaminated area for brief periods and became covered with oil. One of the otters was not cleaned by the researchers and subsequently died.

According to Barabash-Nikiforov (1947), free-ranging sea otters may have avoided areas purposely contaminated with petroleum products by Japanese fishermen to repel sea otters; Barabash-Nikiforov assumed that the petroleum odor caused avoidance. However, sea otters did not avoid a gasoline and diesel fuel spill near Paramushir Island (Kuril Islands) that may have killed >100 otters (Barabash-Nikiforov et al. 1968). Baker et al. (1981) found that free-ranging European otters did not avoid oil slicks in the water or patches of oil on shore (the result of a large oil spill). Polar bears and many pinnipeds do not seem to consistently avoid oil (Englehardt 1983).

Under certain conditions a major oil spill will come ashore (e.g., VanBlaricom and Jameson 1982), trapping sea otters between the shore and the oil slick. This can create a situation in which the otters are forced to swim through or under the oil slick, in which case the animals almost certainly become contaminated with oil.

Exxon Valdez *Oil Spill*. The effects of oil spills on sea otters, until recently, remained largely a matter of speculation since there had been no well-documented case in which an oil spill had come into contact with sea otters. The first such case occurred in December 1988 near Gray's Harbor, Washington. This spill spread northward through the ranges of sea otter populations in Washington and British Columbia. Although several sea otter carcasses contaminated with oil were found on the beaches following this spill, it has not been established that these animals were actually killed by the oil. Subsequent surveys of both populations have indicated no detectable effects on the population.

On 24 March 1989, the *Exxon Valdez* ran aground on Bligh Reef in Prince William Sound, spilling more than 11 million gallons of Prudhoe Bay crude oil and resulting in the largest and most catastrophic oil spill in U.S. history. This spill eventually spread >700 km to the southwest, affecting coastal areas along the Kenai Peninsula, Kodiak archipelago, and Alaska Peninsula. Although much was learned about the effects of oil contamination on sea otters, work is still ongoing, and many of the results

are litigation-sensitive and thus unavailable to us. For these reasons, we provide only a brief and preliminary overview of this event. Much of this information was provided through personal communications from A. DeGange (U.S. Fish and Wildlife Service, Anchorage, Alaska) and G. VanBlaricom (U.S. Fish and Wildlife Service, Santa Cruz, California). A review of the effects of the *Exxon Valdez* oil spill on sea otters is presented in Bayha and Kormandy (1990).

Effects of the *Exxon Valdez* spill on the population and ecosystem of the sea otter are largely unknown, and they are likely to remain so. Although numerous studies had been conducted on sea otters in Prince William Sound, the size and distribution of the population in the area influenced by the spill was poorly known. Limited surveys were conducted in several areas before and after they were affected by spilled oil, but due to the imprecision of sea otter counts and the ability of sea otters to move long distances over short periods, these surveys may be impossible to interpret. Even so, there are several general points to be made about the effects of oil on sea otter populations there (Bayha and Kormandy 1990). First, contrary to initial expectations, local populations were not exterminated over large areas of coastline, even at sites that were very heavily affected. However, many animals died. Eight hundred seventy-eight carcasses were recovered from the area during the response phase of the spill (through 15 September 1989); most of these were killed by oil. An additional 135 animals died during capture and rehabilitation efforts. Thus, at least 1,013 sea otters died as a result of the spill, and the number could be much larger. The known causes of mortality were briefly discussed earlier in this section.

One of the main efforts associated with the *Exxon Valdez* spill was to capture and rehabilitate oiled wildlife. Most of this effort was directed toward sea otters. Many people were involved and the estimated cost for sea otter rehabilitation alone was $18.3 million. Otter rehabilitation facilities were constructed at several sites. Three hundred sixty-one sea otters were brought to the rehabilitation centers, where they were cleaned and cared for; about 45% of these animals were found to be either unoiled or only lightly oiled. One hundred ninety-seven were eventually released back into the wild, 45 of which were instrumented with surgically-implanted radio transmitters for study. These studies are ongoing, but preliminary results indicate that an unexpectedly high number have died or are missing.

