SEA LIONS

See **SEALS**

SEA OTTERS

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Introduction

A century ago sea otters were on the verge of extinction. Reduced from several hundred thousand individuals, the cause of their decline was simply the human harvest of what is arguably the finest fur in the animal kingdom. They persisted only because they became so rare that, despite intensive efforts, they could no longer be found. Probably less than a few dozen individuals remained in each of 13 remote populations scattered between California and Russia. By about 1950 it was clear that several of those isolated populations were recovering. Today more than 100 000 sea otters occur throughout much of their historic range, between Baja California, Mexico, and Japan, although suitable unoccupied habitat remains (**Figure 1**). As previous habitat is reoccupied, either through natural dispersal or translocation, sea otter populations and the coastal marine ecosystem they occupy, can be studied before, during, and following population recovery. Because of concern for the conservation of the species, as well as conflicts between humans and sea otters over coastal marine resources, nearly continuous research programs studying this process have been supported during the past 50 years. Because sea otters occur near coastlines, bring their prey to the surface to consume, and can be easily observed and handled, they may be more amenable to study than most marine mammals. Both the accessibility of the species and the serendipitous 'experimental' situation provided by their widespread removal and subsequent recovery have provided a depth of understanding into the ecological role of sea otters in coastal communities and the response of sea otters to changing ecological conditions that may be unprecedented among the large mammals.

Sea otters are unique, both among the other otters, to which they are most closely related, and the other marine mammals, with which they share the oceans as a common habitat. They are the only fully marine species of Lutrinae, or otter subfamily of mustelids, having evolved relatively recently from their terrestrial and freshwater ancestors. Thus, the natural history of sea otters is a result of both their phylogenetic history and the adaptations required by a life at sea. As a result of these sometimes opposing pressures, sea otters display characteristics of their recent ancestors, the other otters, and also exhibit attributes that result from those adaptations that are common among the other mammals of the sea.

Description

The sea otter is well known as the smallest of the marine mammals but also the largest of the Lutrinae. The sexes are moderately dimorphic with males attaining maximum weights up to 45 kg and 158 cm total lengths. Adult females attain weights up to 36 kg and total lengths to 140 cm. Newborn pups weigh about 2 kg and are about 60 cm in length. Dentition is highly modified with broad, flattened molars for crushing hard-shelled invertebrates, rounded, blunt canines for puncturing and prying prey, and spade-shaped protruding incisors for scraping tissues out of shelled prey (**Figure 2**). The body is elongated and the tail is relatively short (less than one-third of total length) and flattened compared to other otters. The fore legs are short and powerful with sensitive paws used to locate and manipulate prey and in grooming, traits held in common with the clawless otters (*Aonyx* spp. or crab-eating otters) also known to forage principally on invertebrates. The fore legs are not used in aquatic locomotion. The extruding claws present in sea otters are unique among the mustelids and are useful in digging for prey in soft sediment habitats. The hind feet are enlarged and flattened relative to other otters and are the primary source of underwater locomotion. The external ear is small and similar to the ear of the otariid pinniped. Fur color ranges from brown to nearly black and a general lightening from the head downward may occur with aging.

