Sea Otters: Their Role in Structuring Nearshore Communities

Abstract. *A comparison of western Aleutian Islands with and without sea otter populations shows that this species is important in determining littoral and sublittoral community structure. Sea otters control herbivorous invertebrate populations. Removal of sea otters causes increased herbivory and ultimately results in the destruction of macrophyte associations. The observations suggest that sea otter reestablishment indirectly affects island fauna associated with macrophyte primary productivity.*

Destruction of subtidal and intertidal kelp and sea grass beds because of overgrazing by dense populations of sea urchins has been observed over a wide geographical range (*1, 2*). Removal of sea urchins by experimental manipulations (*2*) and by accidental oil spills (*3*) has resulted in the rapid development of marine vegetation. Because community structure differs in the presence and absence of kelp beds (*4–6*) and prey density in marine communities can be significantly influenced by predation (*7*), the structure of a marine community could be determined by the intensity of herbivore predation (*8*).

Speculation regarding the interrelations of sea otters (*Enhydra lutris*) and marine invertebrates has generated controversy in California. However, only slight consideration has extended beyond economic and esthetic arguments by commercial abalone interests and groups concerned with the sea otters' welfare. The observations discussed in this report suggest that sea otters have a profound effect on the structure of marine communities.

Historically, the sea otter occupied a range from the northern Japanese archipelago, through the Aleutian Islands, and along the coast of North America as far south as Morro Hermoso, Baja California (*9*). At present, the sea otter occupies only remote portions of this original range in the Kuril, Commander, and Aleutian islands and parts of southeastern Alaska (*10*). There is an isolated population off the coast of central California, and recent transplants have reintroduced the sea otter into Oregon, Washington, and British Columbia. Continued expansion of the sea otters' range may be expected.

The sea otter population of Amchitka Island, in the Rat Island group (*11*) of the Aleutian archipelago, has been estimated to be 20 to 30 animals per square kilometer of habitat (*12*). The feeding habitat of the sea otter is limited to the intertidal and sublittoral regions within the 60-m depth contour (*10*). Adult, captive sea otters require 20 to 23 percent of their body weight daily in food, and in the natural environment forage species include benthic invertebrates and fish (*10, 13*). Considering the sea otters' average weight as about 23 kg (*10*), we conservatively estimate that 35,000 kg km^{-2} $year^{-1}$ of animal biomass is consumed by foraging sea otters at Amchitka Island. Thus, a high-density sea otter population is an important member of the nearshore marine community.

Such high-density populations have existed in the Rat Island group for about 20 to 30 years, after almost complete annihilation by Russian fur traders during the 18th century. Apparently, the once abundant sea otter population of the Near Islands was extirpated by overexploitation. Until recently, immigrants from the densely populated Rat Islands have been unable to reach the Near Islands, which are located approximately 400 km west-northwest and are separated from the Rat Islands by wide, deep oceanic passes. Since 1959 there have been scattered reports of sea otters in the Near Islands (*10*), although no major population reestablishment has yet occurred.

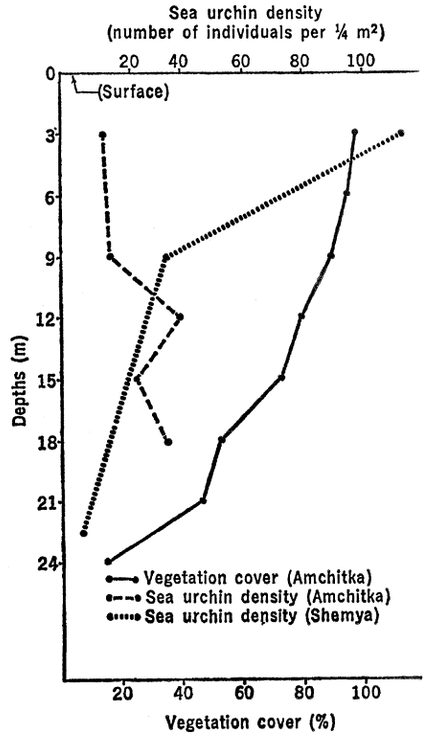

Fig. 1. Vegetation coverage and sea urchin density plotted against depth. The data for Amchitka Island and Shemya Island represent averages from four and three study areas, respectively. Vegetation cover at Shemya Island is coincident with the ordinate.