Finally, the *Exxon Valdez* spill confirmed the fears of many that spilled oil could not be cleaned up or contained. The weather was clear and calm for 2 to 3 days following the spill, so that conditions were ideal for containment. Nonetheless, the oil was not contained and probably could not have been contained with available equipment and technology. Furthermore, most of the spilled oil was never cleaned up and probably never can be. The long-term effects of the oil on the environment of the northern Gulf of Alaska remain to be seen.

Review of Sea Otter Reintroductions in North America

Introduction

As mentioned earlier, sea otters were exterminated along the North American coast from Prince William Sound to central Baja California, except for the remnant population in central California. During the 1960's and early 1970's, in collaboration with various State and Provincial wildlife management agencies, the Alaska Department of Fish and Game attempted to facilitate recovery by reintroducing small numbers of sea otters into areas that otherwise might not have been recolonized for decades or centuries. From 1965 to 1972, 708 sea otters captured at Amchitka Island and in Prince William Sound, Alaska, were reintroduced into unoccupied habitat in Alaska, Canada, Washington, and Oregon (Jameson et al. 1982). In most cases, sex ratios of the initial populations were approximately 2:1, favoring females. In 1969, 17 sea otters captured at Cambria, California, were released about 72 km north into occupied habitat within the sea otter's range. In 1988–89, 19 sea otters were captured at Shell Beach and released at Moss Landing. In 1987, reintroduction of sea otters from central California to San Nicolas Island, in the southern California Bight, was initiated. This project is ongoing. Figure 36 shows the locations of capture areas and reintroduction sites from Alaska to California and indicates the status of each reintroduced population. Results of each reintroduction effort are summarized in Table 11.

Alaska

The first five sea otter reintroductions were attempted in 1951, 1955, 1956, 1957, and 1959. In each of these early instances, otters were captured at Amchitka Island and transported to various sites in Alaska. All of the early reintroductions failed. Most of the relocated otters died in captivity during transport or immediately following release. Death resulted primarily from hypothermia, because the fur of captive animals became soiled and matted during transport and handling (and consequently lost its insulative properties). Therefore, failure of the early reintroductions was due to inadequate transport facilities and insufficient knowledge of the importance of keeping the otters' fur clean (Kenyon and Spencer 1960*; Kenyon 1969).

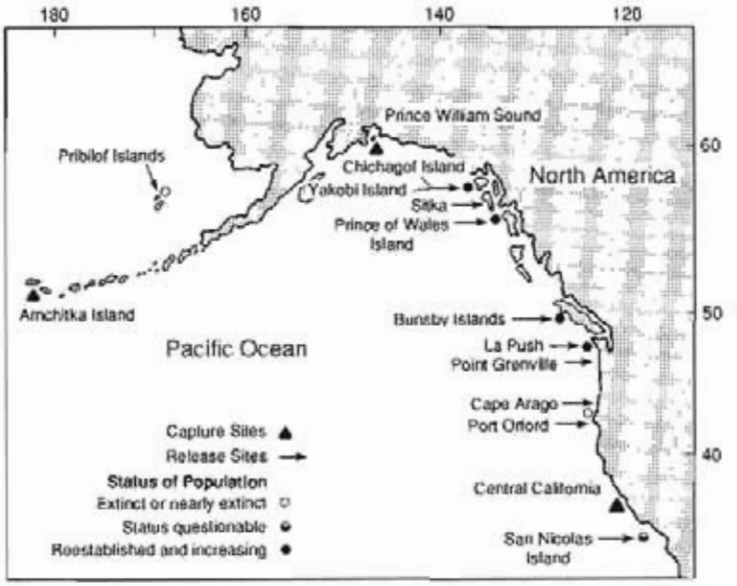


Fig. 36. Location and release sites of translocated sea otter populations.