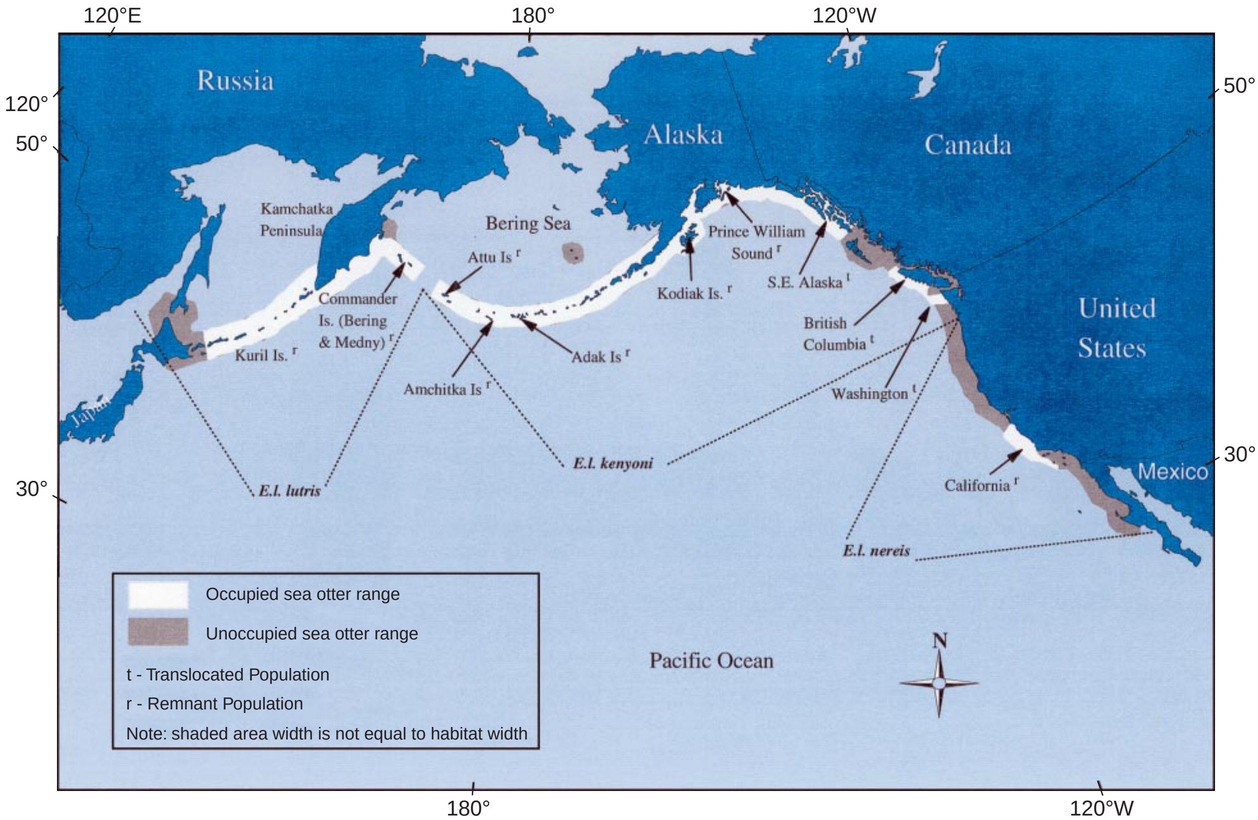


Figure 1 Occupied and unoccupied sea otter habitat in the North Pacific Ocean (2000).

The pelage is composed of bundles made up of a single guard hair and numerous underfur hairs, at a ratio of about 1:70. Hair density ranges to 165 000 cm^{-2} and is the densest hair among mammals. Most marine mammals insulate with a blubber layer, but sea otters are the only one to rely exclusively on an air layer trapped in the fur for insulation. Although air is a superior insulator, it requires constant grooming to maintain insulating quality. It is this means of insulation (fur) that made the sea otter so valuable to humans and makes it susceptible to oil spills and other similar contaminants, that can reduce insulation. Additionally, fur and the air it contains, allow the sea otter to be positively buoyant, a trait shared with some marine mammals but with none of the other otters.

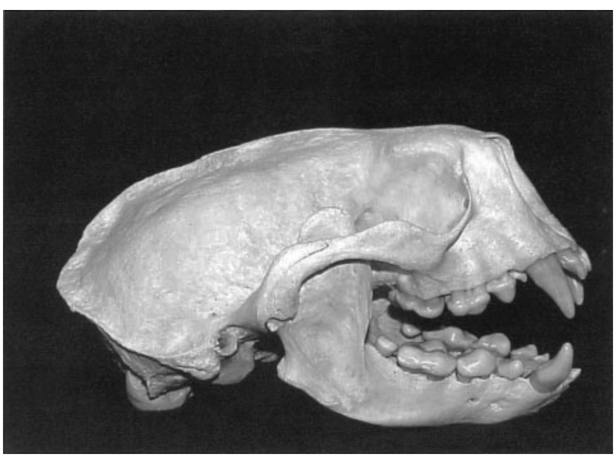


Figure 2 Photo of sea otter skull and dentition.

