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SEA OTTER PREDATION AND COMMUNITY ORGANIZATION IN THE WESTERN ALEUTIAN ISLANDS, ALASKA[1]

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Abstract. Predation by the sea otter *(Enhydra lutris)* limits epibenthic invertebrates, especially sea urchins *(Strongylocentrotus polyacanthus)*, in turn allowing a luxuriant development of the macroalgal canopy. Where sea otters are abundant, sea urchins are small and scarce in shallow water, and the association of fleshy macroalgae apparently is regulated by competition. Sea urchins are larger and more abundant in deeper water, where they are less accessible to sea otters. Macroalgae are most abundant, and competition in the plant association is severest, near the sublittoral fringe where sea otters can remove sea urchins most efficiently. In deeper water, competition among macroalgae is reduced because the light intensity is lower and grazing by sea urchins increases. On islands where sea otters are absent, sea urchins are abundant, large, and are probably limited by intraspecific competition; and they have eliminated fleshy macroalgae.

Available data suggest that the association of *Laminaria* spp. and *Agarum cribrosum* contributes most to primary production in nearshore areas of the western Aleutian Islands. Where sea otters are absent and sea urchins have eliminated this plant association, some higher trophic forms also are absent or less abundant than where sea otters are common and the plant association is well developed.

Earlier studies of sea otter food suggested that low-density populations of sea otters consume primarily sea urchins and mollusks in the western Aleutian Islands. Later studies of high-density populations showed a wider variety of foods consumed, with fish an important component of the diet. These studies support our observations on the differences in availability of these foods between islands with and without sea otters.

Key words: Aleutian Islands; community organization; competition; Enhydra lutris; *macroalgae; Mammalia; predation; primary production; sea otter; sea urchin;* Strongylocentrus polyacanthus.

INTRODUCTION

The sea otter, *Enhydra lutris,* evolved as an integral part of nearshore communities in the northeastern Pacific Ocean and southern Bering Sea. Before white men arrived, sea otters flourished from the northern Japanese archipelago, through the Aleutian Islands, and along the Pacific Coast of North America south to Baja California. Overexploitation by fur traders (from 1741 to 1911) eliminated the species, except for remnant populations in Alaska and the coast of central California. Populations are now growing, and the sea otter has become reestablished over much of the northern part of its original range (Kenyon 1969).

The sea otter is a conspicuous predator in nearshore communities of the northeastern Pacific Ocean. We have estimated that the equilibrium density of sea otters is 20 to 30/km^2 at Amchitka Island (Fig. 1; Estes and Smith 1973), and that a population at this density consumes $\approx$35,000 kg$\cdot$km$^{-2}\cdot$yr^{-1} of animal biomass (Estes and Palmisano 1974).

Predation is an important interaction in many marine communities (Connell 1961*b*, Paine 1966, Dayton 1971, Young et al. 1976, and others). The high trophic status, great abundance, and high nutritional requirements (Kenyon 1969, Morrison et al. 1975) of sea otters suggest that nearshore communities of the northern Pacific Ocean are influenced by intense predation on benthic invertebrates. Sea otters may, therefore, function as a "keystone species" (Paine 1969*a*); i.e., by preying on dominant competitors they may influence the composition and abundance of competitive subordinates.

The reduction or complete destruction of marine plants by intense sea urchin grazing has been documented in many geographical areas (see review by Lawrence 1975). The sea urchin, *Strongylocentrotus polyacanthus,* is the dominant herbivore and an important food for sea otters in the western Aleutian Islands (Barabash-Nikiforov 1947, Lensink 1962, Ken-

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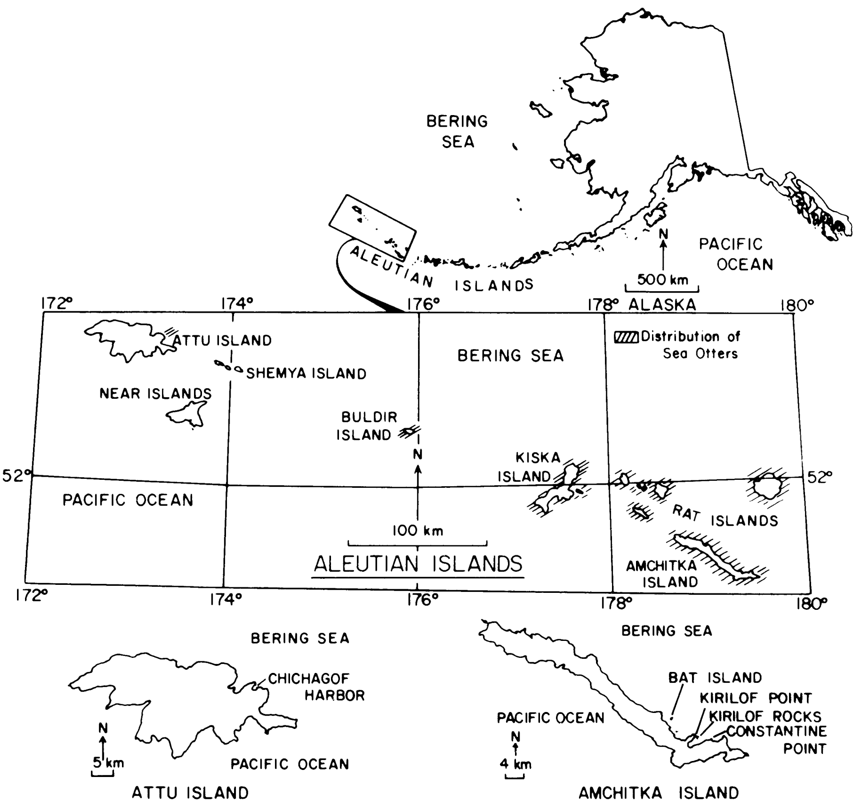

FIG. 1. Location of study areas.

yon 1969). Predation on sea urchins by sea otters in that area may affect vegetation associations, and consequently the dynamics of the entire nearshore community.