On 20 May 1959, seven otters (four females and three males) captured at Amchitka were released at St. Paul Island in the Pribilof Islands. All the otters appeared to be in good health immediately following the release, and subsequent sightings were made near St. Paul Island until spring 1961. However, the relocated population did not survive and reproduce, probably due to its small initial size or to mortality from winter sea ice, which limits the northern extent of the species' range (Schneider and Faro 1975).

In 1968, 55 sea otters captured at Amchitka Island were released at St. George Island in the Pribilof Islands. The St. George population eventually became extinct. During a 1977 survey of the area, only three otters were sighted. Little or no reproduction appears to have taken place within the relocated colony, and no pups have been observed since the 1968 relocation (Jameson et al. 1982). In 1971 and 1972, the sea ice extended unusually far south, to the north side of Unimak Island (Schneider and Faro 1975), and may have reduced or eliminated the population at the Pribilof Islands. It is uncertain whether subsequent sightings are remnants from the reintroduction or animals that dispersed northward from southwestern Bristol Bay. Seven otters were seen at St. George Island by A.L. Sowls during summer 1988, and local residents claim that up to 30 otters are present (A. DeGange, U.S. Fish and Wildlife Service, Anchorage, personal communication).

From 1965 to 1969, 412 otters (89% captured at Amchitka, 11% from Prince William Sound) were reintroduced to various sites in southeastern Alaska (Fig. 37). These efforts were successful, and the sea otter population in southeastern Alaska is currently well established and increasing in size and range. From 1975 to 1987, the southeastern Alaska population increased about eightfold (K.W. Pitcher, Alaska Department of Fish and Game, unpublished data). In a 1988 survey of southeastern Alaska, 4,500 otters were sighted between the Barrier Islands near Dixon Entrance to the south, and north of Cape Spencer (Pitcher, unpublished data). The total population in southeastern Alaska probably contains 5,000 or more sea otters. The ratio of pups to older otters was 1:5. Johnson et al. (1983*) reported that there seemed to be excellent sea otter habitat for future population expansion and predicted that the populations should increase 4- to 5-fold during the 1990's. This population has increased at a rate of 17.6% annually (Estes 1990a).

British Columbia

From 1969 to 1972, 89 sea otters were reintroduced to the Bunsby Islands in British Columbia: 29 in 1969, 14 in 1970, and 46 in 1972. Of the relocated otters, 33% were captured at Amchitka Island, and the remainder were from Prince William Sound (Cameron 1972; MacAskie 1975). Bigg and MacAskie (1978) suggested that the high postrelease mortality that took place during the 1969 relocation occurred due to soiled pelage incurred during transport—the otters were not kept in holding pens before release and were therefore unable to feed or adequately groom and clean their fur before being liberated.

During a 1977 aerial survey, Bigg and MacAskie (1978) sighted 70 sea otters at the Bunsby Islands (55 otters) and Bajo Point (15 otters), including several pups (although they did not specify the number of pups observed). The populations seemed unchanged in 1978 (Breen et al. 1982). Based on the 1977–78 surveys, Farr and Bunnell

Table 11. *Number of sea otters (*Enhydra lutris*) reintroduced into unoccupied habitat in Alaska, Canada, Washington, Oregon, and California, and the size of reintroduced populations during the most recent survey.* [a]

Reintroduction site	Release location	Capture site	Number of otters released	Year of reintroduction	Total number reintroduced	Otters counted during most recent survey (year)[b]	Ratio of pup: independent[c]	Status of reintroduced population
Pribilof Islands (Alaska)	St. George Island	Amchitka	55	1968	55	3 (1977)	0:100	Uncertain
Southeastern Alaska	[d]	89% from Amchitka; 11% from Prince William Sound	23 30 301 58	1965 1966 1968 1969	412	4,520 (1988)	13:100	Established
British Columbia	Bunsby Islands	33% from Amchitka; 67% from Prince William Sound	29 14 46	1969 1970 1972	89	380 (1987)	Some pups observed	Established
Washington	Point Grenville La Push	Amchitka Amchitka	29 30	1969 1970	59	211 (1989)	8:100	Established
Oregon	Point Orford	Amchitka	29 24	1970 1971	93	1 (1981)	0:100	Extinct
	Cape Arago	Amchitka	40	1971				
California	San Nicolas Island	Central California	44	1988–89	103	15 (1990)	13:100	Uncertain