We have studied the nearshore marine communities of Amchitka Island in the Rat Island group and Shemya Island in the Near Island group. Field observations were made at Amchitka at approximately bimonthly intervals from October 1970 to August 1973 and at Shemya for 1 week each in September 1971 and July 1972; observations were also made at Attu in the Near Islands for 4 days in July 1972.

We propose that the sea otter is the primary cause of the differences observed between the nearshore marine communities of the Rat Island and the Near Island groups. Sea urchins (*Strongylocentrotus* sp.) (*14*) are an important sea otter food and are known to be voracious algal grazers which can consume and destroy large quantities of kelp. Our hypothesis is that a dense population of sea otters reduces the sea urchins to a sparse population of small individuals by size-selective predation. The resultant release from grazing pressure permits a significant increase in the size of nearshore and intertidal kelp beds and associated communities.

Benthic macrophytes in the Rat Island group extend from the intertidal region and cover most of the surface of the rock substrate to depths of 20 to 25 m (Fig. 1). Major contributors to these plant communities are Phaeophyta (brown algae), *Alaria fistulosa, Laminaria longipes, L. groenlandica, L. yezoensis, L. dentigera, Agarum cribrosum, Thalassiophyllum clathrus, Desmarestia* sp., and various Rhodophyta (red algae). Sea urchins are generally not conspicuous in shallow areas (0 to 20 m). However, relatively high densities of sea urchins occur in microhabitats along more protected cracks and beneath holdfasts of macrophytic vegetation. Beginning at depths of 10 to 20 m, sea urchin densities increase with depth and vegetation coverage de-

creases in areas of solid substrate (Fig. 1). Densities of sea urchins are highly variable at these depths, but range up to 680 m^{-2} (*15*). The majority of these sea urchins have test diameters of less than 32 mm (*16*). The increase in sea urchin density with depth is probably related to decreased predation by sea otters (and perhaps diving birds). Feeding on small sea urchins at these depths may be energetically infeasible for predators.

Conversely, the Near Island group is characterized by a distinct lack of macrophytic vegetation below the lower intertidal region. In many areas, sea urchins almost completely carpet the sublittoral immediately adjacent to the littoral, but densities decrease as a function of depth (Fig. 1). Differences in size class distribution and biomass between Near Island and Rat Island sea urchin populations are shown in Fig. 2. The larger size (age) classes of sea urchins are missing from the Rat Island group.

Despite the physical similarities and geographical proximity of the Rat Islands and the Near Islands, there are major floral and faunal differences between the marine communities of their lower intertidal rock platforms (benches). The Rat Islands have an almost complete mat of benthic marine brown algae (kelp), predominantly *Hedophyllum sessile* and *L. longipes*, covering these benches. Sessile, filter-feeding invertebrates—barnacles (*Balanus glandula* and *B. cariosus*) and mussels (*Mytilus edulis*)—and motile, herbivorous invertebrates—sea urchins and chitons (*Katharina tunicata*)—are inconspicuous, small, and scarce. At the Near Islands, *H. sessile* and *L. longipes* are heavily grazed by dense populations of sea urchins and chitons, and there are extensive mussel beds and dense populations of barnacles. Less than 1 percent of the attached kelp examined at the Rat Islands was grazed (*17*). At the Near Islands all kelp overhanging channels and tide pools was grazed, and more than 75 percent of the *L. longipes* plots and 50 percent of the *H. sessile* plots sampled contained grazed plants (*17*). Barnacle and mussel densities, respectively, averaged 4.9 m^{-2} and 3.8 m^{-2} at the Rat Islands and 1215 m^{-2} and 722 m^{-2} at the Near Islands (*17*). Sea urchin and chiton densities, respectively, averaged 8 m^{-2} and less than 1 m^{-2} at the Rat Islands and 78 m^{-2} and 38 m^{-2} at the Near Islands (*17*).