Our intent is to elucidate the role of sea otter predation in the organization of nearshore communities in the western Aleutian Islands. By comparing islands with and without sea otters, we propose to test the following hypothesis: Sea otter predation controls epibenthic invertebrate populations (particularly sea urchins), and in turn releases the vegetation association from intense grazing. In addition, our observations provide tentative answers to the following questions:

1) Does predation by sea otters release benthic invertebrates in the nearshore community from limitation by competition, thus affecting the composition, distribution, and dynamics of populations of these invertebrates?

2) Does predation by sea otters indirectly affect the abundance and distribution of macroalgae?

3) Are macroalgae a critical resource for consumers in the nearshore community?

The overexploitation of sea otters by man at similar but isolated islands provided a natural experiment to test these hypotheses. By studying islands with and without sea otters, we have immediate results where a manipulative experiment would have been impractical and time consuming. Furthermore, insular communities are discrete and relatively simple in biotic composition when contrasted with their continental analogues (Simberloff 1974). Therefore, community interactions, as influenced by the presence or absence of sea otters, probably are more clearly observable on islands than in physiographically similar areas along the North American mainland.

THE STUDY AREAS

The Rat and Near Islands are at the western end of the Aleutian Archipelago, between 180° and 170°E and 50° and 55°N. These islands form part of the boundary between the North Pacific Ocean and the Bering Sea (Fig. 1).

The Rat Island group consists of 10 islands; the largest is Amchitka (295 km^2) with 170 kilometres of coastline. Of the 5 islands in the Near Island group, the largest is Attu (905 km^2; 254 km of coastline). Shemya Island is 14 km^2 and has 21 km of coastline.

The climate is maritime and characterized by high winds, persistent overcast skies, and frequent and violent cyclonic storms (Armstrong 1971). Temperatures are moderated by warm water from the Japanese current, and the western Aleutian Islands are far south of the most southerly extension of the polar ice pack.

Geologically, the Aleutian Islands are generally volcanic and of Tertiary or Quaternary origin (Nelson et al. 1974). They were extensively glaciated during the Pleistocene (Black 1976 and references therein).

The biota of the Aleutian Islands is of both Old and New World origin. New World forms predominate at the eastern end of the archipelago and Old World forms at the western end, apparently as the result of post-Pleistocene dispersal. Dense marine vegetation is conspicuous in shallow inshore areas.

Sea otters are abundant throughout the Rat Islands following recovery from near-extinction due to overexploitation. A predictable annual mortality from starvation at Amchitka suggests that this population has been near equilibrium density for the past several decades (Kenyon 1969, Estes and Smith 1973). In contrast, sea otters are scarce or absent throughout the Near Islands, where they were exterminated by fur traders. Deep, wide oceanic passes which surround this island group presumably have limited the influx of sea otters from other areas. Only recently a small population has become reestablished near Chichagof Harbor on Attu Island. These animals apparently came from Buldir Island, 100 km to the east, and probably reached Buldir from Kiska Island, 90 km further to the east (Kenyon 1969).

Climatologically and physiographically, the Near and Rat Islands are similar (Sutton and Wilson 1946, United States Department of the Interior, Fish and Wildlife Service 1966). We believe their primary ecological differences are a consequence of the presence or absence of sea otters. This assumption is our basis for testing hypotheses regarding the function of sea otter predation within these insular communities.

METHODS

We observed nearshore communities at Attu and Shemya Islands in the Near Island group and at Amchitka Island in the Rat Island group (Fig. 1) and collected field data at Amchitka between May and December 1971 and 1972. Shemya was visited for 1 wk in September 1971 and for 1 wk in June 1972, and Attu for 4 days in June 1972.

All data from sublittoral communities were collected by self-contained underwater breathing apparatus (SCUBA) divers. Our observations were restricted to substrata of solid rock because solid rock predominates in the western Aleutians and community structure and composition differ considerably on sand or loose cobble.

Underwater observations at Amchitka, Attu, and Shemya Islands (Fig. 1) were limited by visibility and bottom time, and thus our data from these areas come from only a small portion of the sublittoral habitat in the western Aleutian Islands. However, extensive qualitative observations confirmed the impression that these areas are representative of rocky sublittoral communities throughout respective island groups.

We recorded the percentage cover and vertical distribution of the following species and species groups of epibenthic macroalgae: (1) *Laminaria longipes;* (2) the digitate *Laminaria* life form, including *Laminaria groenlandica, Laminaria dentigera,* and *Laminaria yezoensis;* (3) *Agarum cribrosum;* (4) *Thalassiophyllum clathrus;* (5) *Desmarestia* sp; (6) foliose Rhodophyta; and (7) the total fleshy macroalgal association.

Transects were established during each dive from points arbitrarily selected along the shore. Beginning at a depth of 3 m, and at 3-m depth intervals thereafter, coverage was estimated for each species or species group of macroalgae. When possible, we continued this procedure to a depth of 25 m, at which point we swam parallel to shore a sufficient distance to avoid overlap with the descending transect; the technique was repeated during ascent shoreward. At each estimation point, the observer ascended so that his eye level was ≈2 m above the bottom. The area included in a single coverage estimate varied, depending on clarity of the water and substrate configuration, but seldom exceeded a radius of 3 m.

We tabulated estimates of vegetation coverage and transformed these to arcsin square root percentage values to approximate the normal distribution (Ostle 1963). The mean and 95% confidence interval of the estimates were calculated within the transformation for each element of the vegetation classification and at each depth at Kirilof Point. Only the means were calculated for coverage data collected from the remaining 3 study areas at Amchitka because the samples were small.

Biomass was estimated for each element of the classification. Ten samples of *Laminaria longipes, Agarum cribrosum, Thalassiophyllum clathrus, Desmarestia* sp., and foliose Rhydophyta, and 11 samples of the digitate life form of *Laminaria* spp. (0.25 m^2 each) were collected at Kirilof and Constantine Points from 1 to 8 June 1972 by the following 2-step technique:

1) A 3-sided 0.25-m^2 quadrat was dropped arbitrarily into the patch of vegetation for which the coverage of a particular species or species group was 100%.