[a] Sources of data: Jameson et al. 1982; Johnson et al. 1983*; Jameson, unpublished data; Bigg and MacAskie 1978; Pitcher 1987* and unpublished data; MacAskie 1987; Rathbun et al. 1989*.
[b] Total includes pups.
[c] Number of pups sighted varies according to time of year.
[d] In southeastern Alaska, otters were released at various sites along the exposed west coasts of Yakobi, Chichagof, Baranof, and Prince of Wales islands. Otters were released at Yakutat Bay and Cape Spencer on the Alaska mainland.

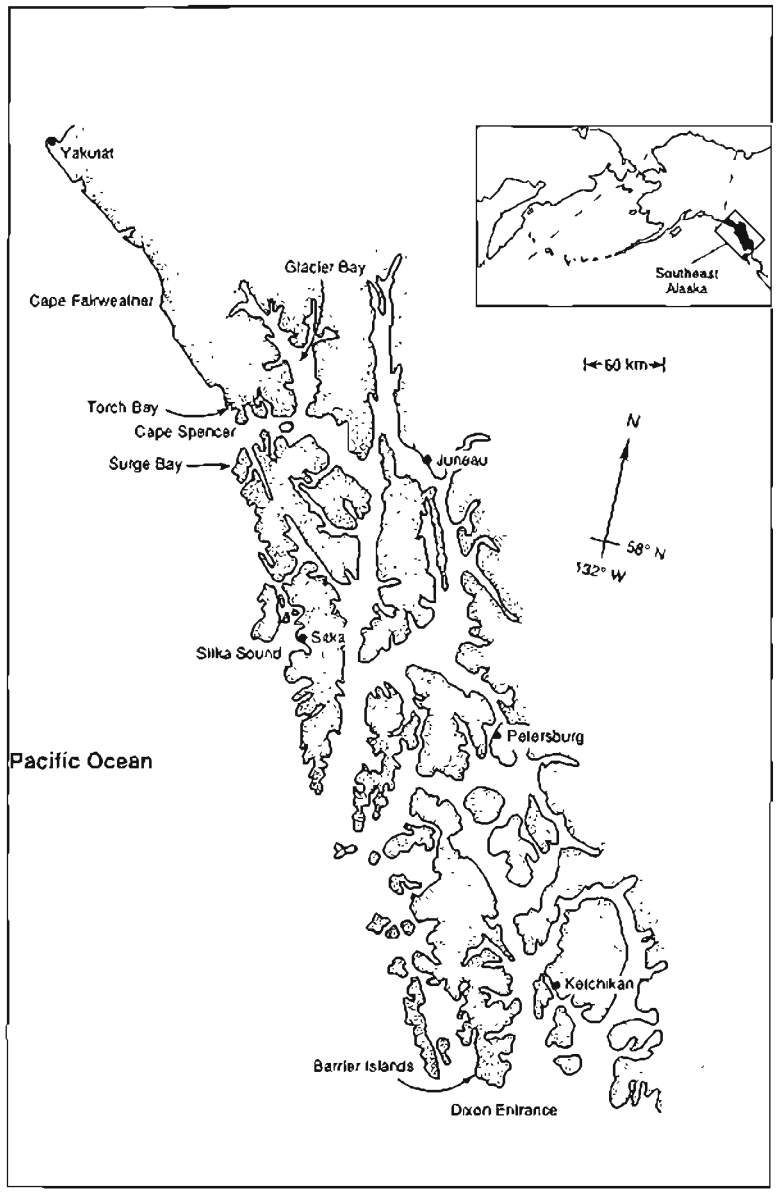


Fig. 37. Southeastern Alaska, indicating areas referred to in text.