Range and Habitat

Primitive sea otters (the extinct *Enhydridon* and *Enhydritherium*) are recognized from Africa, Eurasia, and North America. Specimens of *Enhydra* date to the late Pliocene/early Pleistocene about 1–3 million years ago. The modern sea otter occurs only in the north Pacific ocean, from central Baja California, Mexico to the northern islands of Japan (**Figure 1**). The northern distribution is limited by the southern extent of winter sea ice that can limit access to foraging habitat. Southern range limits are less well understood, but are likely to be related to increasing water temperatures and reduced productivity at lower latitudes and constraints imposed by the dense fur the sea otter uses to retain heat.

Although sea otters occupy and utilize all coastal marine habitats, from protected bays and estuaries to exposed outer coasts and offshore islands, their habitat requirements are defined by their ability to dive to the seafloor to forage. Although they may haul out on intertidal or supratidal shores, their habitat is limited landward by the sea/land interface and no aspect of their life history requires leaving the ocean. The seaward limit to their distribution is defined by their diving ability and is approximated by the 100 m depth contour. Although sea otters may be found at the surface in water deeper than 100 m, either resting or swimming, they must maintain relatively frequent access to the seafloor to obtain food. Sea otters forage in diverse bottom types, from fine mud and sand to rocky reefs. In soft sediment communities they prey largely on burrowing infauna, whereas in consolidated rocky habitats epifauna are the primary prey.

Life History

Following a gestation of about six months, the female sea otter gives birth to a single, relatively large pup. In contrast, all other otters have multiple offspring, whereas all other marine mammals have single offspring. Pupping can occur during any month, but appears to become more seasonal with increasing latitude with most pups born at high latitudes arriving in late spring. The average length of pup dependency is about six months, resulting in an average reproductive interval of about one year. Females breed within a few days of weaning a pup, and thus may be either pregnant or with a dependent young throughout most of their adult life. The juvenile female attains sexual maturity at between two and four years and the male at about age three years, although social maturity, particularly among males may be delayed for several more years. The sea otter is polygynous; male sea otters gain access to females through territories where other males are excluded. The reproductive system results in a general segregation of the sexes; most adult females and few territorial males occupy most of the habitat and nonterritorial males reside in dense aggregations. Similar reproductive systems are common among the pinnipeds, whereas most otter species are organized around family units consisting of a mother, her offspring and one or more males.

Survival in sea otters is largely age dependent. Survival of dependent pups is variable ranging from about 0.20 to 0.85, and is likely dependent on maternal experience, food availability, and environmental conditions. Among dependent pups, survival is lowest in the first few weeks after parturition, then increasing and remaining high through dependency. A second period of reduced survival follows weaning and may result in annual mortality rates up to 0.60. Once a sea otter attains adulthood, survival rates are high, around 0.90, but decline later in life.

Maximum longevity is about 20 years in females and 15 years in males. Sources of mortality include a number of predators, most notably the white shark (*Carcharadon charcharias*) and the killer whale (*Orca orcinus*). Bald eagles (*Haliaeetus leucocephalus*) may be a significant cause of very young pup mortality. Terrestrial predators, including wolves (*Canis lupus*), bears (*Ursos arctos*) and wolverine (*Gulo gulo*) may kill sea otters when they come ashore, although such instances are likely rare. Pathological disorders related to enteritis and pneumonia are common among beach-cast carcasses and may be related to inadequate food resources, although such causes of mortality generally coincide with late winter periods of inclement weather. Nonlethal gastrointestinal parasites are common and lethal infestations are occasionally observed. Among older animals, tooth wear can lead to abscesses and systemic infection, eventually contributing to death.

Adaptations to Life at Sea

Locomotion

Adaptations seen in the sea otter reflect a transition away from a terrestrial, and toward an aquatic existence. The sea otter has lost the terrestrial running ability present in other otters, and although walking and bounding remain, they are awkward. The reduced tail length decreases balance while on land. The sea otter is similar to other otters in utilizing the tail as a supplementary means of propulsion, but more similar to the phocid seal in primarily relying on the hind flippers for aquatic locomotion. The hind feet of the sea otter are more highly adapted compared to other otters, but less modified than the hind legs of both pinnipeds and cetaceans. The hind feet are enlarged through elongation of the digits, flattened and flipper like and provide the primary source of underwater locomotion. While swimming, the extended hind flippers of the sea otter approximate the lunate pattern and undulating movement of the fluke of cetaceans.