2) Each plant whose holdfast fell within the quadrat was removed at the substratum. *Laminaria longipes* was removed by cutting the stipe immediately above the holdfast; we estimate that ≈10% of the biomass of this species was lost. All specimens from a single quadrat were put in a plastic bag, taken to the surface, and labeled. Each 0.25-m^2 sample was shaken dry and fresh weights were recorded. Samples were dried to constant weight at 106°C. Most specimens of *Laminaria* exuded copious amounts of mucilage shortly after their removal from the sea, and some of this material inevitably was lost during handling.

Sea urchin densities and size-class distributions were estimated by arbitrarily placing a 0.25-m^2 quadrat on the ocean floor and removing all sea urchins within the quadrat for counts and measurements in the field laboratory. (All diameters of sea urchins given herein

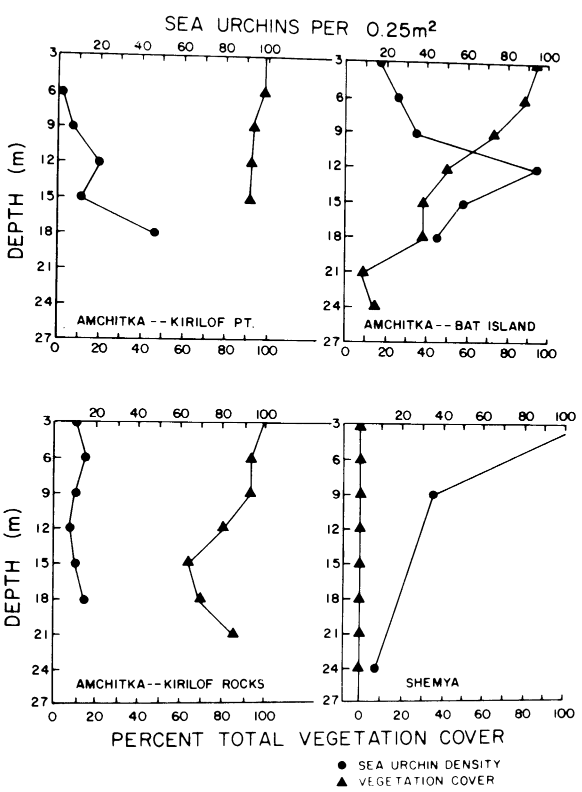

FIG. 2. Total macroalgal coverage and sea urchin density as a function of depth at 3 stations at Amchitka Island—Kirilof Point, Bat Island, and Kirilof Rocks—and 1 at Shemya Island.

refer to outside test diameter.) Estimations of size-class distribution and maximum density of the sea urchin population at Amchitka are from Barr (1971). We measured sea urchin densities at 3-m depth intervals between depths of 3 and 18 m at Bat Island, and at Kirilof Point and Kirilof Rocks on Amchitka (Fig. 1) where, at each depth, 10 arbitrarily placed 0.25-m² quadrats were sampled. Data on size-class distributions of sea urchins were also collected from Shemya (Near Islands), where we measured densities at depths of 3, 9, and 23 m (n = 15, 10, and 5, respectively).

The relation between fresh weight (blotted dry) and diameter of sea urchins was defined by the linear model $Y_i = \alpha + \beta X_i + \epsilon_i$, where Y_i = logarithm sea urchin mass, X_i = logarithm sea urchin diameter and ϵ_i = residual error. By the method of least squares, $\hat{\alpha} = -7.857$ and $\hat{\beta} = 2.992$. The correlation coefficient ($r = .992$) indicates a nearly perfect linear fit of the log-log transformation. By using this model as our estimator, biomass was superimposed on each size class distribution of sea urchins.

Sea urchins were collected between depths of 3 and 21 m and from as deep as 80 to 90 m (with a bottom trawl operated by the R/V Commander, University of Washington) at Amchitka, and from depths between 3 and 9 m at Shemya and Attu. All specimens were preserved in 10% Formalin. Later, we measured individual diameters (n = 319) and estimated ages according to the technique of Jensen (1970).

Growth curves (age as the independent variable, diameter as the dependent variable) were plotted separately for sea urchins collected at different locations. Later, we pooled all data because there was no apparent difference in growth rate between populations from the various sampling locations.

RESULTS

Macroalgae

The association of sublittoral macroalgae at Amchitka generally covers the solid rock substratum from the sublittoral fringe to a depth beyond 25 m (Fig. 2). Primary components of this association are *L. longipes*, *L. groenlandica*, *L. yezoensis*, *L. dentigera*, *Agarum cribrosum*, *Thalassiophyllum clathrus*, *Desmarestia* sp., and various Rhodophyta. *Laminaria* and *Agarum* are the dominant genera (Fig. 3). Also, *Alaria fistulosa* forms a dense surface canopy in many areas.

Laminaria longipes is most abundant from the sublittoral fringe to a depth of 3 m. The association of *L. groenlandica*, *L. dentigera*, and *L. yezoensis* grows between mean low water (MLW) to depths >24 m. This association of species predominates between 3 and 12 m. *Agarum cribrosum* occurs from 6 to >25 m and is most abundant between 12 and 18 m. *Thalassiophyllum clathrus* and *Desmarestia* sp. are relatively minor components of the association of sublittoral macroalgae and cover <10% of the rocky substratum. *Thalassiophyllum* is distributed between depths of ≈3 and 18 m and is most abundant at a depth of ≈10 m. *Desmarestia* also is distributed between depths of ≈3 and 18 m, but it shows no peak in percentage cover. Foliose Rhodophyta are distributed between the sublittoral fringe to depths >25 m. In shallow water these forms grow beneath the *Laminaria* canopy as well as epiphytically on phaeophtyes. Rhodophytes were continuously abundant from the sublittoral fringe to depths >24 m but they appear to be most abundant in the deeper areas.

Estimates of vegetation biomass from the sublittoral zone at Amchitka Island (Table 1) were used to estimate percentage of the macroalgal biomass contributed by each species or species group (T_j) in areas of solid rock substratum by the formula

$$T_j = 100b_j \sum_{i=1}^{n} p_i \Big/ \sum_{j=1}^{k} \sum_{i=1}^{n} p_i b_j,$$

where p_i = the coverage estimate of species j at the i^{th} point (study area and depth), and b_j = grams dry weight per 0.25 m^{-2} of the j^{th} species.