(1980) estimated that the population contained 70–120 animals. In 1984, MacAskie (1984) found that the population in British Columbia had split into two main groups, which together contained an estimated 345 individuals; 370 otters were counted in a 1987 survey (MacAskie 1987). From these data, Estes (1990a) estimated that the British Columbia sea otter population increased at 17.7% annually.

Since the relocations to British Columbia, sea otters have been sighted as far northwest of the reintroduction site as 320 km (to the Queen Charlotte Islands and northern mainland) and 220 km southeast along the Vancouver Island coast. However, sightings extralimital to the main British Columbia population may represent sea otters from reintroduced populations in southeastern Alaska and western Washington, since these reintroduction sites are located about the same distance away from these areas as are the Bunsby Islands (Bigg and MacAskie 1978).

Washington

From 1969 to 1970, 59 sea otters were relocated from Amchitka Island to Washington. In 1969, 29 sea otters were released at Point Grenville; at least 16 died within 2 weeks of the reintroduction (Jameson and Kenyon 1977*; Jameson et al. 1982). Most of the mortalities occurred among otters whose fur became soiled in transit (Farr and Bunnell 1980). A second reintroduction of 30 otters was made to La Push in 1970. During a 1983 survey of the Washington coast, 52 otters (including 4 pups) were sighted, from the Destruction Islands in the south to the

Bodelteh Islands in the north. The Washington population was again surveyed in 1985, during which 65 animals were counted (Jameson et al. 1986), of which 5 were dependent pups. A 1987 survey recorded 90 sea otters, including 12 dependent pups. More than 200 otters were counted during a 1989 survey (Jameson, personal communication), although some of these were in a large group offshore in an area that had not been examined in previous surveys. The small proportion of pups (8%) observed in the Washington population during the 1983 survey probably reflects the fact that the survey was conducted in September, when most pups had been weaned (Jameson, unpublished data). Jameson et al. (1986) reported that from 1977 to 1983, the average rate of population growth was 18.3% and predicted that the population should contain >160 otters by 1990. Estes (1990a) estimated that the Washington population increased at 20.6% annually from 1978 to 1987, a rate similar to that of other increasing populations in Alaska and British Columbia.

Oregon

In 1970 and 1971, 93 sea otters from Amchitka Island were released in Oregon in three relocations: 29 at Port Orford in 1970, 24 at Port Orford in 1971, and 40 at Cape Arago in 1971. From 1972 to 1974, 21–23 otters were sighted during surveys of the Oregon coastline; pup-to-independent otter ratios varied from 1:20 to about 1:3. The Oregon populations declined dramatically after 1975 (Jameson 1975; Jameson et al. 1982). In a 1981 survey, only one otter was sighted (Jameson et al. 1982). Sea otters have not been seen since, and the population is considered extinct (Jameson, personal communication).

Eleven sea otter mortalities (including one stillborn pup) were recorded in the Oregon population (Jameson and Kenyon 1977*; Jameson et al. 1982). Although little postrelease mortality was documented, it is possible that the incidence of mortality immediately following the two 1971 translocations was high. High postrelease mortality caused by exposure and thermoregulatory distress may have resulted from an unseasonal storm, which prevented the otters from recuperating (by cleaning their fur and feeding) in holding pens; instead, the animals were released directly into open water from their carrying cages (Jameson 1975).

Jameson and Kenyon (1977*) and Jameson et al. (1982) suggested that failure of the Oregon reintroductions may have been due to emigration, mortality, or habitat unsuitability. Several sightings were made considerable distances from the Oregon reintroduction sites. In 1972, 4–5 otters were observed 204 km north of Cape Arago in June, and 3 otters were reported 290 km north of Cape Arago in August; the same otters could have been involved in both sightings (Jameson et al. 1982).