Kelp beds at the Rat Islands shelter the shore from wave action to an appreciable extent. Populations of sessile intertidal invertebrates decline drastically at the Rat Islands since they cannot compete successfully with kelp for space and they are hampered by silt which accumulates because wave-induced turbulence has been reduced (*18*).

Climate, sea state, tidal ranges, and mean tidal levels are similar at both island groups (*19, 20*), and we compared only coastlines of similar structure (with wide intertidal benches). We conclude that the differences observed between benthic communities of the Near Islands and Rat Islands are probably related to the presence or absence of sea otters. The otters effectively control sea urchin populations, and the absence of grazing pressure allows vegetational communities to flourish. Reducing the population of sea otters makes it possible for the sea urchin population to increase, and this leads to a significant reduction in the size of the kelp beds and associated communities.

More far-reaching consequences of these relations are suggested by comparing food webs and faunal distributions between the island groups. Benthic macrophytes are of considerable importance to nearshore productivity in temperate waters (*21*). Species whose food webs originate from macrophytic algal productivity would certainly be adversely affected by its removal. We believe that some faunal differences between the Near Islands and Rat Islands are related to the presence or absence of benthic macrophytes as a nutritional base. Rock greenling (*Hexagrammos lagocephalus*), harbor seals (*Phoca vitulina*), and bald eagles (*Haliaeetus leucocephalus*) are abundant in the Rat Islands but are scarce or absent in the Near Islands (*19, 22*). These species depend largely on nearshore marine productivity in the Aleutians (*23*). We propose that reduced populations of these (and perhaps other) species in the Near Islands may be related to reduced macrophyte productivity.

Our results suggest that reestablishment of sea otters along the Pacific coast of North America will have pro-