The primary method of aquatic locomotion in sea otters while submersed is accomplished by craniocaudal thrusts of the pelvic limbs, including bending of the lumbar, sacral, and caudal regions for increased speed. The sea otter loses swimming efficiency in the resistance and turbulence during the recovery stroke and through spaces between the flippers and tail. Travel velocities over distances less than 3 km are in the range of about 0.5–0.7 $\mathrm{m\,s^{-1}}$, with a maximum of about $2.5\,m\,s^{-1}$. Estimated sustainable rates of travel over longer distances are in the range of $0.16–1.5\,m\,s^{-1}$. Rates of travel during foraging dives average about $1.0\,m\,s^{-1}$.

A unique paddling motion, consisting of alternating vertical thrusts and recovery of the hind flippers is a common means of surface locomotion. The tail is capable of propelling the sea otter slowly, usually during either resting or feeding.

Thermoregulation

Sea otters, similar to all homeotherms, must strike a balance between conserving body heat in cold environments, and dissipating heat when internal production exceeds need. This process is particularly sensitive in the high latitudes where water is cold and heat loss potential is high and when a relatively inflexible insulator such as air is used. The small size of the sea otter magnifies the heat loss problem because of a high surface area to volume ratio. One way to offset high heat loss is through the generation of additional internal heat. The sea otter accomplishes this through a metabolic rate 2.4–3.2 times higher than predicted in a terrestrial mammal of similar size. This elevated metabolic rate requires elevated levels of energy intake. As a result of this increased energy requirement, sea otters consume 20–33% of their body mass per day in food. In northern latitudes, sea otters may haul-out more frequently during the winter as a means to conserve heat.

Although air is a more efficient insulator than blubber (10 mm of sea otter fur is approximately equal to 70 mm of blubber), the fur requires high maintenance costs and does not readily allow heat dissipation that may be required following physical exertion. To maintain the integrity of the fur, up to several hours per day are spent grooming, primarily before and after foraging, but also during foraging and resting activities. To dissipate excess internal heat, and possibly absorb solar radiation the sea otter's hind flippers are highly vascularized and with relatively sparse hair. Heat can be conserved by closing the digits and placing the flippers against the abdomen, or dissipated by expanding the digits and exposing the interdigital webbing to the environment. Because air is compressible, sea otters likely lose insulation while diving, and may undergo unregulated heat loss during deep dives, however the heat loss may be offset to some extent by the elevated metabolic heat produced during diving.

Diet and Diving

Sea otters prey principally on sessile or slow-moving benthic invertebrates in nearshore habitats throughout their range, from protected inshore waters to exposed outer coast habitats. In contrast, most other otters and most pinnipeds and odontocete cetaceans rely largely on a fish-based diet. Although capable of using vision to forage, the primary sensory modality used to locate and acquire prey appears to be tactile, since otters feed in highly turbid water, and at night. Foraging in rocky habitats and kelp forests consists of hunting prey on the substrate or in crevices. Foraging in soft sediment habitats often requires excavating large quantities of sediments to extract infauna such as clams.

Although the number of species preyed on by sea otters exceeds 150, only a few of these predominate in the diet, depending on latitude, habitat type, season, and length of occupation by sea otters. Generally, otters foraging over rocky substrates and in kelp forests mainly consume decapod crustaceans (primarily species of *Cancer*, *Pugettia*, and *Telmessus*), mollusks (including gastropods, bivalves, and cephalopods) and echinoderms (species of *Strongylocentrotus*). In protected bays with soft sediments, otters mainly consume infaunal bivalves (species of *Saxidomus*, *Protothaca*, *Macoma*, *Mya*, and *Tresus*) whereas along exposed coasts of soft sediments, *Tivela stultorum*, *Siliqua* spp. are common prey. Mussels (species of *Mytilus* and *Modiolis*) are a common prey in most habitats where they occur and may be particularly important in providing nourishment for juvenile sea otters foraging in shallow water. Sea urchins are relatively minor components of the sea otter's diet in Prince William Sound and the Kodiak archipelago, but are a principal component of the diet in the Aleutian Islands. In the Aleutian, Commander and Kuril Islands, a variety of fin fish (including hexagrammids, gaddids, cottids, perciformes, cyclopterids, and scorpaenids) are present in the diet. For unknown reasons, fish are rarely consumed by sea otters in regions to the east of the Aleutian Islands.