Jameson et al. (1982) speculated that the sea otters relocated from Amchitka might have been better adapted for survival in northern waters. Because Oregon and Washington lie within a transitional zoogeographic province between the Aleutian and California provinces (Ekman 1953), the more southerly habitat may have been less than suitable for otters originating from the Aleutian Islands. However, the reason for failure of this relocation effort is, in fact, unknown.

California

In 1969, the California Department of Fish and Game relocated 17 sea otters, captured and tagged near Cambria, to Big Creek, located about 72 km north of Cambria. This relocation differed from those discussed previously: the California otters were released a fairly short distance from the capture site and into habitat already occupied by sea otters. In addition, whereas the other relocations were done to expand the otter's range, this one was done to limit it. The relocations in California took place during January, April, July, and August. At least 30% (5) of the relocated sea otters returned to the capture site at Cambria within 9 months of their release (Wild and Ames 1974). On 25 September 1969, the first relocated otter was observed off Cambria (Odemar and Wilson 1969b*). On 12 October 1969, four otters released at Big Creek were sighted 6 km south of Cambria. According to Wild and Ames (1974), it is likely that the proportion of otters that returned to the capture site was greater than indicated by the five otters actually sighted.

Another translocation of California sea otters from the southern to the northern part of their current range was conducted in 1988–89 by Doroff et al. (1989*), who investigated the movement patterns of the translocated animals. Sea otters from the southern part of the range were captured and moved, because animals in this area may be at higher risk to oil spills if the proposed oil development in the Santa Maria basin takes place. If an oil spill occurred in this area, attempts would be made to capture, clean, and relocate oil-contaminated otters; therefore, the movements of such relocated otters after release in the northern part of the range are of interest; if they return to their capture site, they may risk oil recontamination.

Doroff et al. (1989*) captured 19 sea otters at Shell Beach and released them at Moss Landing during 3 periods: 9 during 17–20 May 1988, 6 during 18–19 January 1989, and 4 during 27 April–2 May 1989. A 60-day radio-transmitter tag was attached to each otter's hindflipper. One of the otters was a juvenile female, and the rest were juvenile, subadult, or adult males. Nine of the otters were released soon after being moved to Moss Landing, while the remaining 10 were held in a flotation

pen at Moss Landing harbor for 48 h to determine the effect of such containment on homing behavior.

All otters detained in the holding pen remained between Monterey and Point. Año Nuevo for the entire study. Yet 56% (five) of the nine otters not held returned to the Shell Beach capture site, about 291 km south of Moss Landing, traveling this distance in an average of 12 days (range = 7–21 days). The remaining four otters moved southward only once during the monitoring period. Four of the otters that returned to Shell Beach immediately moved north to Soquel Point (an area inhabited primarily by males, 27 km north of the Moss Landing release site) before returning to Shell Beach.

After being released without being held for 48 h, one adult male (captured 17 May 1988) moved 27 km north to Soquel Point where he remained for 6 days; he was found back at Shell Beach 7 days later. Interestingly, after 34 days, he returned to Soquel Point, and was last located 28 days later near Cayucos, 250 km south of Soquel Point. After the expiration of his radio-transmitter, the otter was again sighted 3 times at Soquel Point, identified by his hindflipper tags; the last sighting was 12 May 1989.

One old adult male died during the monitoring period, and two old adult males were found dead after the study ended, at Half Moon Bay (116 km north of Moss Landing) and San Gregorio Beach (100 km north of Moss Landing); causes of all three deaths were unknown. This translocation experiment indicates that holding sea otters for a period of time before they are released influences homing behavior, possibly making them less likely to return to their capture site.