Sublittoral macroalgae essentially were absent from the solid rock substratum at Attu and Shemya (Fig. 2). They were found only as small, isolated patches on submarine pinnacles and were often heavily damaged from sea urchin grazing.

Sea urchins

Beginning at the sublittoral fringe at Amchitka, we found that the abundance of sea urchins generally increased with depth (Fig. 2). Sea urchins were rare immediately below MLW, except for those associated with algal holdfasts or small cracks and crevices in the substratum. At depths of 6 to 9 m, sea urchins were more frequently exposed, but were not abundant. Beyond 15 to 18 m, sea urchins were even more abundant and openly exposed in many areas. In a size-class distribution from an area of high sea urchin density at Amchitka (18–23 m), animals with a test diameter of ≈25 mm dominated in both numbers and biomass.

The structure and distribution of sea urchin populations differed remarkably between Amchitka and Attu–Shemya. At Attu and Shemya, the abundance of sea urchins decreased, rather than increased, with depth (Fig. 2, Shemya). Immediately below MLW, sea urchins commonly covered the entire substratum and the size-class distribution at a depth of 3 metres (Fig. 4) peaks at ≈15-mm and again at 65-mm test diameter. The maximum diameter of sea urchins from this sample was 87 mm although animals >100 mm in diameter were found when we specifically searched for large individuals. The estimated biomass of all size classes combined was 3,082 g/0.25 m². In obvious contrast, the maximum biomass of sea urchins at Amchitka (at 18–23 m) was estimated to be 374 g/0.25 m².

At depths of 9 to 14 m at Shemya, sea urchins were much less abundant than near the sublittoral fringe (Fig. 4). The peak in abundance at 15 mm test diameter was lower and no peak occurred at 65 mm, in contrast to the high peak at this diameter near the sublittoral fringe. The biomass at this depth was 206 g/0.25 m².

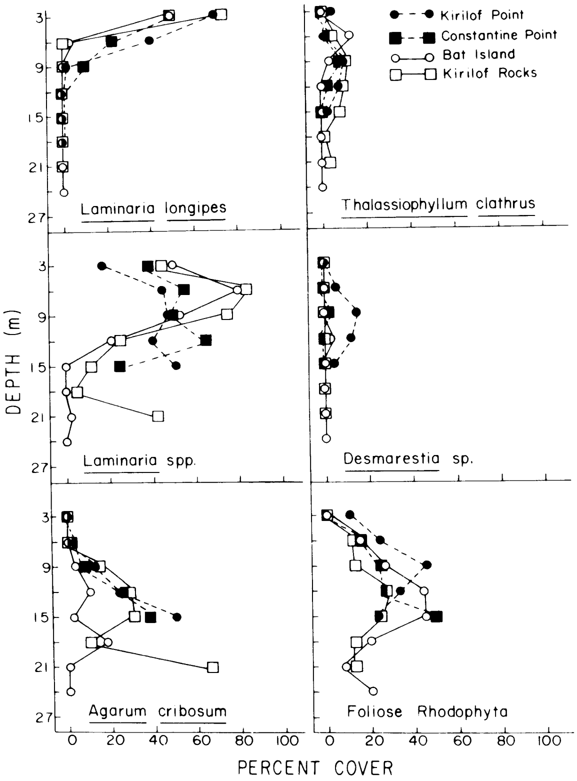

FIG. 3. Coverage estimates of each species or species group of macroalgae at Amchitka Island, as a function of depth.

At 18 to 23 m, Shemya sea urchins were even less abundant, and no peaks in the size class distribution were apparent (Fig. 4). The biomass was 53 g/0.25 m².

In summary, the distribution of sea urchins at Amchitka and Attu-Shemya differed widely. At Attu and Shemya, the maximum abundance of sea urchins was

TABLE 1. Vegetation biomass from the rocky sublittoral at Amchitaka Island. U = upper; L = lower; C.I. = confidence interval

Species[a]	Wet wt (g/0.25 m²)		Dry wt (g/0.25 m²)		Percent total biomass
	$\bar{x} \pm$ SE	95% C.I.[c]	$\bar{x} \pm$ SE	95% C.I.[c]	
Laminaria spp.[b]	1,486 ± 251	U = 2,046 L = 926	209 ± 38	U = 294 L = 124	36.3
Laminaria longipes	2,646 ± 272	U = 3,261 L = 2,032	452 ± 28	U = 516 L = 388	21.6
Agarum cribrosum	792 ± 78	U = 968 L = 616	147 ± 14	U = 179 L = 115	9.4
Thalassiophyllum clathrus	881 ± 112	U = 1,134 L = 628	164 ± 19	U = 207 L = 121	2.9
Desmarestia	984 ± 165	U = 1,357 L = 611	188 ± 30	U = 257 L = 119	1.4
Foliose Rhodophyta	1,551 ± 186	U = 1,971 L = 1,131	250 ± 28	U = 313 L = 187	23.8

[a] Samples were taken at various depths where coverage estmates for a single species or species group were 100%.

[b] *Laminaria groenlandica*, *Laminaria dentigera*, *Laminaria yezoensis*.

[c] 95% C.I. = $\bar{x} \pm (s_x/\sqrt{n})$ $(t_{\eta,.025})$: 10 degrees of freedom: $t_{.025}$ = 2.228; 9 degrees of freedom, $t_{.025}$ = 2.262.