Sea otters also exploit normally rare, but episodically abundant prey. Examples include squid (*Loligo* sp.) and pelagic red crabs (*Pleuroncodes planipes*) in California and smooth lumpsuckers (*Aptocyclus ventricosus*) in the Aleutian Islands. The presence of abundant episodic prey may allow temporary release from food limitation and result in increased survival. Sea otters, on occasion, attack and consume sea birds, including teal, scoters, loons, gulls, grebes, and cormorants, although this behavior is apparently rare.

The sea otter is the most proficient diver among the otters, but one of the least proficient among the other marine mammals. Diving occurs during foraging but also while traveling, grooming, and during

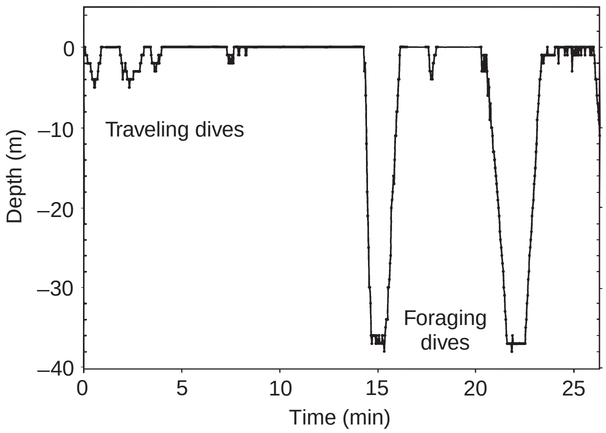


Figure 3 Examples of foraging and traveling sea otter dive profiles. Ascent/descent rates and percentage of dive time at bottom vary between dive types.

social interactions. Foraging dives are characterized by rapid ascent and descent rates with relatively long bottom times. Traveling dives are characterized by slow ascent and descent rates and relatively short times at depth (**Figure 3**). The maximum recorded dive depth in the sea otter is 101 m and most diving is to depths less than 60 m. Mean and maximum dive depths appear to vary between sexes and among individuals. Generally, males appear to have average dive depths greater than females, although some females regularly dive to depths greater than some males. Maximum reported dive duration is 260 s. Average dive durations are in the range 60–120 s and differ among areas and are likely influenced by both dive depth and prey availability. Foraging success rates are generally high, from 0.70 to > 0.90 although the caloric return per unit effort probably varies relative to prey availability.

Reproduction

In contrast to the pinnipeds and polar bears, as well as the other otters, sea otter reproduction has no obligatory terrestrial component. In this regard, the sea otter is more similar to the cetacea or sirenia. Sea otters throughout their range are capable of reproducing throughout the year. Alternatively, most pinnipeds and cetaceans display strong seasonal, synchronous reproductive cycles. Likely the most conspicuous reproductive adaptation that separates sea otters from the other lutrines and aligns them with the other marine mammals is reduction in litter size. All other lutrines routinely give birth to and successfully raise multiple offspring from a single litter. Although sea otters infrequently conceive twin fetuses, there are no known records of a mother successfully raising more than one pup. This trait of single large offspring appears to be strongly selected for in marine mammals (**Figure 4**) with the exception of polar bears.

The Role of Sea Otters in Structuring Coastal Marine Communities

A keystone predator is one whose effects on community structure and function are disproportionately large, relative to their own abundance. Sea otters provide one of the best documented examples of the keystone predator concept in the ecological literature. Although other factors can influence rocky nearshore marine communities, particularly when sea otters are absent, the generality of the sea otter effect is supported with empirical data from many sites throughout the North Pacific rim.

There are several factors that have contributed to our understanding of the role sea otters play in structuring coastal communities. First, sea otters are distributed along a narrow band of relatively shallow habitat where they forage almost exclusively on generally large and conspicuous benthic invertebrates. Because water depths are shallow, scientists, aided with scuba have been able to rigorously characterize and quantify coastal marine communities where sea otters occur. Because sea otters bring their prey to the surface prior to consumption, the type, number, and sizes of prey they consume are straightforward to determine. Furthermore, many of the preferred prey of sea otters are either ecologically (e.g., grazers) or economically (e.g., support fisheries) important, prompting a long-standing interest in the sea otter and its effect on communities. And finally, because sea otters were removed from