The 1969 and 1988–89 California experiments demonstrated that relocations across continuous rocky substrate–kelp forest habitat (apparently preferred by sea otters) could not effectively prevent otters from dispersing from the release site and traveling back to the original capture site (Wild and Ames 1974). However, other factors such as the age of animals, presence of territorial males, and seasonal movements of males to and from the range peripheries (Jameson 1989), may have influenced attempts to relocate male otters to a specific area within the established range in California. Doroff et al. (1989) pointed out that all five otters that returned to their Shell Beach capture site were released in spring (late April to mid-May).

Jameson et al. (1982) suggested that sea otters (especially adults) have an affinity for a specific home range. Those most likely to return to their capture site when relocated to an unfamiliar area, therefore, may be the adult otters. Jameson (1989) found that some adult males near San Simeon, California, returned to the same territories for 6 consecutive years. Jameson et al. (1982) suggested that subadult otters, especially males, may be more likely to remain at the relocation site due to their tendency to disperse to new areas from their natal site. In many species of mammals, it is the juveniles, particularly

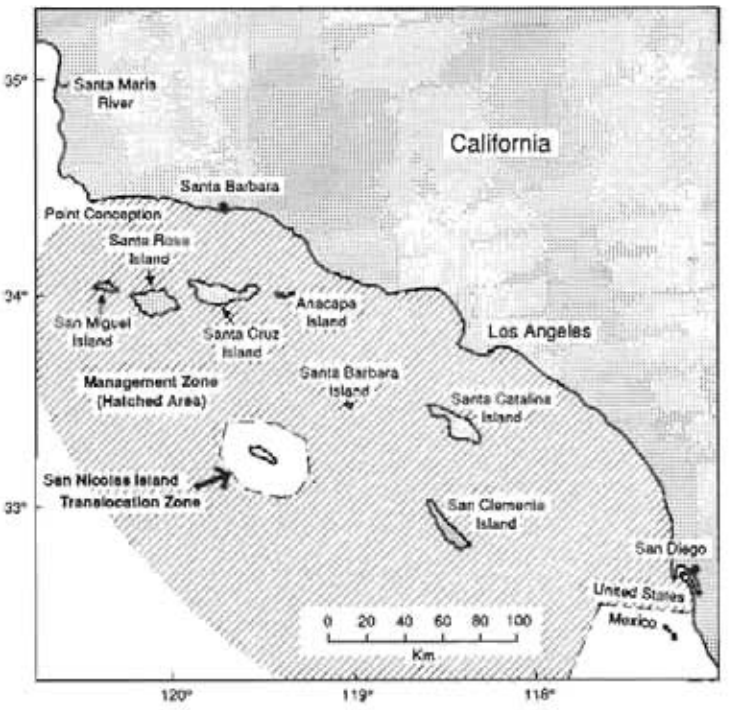


Fig. 38. San Nicolas Island translocation zone, where the relocated population of California sea otters is protected. Sea otters in the management zone are to be removed and transported back to the sea otter range north of Point Conception.

juvenile males, that disperse from the natal area seeking reproductive opportunities (Murray 1967; Gadgil 1971; Hamilton and May 1977; Horn 1978). In the California sea otter population, evidence suggests that juvenile males tend to disperse a greater distance from the natal area than juvenile females (Ralls et al. 1988a*; Riedman et al. 1988*; Jameson, unpublished data). However, Doroff et al. (1989*) found that 30% (3) of their sample of 10 subadult males returned to their capture site within their monitoring period.

San Nicolas Island

In August 1987, the U.S. Fish and Wildlife Service began a major effort to reintroduce sea otters to San Nicolas Island in the southern California Bight (Fig. 38). This effort is ongoing. Unlike all previous sea otter reintroductions, this project included an intensive follow-up study of the fate and behavior of the relocated otters (Rathbun et al. 1989*). As of June 1990, 137 animals had been moved to San Nicolas Island (U.S. Fish and Wildlife Service 1990). Each of these animals was marked with color-coded flipper tags, and some were instrumented with radio transmitters. By June 1990, 15 animals were known to have remained at San Nicolas Island. Of the other translocated animals, 30 returned to the mainland, 9 died from human-related causes (including capture stress), 3 were recaptured and returned to their original capture site (after they swam into the "no-otter" zone near the southern California mainland), and 80 were unaccounted for (Rathbun et al. 1989*). Adults (>1.8 kg) seem to be more likely to return to their capture sites than do subadults and juveniles. Eight pups were born on San Nicolas Island; of these, one was weaned, three are still with their mothers, and the fate of the remaining four is unknown (U.S. Fish and Wildlife Service 1990*). The success or failure of this project is still undetermined.