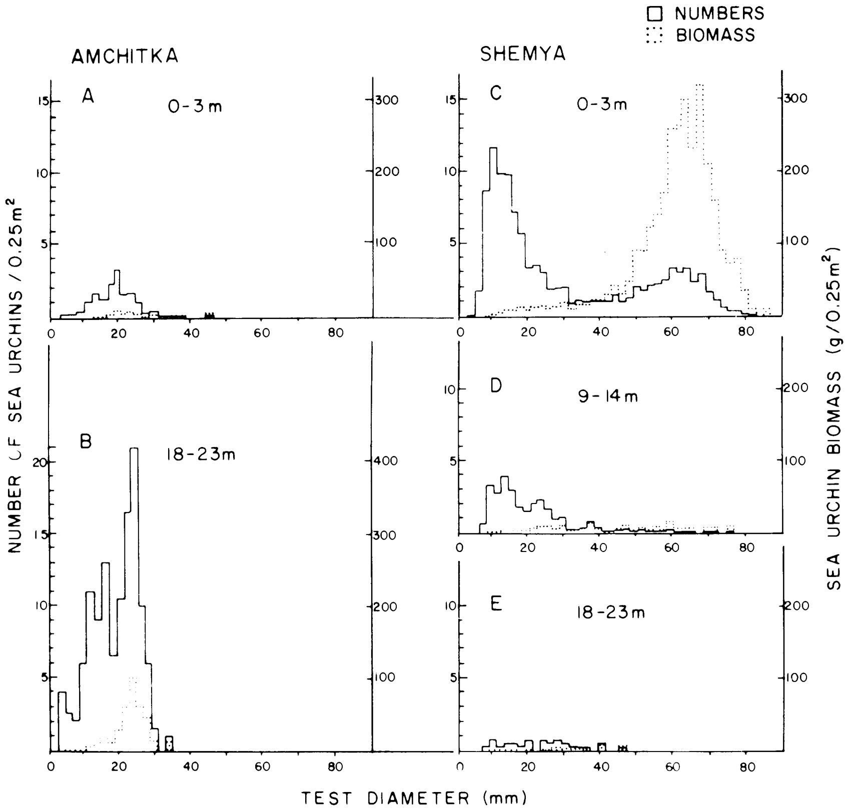

FIG. 4. Size class and biomass distribution of sea urchins at 0–3 m (A) and 18–23 m (B)—at Amchitka Island, and 0–3 m (C), 9–14 m (D), and 18–23 m (E)—at Shemya Island.

at or slightly below the sublittoral fringe and decreased rapidly with increased depth; at Amchitka, the sea urchins were least abundant at the sublittoral fringe, and abundance generally increased with depth.

A growth curve based on estimated ages of 319 sea urchins (Fig. 5) shows that sea urchins at Attu and Shemya commonly attained ages in excess of 15 yr and some exceeded 20 yr. Sea urchins at Amchitka, however, rarely live longer than 5 or 6 yr except in deep water (80 to 90 m).

DISCUSSION

The absence of a basic principle of experimental design—local control—is a weakness of our natural experiment. Indeed, the presence or absence of sea otters was not the only ecological difference between the Near and Rat Islands. However, the following evidence supports our contention that sea otter predation was largely responsible for differences in epibenthic invertebrate associations between the 2 groups of islands.

R. D. Jones (in Kenyon 1969:128) reported that sea urchins were "abundant and obvious" at Adak Island in 1957 before the reestablishment of an abundant population of sea otters. After sea otters reoccupied Adak, Jones was unable to find sea urchins there. Kenyon (1969) reported similar observations at the Sandman and Sanak Reefs in the eastern Aleutian Islands and at Amchitka after the reappearance of sea otters.

The most striking characteristic of sea urchin remains in Aleut kitchen midden sites at Amchitka (Desautels et al. 1970) is their larger size compared with those in current populations in shallow water at Amchitka. Aboriginal Aleuts apparently locally reduced or eliminated sea otters and most urchins in these middens are about the same size as the larger sea urchins we observed at Attu and Shemya (Simenstad et al. 1978).

Finally, the maximum test diameter of sea urchins collected from a depth of 80 m at Amchitka, and thus beyond the effective foraging depth of sea otters, was ≈100 mm. This is equivalent to the maximum size of sea urchins from the sublittoral fringe at Attu and Shemya, and probably represents the maximum size that individuals from undisturbed populations of this species are capable of attaining in this geographical area.

Sea urchin populations

Strikingly different size structures and densities of sea urchin populations are correlated with the distribution of sea otter populations in the western Aleutian

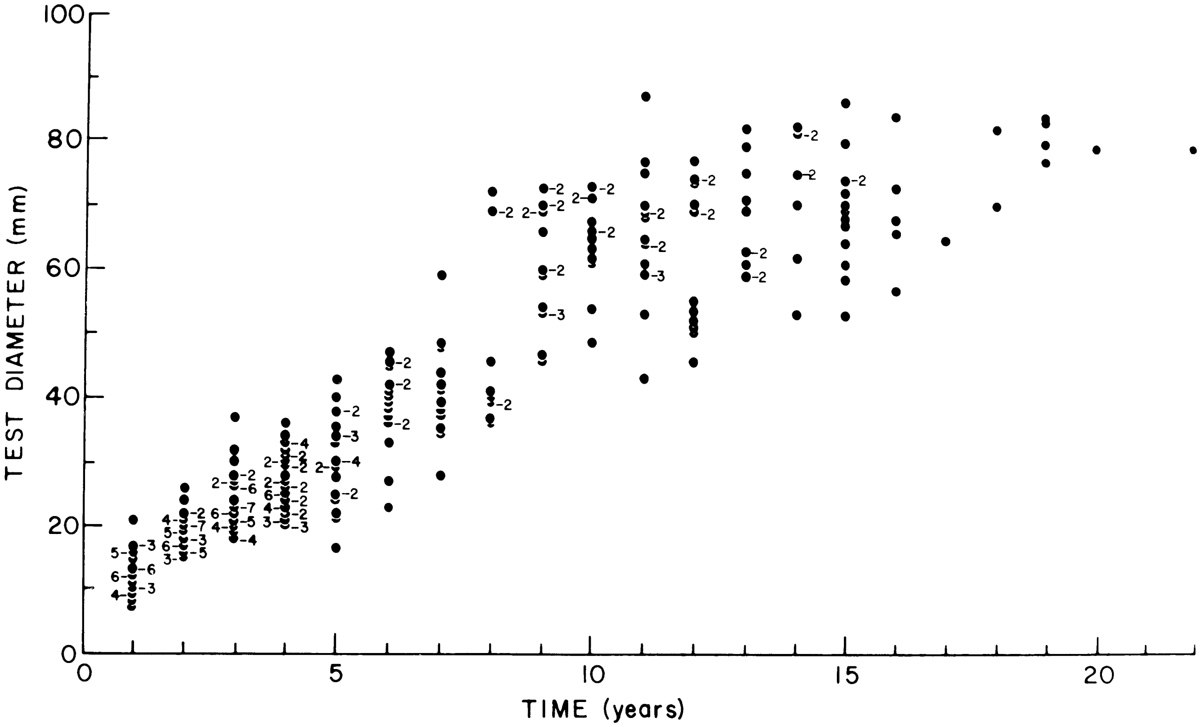

FIG. 5. Sea urchin size as a function of age.