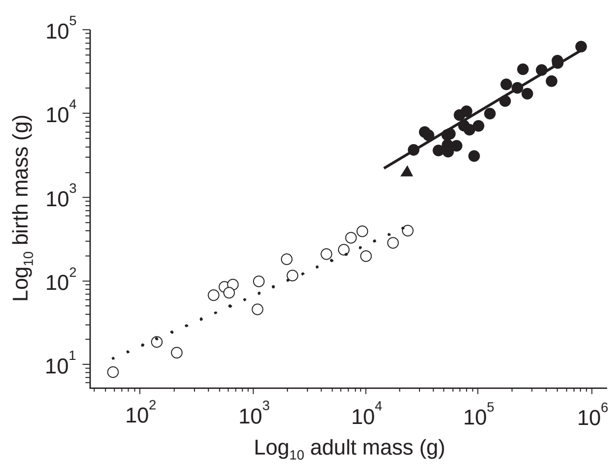


Figure 4 Birth mass versus adult female mass of sea otters relative to the other mustelids and marine mammals. ●, Pinnipeds; ○, Mustelids; ▲, *Enhydra lutris*; —, Pinniped, regression, …, mustelid regression.

most of their range prior to 1900, but have recovered most of that range during the last half of the twentieth century, we have been afforded the opportunity to repeatedly observe coastal communities both with and without sea otters present, as well as before and after sea otters recolonize an area. This combination of factors may be nearly impossible to duplicate in other communities that support large carnivores.

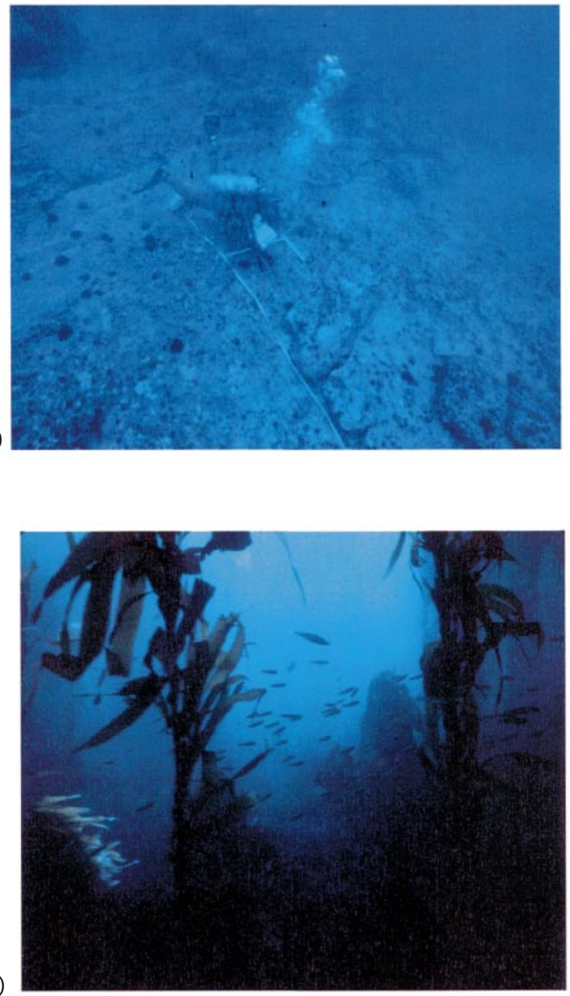
Kelp Forests

The majority of studies on sea otter ecosystem effects has taken place in kelp forest communities that occur over rocky reefs and has led to a generalized sea otter paradigm. This scenario describes the rocky reef community in the absence of sea otters as being dominated by the effects of the herbivorous sea urchins (*Strongylocentrotus* spp.) that can effectively eliminate kelp populations, resulting in what have come to be termed 'urchin barrens' (**Figure 5A**). The urchin barren is characterized by low species diversity, low algal biomass, and abundant and large urchin populations. In areas of the Aleutian Islands dominated by urchin barrens the primary source of organic carbon in nearshore food webs results from fixation of carbon by phytoplankton or microalgae.