Summary and Conclusions

Failure of all efforts to reintroduce sea otters in the 1950's was principally due to a high mortality that occurred during and immediately after transportation to the release site. Mortality in transit was caused by thermoregulatory distress resulting from soiled and matted fur, which lost its insulative properties when the otters were released into open water. During subsequent attempts, this problem was largely resolved by preventing the animals from becoming soiled in transit and by placing them in holding facilities containing clean seawater before release allowing the animals to feed and to clean and groom their fur.

From 1965 to 1972, attempts to reestablish populations of sea otters into unoccupied habitat were successful in southeastern Alaska, British Columbia, and probably Washington. Reintroductions to Oregon and to the Pribilof Islands in Alaska failed. The reasons some attempts succeeded and others failed are largely unknown, although postrelease dispersal has occurred in all the relocation efforts (Estes et al. 1989); failure of the reintroduction to St. George Island in the Pribilof Islands may have been due to mortality caused by unseasonal winter sea ice in the area (Kenyon 1969; Jameson et al. 1982).

The Oregon reintroduction probably failed because of emigration from the release area coupled with a high mortality rate. Some degree of habitat unsuitability for the transplanted Amchitka otters may possibly have promoted the decline in the Oregon population (Jameson et al. 1982), although there is no evidence for this. The reintroductions to southeastern Alaska, British Columbia, and Washington apparently succeeded because of the larger number of otters relocated (although the Oregon reintroduced population was larger than the one to Washington and comparable in size to the British Columbia population), immigration of otters from other populations, or highly suitable habitat available at the reintroduction site (Jameson et al. 1982)

Based on the results of previous reintroduction efforts for sea otters, Jameson et al. (1982) concluded the following: (1) Soon after release, the number of sea otters at a reintroduction site may decline substantially; (2) emigration probably is the main cause of the decline; (3) it is difficult to predict specific locations where the relocated populations will become established, although it is possible to reintroduce otters to a general area; and (4) the successful reintroduction of sea otters into unoccupied habitat probably will require a fairly large nucleus population. Jameson et al. (1982) suggested that relocation of 25–30 otters annually over 3–5 years would be necessary to ensure adequate growth of the reintroduced population.

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Personal Communications

Jack A. Ames, California Department of Fish and Game, Monterey, California.

Alan Baldridge, Hopkins Marine Station, Pacific Grove, California.

James L. Bodkin, U.S. Fish and Wildlife Service, Institute of Marine Sciences, University of California, Santa Cruz, California.

Donald Croll, Moss Landing Marine Laboratories, Moss Landing, California.

Charles Deutsch, Institute of Marine Sciences, University of California, Santa Cruz, California.

Larry Espinosa, California Department of Fish and Game, Monterey, California.

Connie Grey, Monterey Bay Aquarium, Monterey, California.

Robert A. Hardy, California Department of Fish and Game, Morro Bay, California.

Brian Hatfield, U.S. Fish and Wildlife Service, San Simeon, California.

Julie Hymer, Monterey Bay Aquarium, Monterey, California.

Ronald J. Jameson, U.S. Fish and Wildlife Service, San Simeon, California.

Kathy Lyons, Institute of Marine Sciences, University of California, Santa Cruz, California.

Bruce Steele, California Urchin Divers Association, Santa Barbara, California.

Judson E. Vandevere, 93 Via Ventura, Monterey, California.

Fredrich E. Wendell, California Department of Fish and Game, Morro Bay, California.

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