Islands. Sea urchins are important sea otter prey. Therefore sea otters probably are principal determinants to the structure and abundance of urchin populations.

Sea urchins at Attu and Shemya are abundant and large. Two sources of evidence support the conclusion that these populations are limited by competition. The first is that predation on sea urchins was not observed, except in the upper reaches of the sublittoral fringe where on several occasions we observed predation by Glacous-winged Gulls (*Larus glaucescens*) and arctic foxes (*Alopex lagopus*). The second is that the size-class distribution is skewed toward older animals, suggesting depressed reproduction or low recruitment compared with the population at Amchitka (Fig. 4). Food probably limits sea urchins at Attu and Shemya. This conclusion is supported by the observations that (1) kelp beds have been grazed to destruction there, (2) sea urchins cluster about drift kelp, and (3) the sea urchin density was highest near the sublittoral fringe immediately adjacent to the large standing crop of littoral algae.

Directly in contrast to the pattern at Attu and Shemya, the population density and maximum size of sea urchins at Amchitka increase with depth (Fig. 2). Limitation of these urchins by competition for food seems unlikely in view of the abundant standing crop of algae. Competition for space with the algal association also is unlikely because abundant space is available beneath the epibenthic canopy, although the physical and biological configuration of the bottom may influence larval settling (Crisp and Barnes 1954). Predation by birds, fish, or other invertebrates may occur but the relative abundance and food habits of the most conspicuous species in this community indicate that sea otter predation is the most important limiting factor.

At Amchitka, where predation by sea otters is intense, the sea urchins are held to a density and size well below that which can have a destructive impact on their food: the strategy for an iteroparous species, where food is not limiting and the natural mortality rate is high, should be to devote a relatively large amount of energy to reproduction and to begin reproducing at a young age (Giesel 1976 and references therein). The large number of small (young) animals in the sea urchin population at Amchitka (Fig. 4), in contrast with the populations of Attu and Shemya, is evidence in support of this argument. However, if the intensity of predation were uniform regardless of depth, the abundance and population structure of sea urchins also should be constant or, if not, the highest density and largest animals should be in shallow areas where algal (food) abundance is greatest (Fig. 2). Exactly the opposite pattern exists at Amchitka, and the simplest explanation is that sea otters are less efficient predators in deep than in shallow water—a logical assumption considering that they must come to the surface both to breathe and to consume food, and thus must expend more energy to feed in deeper water.

In this system then, the intensity of exploitation of sea urchins declines with depth from a maximum at the sublittoral fringe. In the zone of intense predation, few urchins live to reproduce and their contribution to future generations is less than that of those living in deeper water, where the sea otter is a less effective predator. Under these circumstances, selection should favor a large investment in reproduction and perhaps the tendency to migrate downward.

Strong selection of the kind described might eventually produce a pattern of complete spatial separation between sea otters and sea urchins; however, there are at least 3 reasons why this has not occurred. First, food availability in this community is highest at the sublittoral fringe and declines rapidly in deeper water (the distribution of phaeophytes ends at depths of ≈18–24 metres). Our observations at Attu and Shemya indicate that reproduction or recruitment is diminished where kelp is absent (Fig. 4). Thus, it might be advantageous to risk predation, provided that risk is not too great, to gain reproductive advantages in an area where food is more abundant. Second, the risk of predation by a diving predator, such as a sea otter, must decline in deeper water. Therefore, at some depth in this community, the disadvantage of predation is surpassed by the advantage of increased reproduction. Third, the hierarchy of sea otter food preference varies with the density of sea otters in a complex way that is itself related to the sea otter–sea urchin–kelp interaction. As sea otters become abundant in a community, fish production is enchanced and fish assume an increasingly important role in their diet (see following discussion). This complex interaction probably decreases the intensity of sea otter predation on sea urchins and, therefore, favors coexistence.

Where sea urchins are not subjected to predation by sea otters, patterns of reproduction and motility appear to be reversed. Because food probably is limiting to sea urchins at Attu and Shemya, relatively less energy should be invested in reproduction than at Amchitka. Furthermore, food is most available at Attu–Shemya at the sublittoral fringe, not only because it is adjacent to the littoral zone (which supports an abundant algal association), but because drifting kelp frequently settles there. An upward migration should therefore occur. The data in Figs. 2 and 4 support these hypotheses. Reproductive success is greater where food is more abundant (i.e., for the density of young animals in Fig. 4, B > C > D > E) and the fact that both the total density and the density of large (50- to 90-cm diameter) animals at Attu and Shemya decrease at greater distances (depths) from the sublittoral fringe suggests an upward migration.

The macroalgal association

Recently Dayton (1975*a*), who elucidated the major competitive interactions among macroalgae at Amchitka Island, found that *Laminaria* spp. competitively dominated *Alaria fistulosa*, *Agarum* sp. and foliose red algae, and that *Agarum* dominated both *Alaria* and foliose red algae. Consistent with these results, our general impression was that *Alaria* is relatively more common on cobble substratum and in protected areas than in exposed areas of solid substratum. Apparently unstable substrata are frequently disturbed by heavy seas and protected areas are suboptimum habitat for *Laminaria* spp. and possibly *Agarum;* both conditions permit *Alaria* to establish itself.