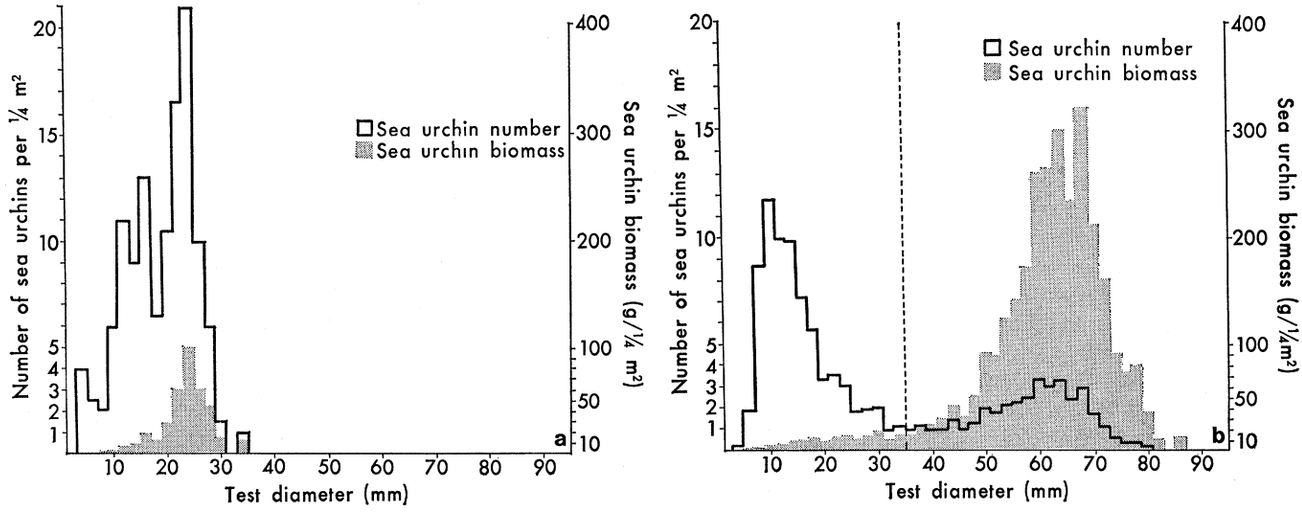

Fig. 2. Sea urchin size class distributions and associated biomass contributions. (a) Data collected from Amchitka Island (high-density sea otter populations). (b) Data collected from Shemya Island (sea otters absent). The dotted line represents the largest sea urchin size class observed at Amchitka Island.

found ecological effects. That this is currently happening is indicated by the sea otter–abalone controversy in California. A decrease in sport and commercial abalone fisheries has been reported following the influx of sea otters into areas of previously unoccupied habitat (*24*). Surveys conducted in 1967 by the California Department of Fish and Game revealed that throughout the sea otters' range preferred sea otter forage items were reduced in number and restricted to protected habitat as compared with habitat outside the range (*25*). Also, an increased diversity in sea otter forage items has been reported in areas long inhabited by sea otters. This is apparently the result of reduced availability of preferred sea otter forage items (*24*).

The sea otter may also be important in restoring kelp beds (and associated species of animals) in southern California. Sea otters in California completely remove large sea urchins (*Strongylocentrotus franciscanus*) from areas by predation, permitting luxuriant development of the *Nereocystis-Pterygophora* (brown algae) association (*4*). Recent increases in sea urchin populations are correlated with kelp bed reduction (*5*). Although kelp bed reductions are obviously related to phenomena more recent than the disappearance of sea otters (*26*), the reestablishment of sea otters should decrease invertebrate populations and increase vegetational biomass.

The sea otter is an important species in determining structures and dynamic relations within nearshore communities, and so fits Paine's (*27*) concept of a keystone species. Many changes have resulted from the near extinction of the sea otters in these communities during the 18th and 19th centuries. In modern biological studies of nearshore marine communities along the Pacific coast of North America the species' ecological importance has not been considered in sufficient detail. We believe that the sea otter is an evolutionary component essential to the integrity and stability of the ecosystem.

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Puromycin: A Questionable Drug for Studying the Mechanism of Thyroid Calorigenesis in vivo

Abstract. *Puromycin fails to alter minimal oxygen consumption of rats treated with thyroxine, provided the rectal temperatures of these rats are maintained at 37.8° to 38.1°C. The previously reported puromycin-induced decline in basal metabolic rate of thyroxine-treated rats may have been due to the hypothermia produced by this drug.*

Thyroid hormone–induced alteration of the rate of protein synthesis is a familiar hypothesis proposed to explain the elevated consumption rate of O_2 observed after administration of thyroid hormones (*1, 2*). This hypothesis is based on the results of experiments that measured basal metabolic rate (BMR) before and after the use of inhibitors of protein synthesis (such as puromycin) in vivo (*1, 2*).

Because of the importance of this hypothesis, we tried to confirm the original findings (*2*) by using a new parameter—minimal oxygen consumption (MOC) (*3–6*). Among the 70 endocrine and nonendocrine factors studied, the MOC appears to measure changes in thyroid state more specifically than the BMR (*6*). Unlike various BMR methods, MOC is measured in sleeping or anesthetized rats, at their thermoneutral temperature (*3, 6*). Thermoneutrality is defined as the highest test chamber temperature that maintains a normal rectal temperature (37.8° to 38.1°C) (*3, 6*). Oxygen consumption was detected volumetrically with a precision-bore glass tube (*6*); a servosystem corrected for extraneous variations in ambient temperature and pressure (*4*). The MOC was expressed in