Sea urchins may be the most preferred of the many species preyed on by sea otters. As a result, when sea otters recolonize urchin-dominated habitat, urchin populations are soon reduced in abundance with few if any large individuals remaining. Following reduced urchin abundance, herbivory on kelps by urchins is reduced. In response to reduced herbivory, kelp, and other algal populations increase in abundance often forming a multiple-layer forest culminating in a surface canopy forming kelp forest (**Figure 5**). The kelp forest in turn supports a high diversity of associated taxa, including gastropods, crustaceans, and fishes. The effects of the kelp forests may extend to birds and other mammals that may benefit from kelp forest-associated prey populations. In areas of the Aleutian Islands dominated by kelp forests, the primary source of organic carbon in nearshore food webs results from fixation of carbon by kelps, or macroalgae.

Soft-Sediment Subtidal

Studies throughout the North Pacific indicate that sea otters can have predictable and measurable effects on invertebrate populations in sedimentary communities. The pattern typically involves a predation-related reduction in prey abundance and a shift in the size-class composition toward smaller individuals, similar to patterns seen in rocky reefs. This pattern has been observed for several species of bivalve clams and Dungeness crabs (*Cancer magister*). The green sea urchin (*Strongylocentrotus droebachiensis*) can be common and abundant in sedimentary habitats in Alaska, particularly where sea otters have been absent for extended periods of time. In such areas, as sea otters recover prior habitat, the green urchin may be a preferred prey. The effect of sea otter foraging on the green urchin in sedimentary habitats is similar to the otter effect observed on urchins in rocky reefs. Urchin abundance is reduced and surviving individuals are small and may achieve refuge by occupying small interstitial spaces created by larger sediment sizes. Although sea urchins may provide an abundant initial resource during sea otter recolonization, clams appear to be the primary dietary item in soft sediment habitats occupied for extended periods.



(A) (B)

Figure 5 Photos of (A) urchin barrens and (B) kelp forest.

Cascading trophic effects of sea otter foraging are less well described in sedimentary habitats, when contrasted to rocky reefs. It is likely that the reduction of urchins has a positive effect on algal productivity, especially where the larger sediment sizes (e.g., rocks and boulders) required to support macroalgae are present. In the process of foraging on clams, sea otters discard large numbers of shells after removing the live prey. These shell remains provide additional hard substrate that can result in increased rates of recruitment of some species such as anemones and kelps.

The effects of otter foraging in sedimentary habitats include disturbance to the community in the form of sediment excavation and the creation of foraging pits. These pits are rapidly occupied by the sea star (*Pycnopodia helianthoides*). *Pycnopodia* densities are higher near the otter pits where they may prey on small clams exposed, but not consumed, by sea otters.

Responses to Changing Ecological Conditions

Contrasts between sea otter populations at recently (below equilibrium) and long-occupied sites (equilibrium) as well as contrasts at sites over time provide evidence of how sea otters can modify life history characteristics in response to changing population densities and the resulting changes in ecological conditions. The data summarized below were collected at sites sampled over time, both during and following recolonization, and also at different locations where sea otters were either present for long or short periods of time.

Diet

In populations colonizing unoccupied habitat, sea otters feed largely on the most abundant and energetically profitable prey. Preferred prey species likely differ between areas but include the largest individuals of taxa such as gastropods, bivalves, echinoids, and crustaceans. Over time, as populations approach carrying capacity and the availability of unoccupied habitat diminishes, preferred prey of the largest sizes become scarce and smaller individuals and less preferred prey are consumed with increasing frequency. Several consequences of this pattern of events are evident, and have been repeatedly observed. One is an increase in dietary diversity over time as otter populations recolonize new habitats and grow toward resource limitation. A relatively few species are replaced by more species, of smaller size, and at least in the Aleutian Islands, a new prey type (e.g., fish) may become prevalent in the diet. This in turn may eventually lead to a new and elevated equilibrium density. Another result of declining prey is an increase in the quantity of time spent foraging as equilibrium density is approached. In below-equilibrium populations, sea otters may spend as little as 5 h each day foraging, whereas in equilibrium populations 12 h per day or more may be required. Finally, declining body conditions and total weights have been seen in sea otters as equilibrium density is attained. Mass/length ratios are consistently greater in below-equilibrium populations compared to those at or near equilibrium. At Bering Island as the population reached and exceeded carrying capacity over a 10 year period (**Figure 6**), average weights of adult males declined from 32 kg to 25 kg.