Our data (Fig. 3) suggest that *Laminaria* spp. completely excludes *Agarum* from areas shallower than ≈6-m depth. Depths >6 m apparently are suboptimum for *Laminaria* spp. either because light is reduced or grazing by more abundant sea urchins is increased. Consequently, *Agarum* becomes more abundant at depths >6 m where competition with *Laminaria* spp. is not so intense. This conclusion is similar to that reached by Vadas (1968), who found that *Laminaria* was dominant over *Agarum* in undisturbed areas of the San Juan archipelago. Vadas (1968) also concluded that *Agarum* was more resistant to grazing by sea urchins than *Laminaria* and could become established in the presence of moderate grazing pressure. Rhodophytes, which can use reduced light beneath the epibenthic canopy (Dawson et al. 1960) and deep-penetrating green light (Blinks 1955) are abundant throughout and beyond the depth range of the kelps.

Sublittoral macroalgae at Attu and Shemya are essentially absent because of intense overgrazing by the abundant sea urchins. We have noticed, however, that where small patches of algae exist, species diversity is high. Here *Agarum* and *Thalassiophyllum* occur near the sublittoral fringe, whereas at Amchitka they are competitively excluded by *Laminaria*.

At the sublittoral fringe of Amchitka, where predation by sea otters apparently is so intense that it virtually eliminates the effect of grazing invertebrates, competitive interactions within the macroalgal association are intense enough to exclude such species as *Agarum* and *Alaria fistulosa*. Furthermore, the fact that 3 species of *Laminaria* coexist here suggests that strong competitive relationships have persisted and perhaps have affected the evolution of this complex of species (see Pianka 1966, and Menge and Sutherland 1976 for details of theoretical arguments). If the coexistence of the *Laminaria* guild is maintained by disturbance (e.g., wave shock), then exclusion of phylogenetically more divergent competitive subordinates, such as *Agarum* and *Thalassiophyllum*, would not be expected.

The important general conclusion from these results is that the macroalgal association at Amchitka is dominated by competitive interactions because of the virtual absence of herbivores. When the sea otter is removed from this system, the predominant roles of competition and predation are transposed: macroalgae are limited by predation (grazing) and the epibenthic invertebrates (most of which are herbivorous) by competition.

Productivity of the nearshore community

What are the consequences of the elimination of kelp beds by sea urchins? If kelp is an important source of food or cover to certain fauna of the Aleutian Islands, then these animals should be affected by the absence of kelp beds.

Benthic macrophytes are principal contributors to nearshore productivity of temperate oceans (Blinks 1955, Mann 1972, 1973) and support an abundant growth of higher trophic forms. In nearshore communities of the western Aleutian Islands, benthic macrophytes, phytoplankton, and terrestrial plant associations are the main sources of primary production. Each of these can be estimated either by direct measurement (terrestrial plants, 1–100 $\mathrm{g \cdot Cm^{-2} \cdot yr^{-1}}$ [Amundsen and Clebsch 1971]; phytoplankton, 27–55 $\mathrm{g \cdot cm^{-2} \cdot yr^{-1}}$ [Koblents-Mishke 1965, McAlister 1971]) or indirectly (Mann 1973) from biomass density (littoral macrophytes, 438–784 $\mathrm{g \cdot cm^{-2} \cdot yr^{-1}}$ [Weinmann 1969, Palmisano 1975]; sublittoral macrophytes, 1275–2840 $\mathrm{g \cdot Cm^{-2} \cdot yr^{-1}}$—Fig. 3 and Table 1). These data indicate that primary production may be greatly reduced in communities lacking macroalgae. Therefore, there can be little doubt that the indirect role played by sea otters in maintaining the macroalgal association is of major importance.

Consequently, communities without sea otters predictably should be depauperate of higher trophic forms. A comparison of communities between the Rat and Near Islands supports this hypothesis.

Quast (1968) speculated that kelp beds off coastal California provide food and protection to many fishes, and we suspect that kelp associations in the Aleutian Islands are functionally similar. Nearshore fishes at Amchitka Island are supported by a detritus-based food web (Simenstad et al. 1977) and we have recently found that nearshore fishes are much more abundant at Amchitka than they are at Attu and Shemya (C. A. Simenstad, *personal communication; personal observation*). Therefore, we are not surprised that the abundance and foraging of species with higher trophic status, particularly those dependent on fish in some part of their food web, are related to the abundance of macroalgae. For example, where sea otters are abundant, they consume more fish than in areas where they are rare (Lensink 1962, Kenyon 1969). Harbor seals, *Phoca vitulina,* feed largely on nearshore fishes and invertebrates (Scheffer and Sperry 1931, Scheffer and Slipp 1944, Wilke 1957, Kenyon 1965). Frequently, we have seen large numbers of harbor seals on Amchitka but apparently they are less abundant at Attu and Shemya (Kenyon and King 1965, *personal observation*).

Bald Eagles, *Haliaeetus leucocephalus*, are largely dependent on marine food webs in the Aleutian Islands. They feed mostly on fish, marine mammals, and marine birds (White et al. 1971). Eagles are abundant at the Rat Islands, but are absent from the Near Islands (Sekora 1973) and although conceivably this could be explained as part of an immigration pattern (Darlington 1957) from North America, the absence of eagles from the Near Islands may be related to the greatly reduced abundance of macroalgae. The absence of eagles from the Near Islands probably is not a result of an inability to immigrate because the Near Islands are only 300 km west of the robust population inhabiting the Rat Islands. Extinction by random chance also is not likely, considering that Agattu and Attu in the Near Islands are both large and should support eagle populations similar to those on the Rat Islands. Extinction probabilities vary strongly and nonlinearly as a function of carrying capacity (K) and the expected time to extinction of a single propagule with the life history of a Bald Eagle (White et al. 1971) is between 1,000 and 10,000 yr (MacArthur and Wilson 1967), assuming $K = 50$, which is about the number of breeding pairs of Bald Eagles at Amchitka. Furthermore, the fact that the Near Islands are composed of 2 large islands and a group of smaller islands makes the probability of local extinction even less likely. The physical environments of the Rat and Near Islands are not obviously different. However, sea otters are responsible for indirectly maintaining the macroalgal association and consequent high primary production in the nearshore community, and these clearly differ greatly between the 2 island groups.