Reproduction

Studies of age specific reproductive rates have produced generally consistent results in populations both below and at equilibrium densities. Although a small proportion of females may attain sexual maturity at age two most are mature at age four, regardless of population status. Annual adult female reproductive rates are uniformly high, at around 0.85–0.95, among all populations despite differences in availability of food resources. Under the range of ecological conditions studied, sea otter reproductive output does not appear to play a major role in population regulation, although it seems likely that as ecological or environmental conditions deteriorate, at some point reproductive output should be adversely affected.

Survival

Greater food availability, and the resulting improved body condition can result in significantly higher juvenile sea otter survival rates in below-equilibrium populations. Coupled with high reproductive output, high survival has resulted in sea otter population growth rates in several translocated or recolonizing populations that have approached the theoretical maximum for the species of about 0.24 per year. Declining prey availability does not appear to affect the ages and sexes equally. Survival of dependent pups was nearly twice as high (0.83) in a population below equilibrium, compared to one at equilibrium (0.47). Postweaning survival appears similarly affected, increasing during periods of increasing prey availability. Adult survival appears high and uniform at about 0.90, among both equilibrium and below-equilibrium populations. Survival appears to be greater among females of all age classes, compared to males. At Bering Island in

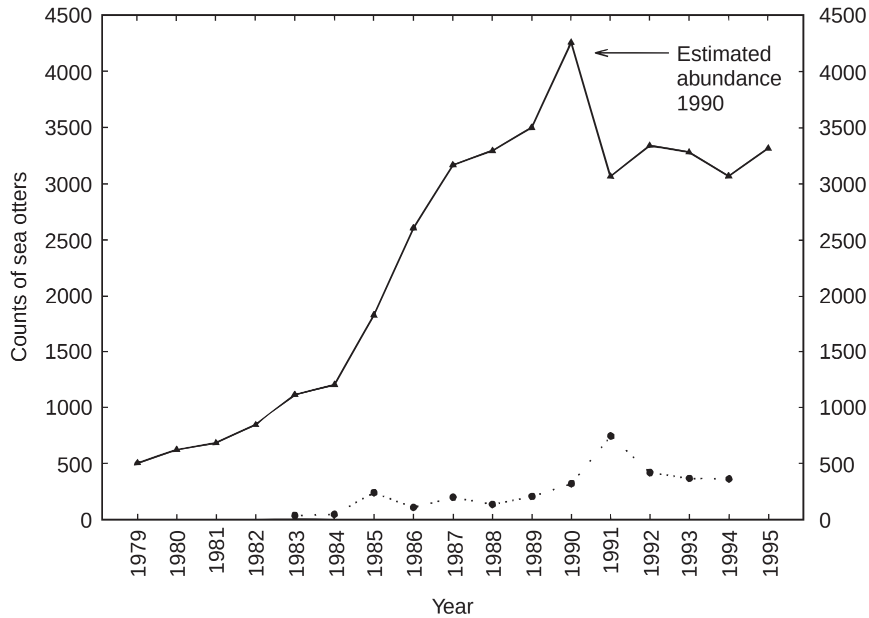


Figure 6 Sea otter abundance (▲, average annual growth 1979–1989 = 0.24) and carcass recovery rates (●) during a period of recolonization and equilibration with prey resources, Bering Island, Russia.

Russia (**Figure 6**) during a year when about 0.28 of the population was recovered as beach cast carcasses, 0.80 of the 742 carcasses were male. Higher rates of male mortality are associated with higher densities of sea otters in male groups and increased competition for food. Thus sex ratios in populations of sea otters are generally skewed toward females. Available data suggest that survival, particularly among juveniles, is the primary life history variable responsible for regulating sea otter populations.

Populations

Trends in sea otter populations today vary widely from rapidly increasing in Canada, Washington and south east Alaska, to stable or changing slightly in Prince William Sound, the Commander Islands, and California, to declining rapidly throughout the entire Aleutian Archipelago. Rapidly increasing population sizes are easily understood by abundant food and space resources and increases should continue to be seen until those resources become limiting. Relatively stable populations can be generally characterized by food limitation and birth rates that approximate death rates. The recent large-scale declines in the Aleutian Archipelago are unprecedented in recent times. Our view of sea otter populations has been largely influenced by events in the past century when food and space were generally unlimited. However, as resources become limiting, it is likely that other mechanisms, such as predation or disease will play increasingly important roles in structuring sea otter populations.

See also

Marine Mammals, History of Exploitation.

Further Reading

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