In summary, if macroalgae are the limiting resource to many faunal elements in the western Aleutian Islands, then sea otters may locally and indirectly elevate the carrying capacities of those species. For some species this may simply influence their population abundance, e.g., nearshore fishes and harbor seals. For others, e.g., Bald Eagles, it may mean the difference between rapid extinction or extremely long periods of survival.

Evidence from sea otter food

Paine (1966) found that species diversity was directly related to the efficiency with which predators prevented monopolization of major environmental requisites by competitively superior species. Studies of sea otter food in the Commander and western Aleutian Islands (Table 2) indicate a direct relation between intensity of sea otter predation and the diversity of food. At Amchitka, Kenyon (1969) found at least 42 species of animals in sea otter stomachs, and Burgner and Nakatani (1972) found 15, although they did not report them as individual species. Stomachs in both studies were collected at times when the sea otter population at Amchitka was at equilibrium density—Kenyon's in 1962–63 and those of Burgner and Nakatani in 1970. Lensink (1962), who summarized the analyses of sea otter fecal samples collected at the Commander

TABLE 2. Occurrence of prey items in sea otter stomachs and feces (after Palmisano 1975)

Source	Wilke 1957	Kenyon 1969	Kenyon 1969	Burgner and Nakatani 1972	Barahash-Nikiforov 1947	Williams 1938
Location	Amchitka	Amchitka	Amchitka	Amchitka	Commander Islands	Western Aleutians
Sample period	1954	1962–1963	1962–1963	1970	1930–1932	1936
Sample type	Stomach	Stomach	Stomach	Stomach	Feces	Feces
Sample size	5	309	309	49	500	70
Analysis	Percent of total volume	Percent of total volume	Percent of total number of prey item	Percent of stomachs containing food item[a]	Percent of total volume	Percent of total volume
Prey item						
Annelids	0	1	2	2	0	0
Arthropods						
Crabs	0	<1	4	22	10	4
Others	0	0	3	0	0	0
Mollusks	8	37	31	38	23	13
Echinoderms						
Sea urchins	86	11	21	82	59	78
Others	0	0	16	0	0	0
Fish	6	50	22	44	7	3
Others	0	<1	1	0	1	2
Total	100	100	100	...	100	100

[a] Percent of total volume: carnivores 65 (including fish 62.2) and herbivores 35.

and Aleutian Islands in the 1930s and 1940s as well as some later observations of stomach contents, reported only 6 food items from Amchitka, and sea urchins and mussels made up nearly the entire volume. Lensink's (1962) studies suggest that sea urchins were the dominant sea otter food item at Amchitka and other Aleutian Islands during the late 1930s and 1940s, when sea otters were less abundant than today. The later studies by Kenyon (1969), and Burgner and Nakatani (1970), showed an increase in diversity of food items consumed by the sea otter. Of particular interest is the increased amount of fish in the sea otter's diet in more recent years. The data in Table 2 indicate that the percentage of fish by volume in the sea otter's diet increased from 6% in 1954 to 50% in 1962–63 and 62% in 1970. The abundance of nearshore fishes probably reflects the abundance of macroalgae which we claim has increased concurrently with the sea otter population.

Although the techniques used in these various investigations are not strictly comparable, the general pattern of change in sea otter food through time is significant. Apparently, as sea otters foraged during early stages of population recovery, sea urchins were the primary food because they were abundant and easily captured. Later, as the sea urchin population was reduced by sea otter predation, benthic community structure and sea otter foraging changed. This change is reflected as an increased diversity in sea otter food, temporally paralleling the development and establishment of high-density sea otter populations.

CONCLUSIONS

The observations discussed herein provide another example of the importance of predation and competition to the organization of marine benthic communities. Island biogeography has provided an impetus to develop techniques (Simberloff 1974) which can be used to examine the contribution of sea otters to the organization of nearshore communities in the western Aleutian Islands. Predation by sea otters reduces competition for food or space, or both, among benthic invertebrates (Estes and Palmisano 1974) and results in the opposite interaction within the next lower trophic level (the macrophyte association). Stated otherwise, where communities are dominated by sea otters, competition apparently is the principal interaction within the plant association (Dayton 1975*a*).

Additional indirect community interactions are suggested by differences in faunal composition and abundance between islands dominated by sea otters and islands where sea otters are absent. Higher level interactions are more difficult to understand, and to demonstrate experimentally, than are direct consequences of biological processes such as those reported by Connell (1961*a*, 1961*b*), Paine (1966, 1969*b*, 1974), Janzen (1970), Dayton (1971), and others. Clearly, however, the neighborhood stability (Lewontin 1969) of many communities is controlled largely by a key predator (Brooks and Dodson 1965, Holling 1973, Sutherland 1974).

The sea otter is a key predator in nearshore communities of the North Pacific Ocean. Since the mid-

1700s these communities have experienced several major changes, which were induced by the arrival of the white man. Aboriginal people, who occupied the Aleutian Islands for at least 8,400 yr (Laughlin 1972) and who preyed on sea otters and perhaps competed with them for food, are now virtually extinct. Thus, we may only speculate from archeological evidence on the interplay between Aleuts, sea otters, and food resources. Where sea otters are now probably limited by food, they perhaps were once limited by native hunting. The vertebrate fauna of this area have suffered several recent extinctions (e.g., Stellar's sea cow and Aleutian Canada Goose) and exotic introductions (e.g., Arctic fox and brown rat) (Murie 1959, Sekora 1973). The question remains: To what extent was natural selection responsible for present structural patterns in these communities and to what extent are these patterns the product of recent extinctions and introductions?

An equally interesting question is: What sorts of evolutionary adaptations affecting ecological interactions have taken place in this community since the departure of the sea otter? The relaxation of such a dynamic disturbance (sea otter predation) would seem to be important in this regard. These questions are pertinent when evaluating conclusions from prior investigations of nearshore communities within the historical range of the sea otter, particularly over those large expanses of coastline where sea otters currently do not occur. For example, Ebert (1968) concluded that productivity, growth rate, and the ultimate size of sea urchins *(Strongylocentrotus purpuratus)* in Oregon were determined by available food. Ebert (1968) further argued that his conclusions were in opposition to the contention of Hairston et al. (1960) that herbivores are not limited by food, but by predation. We suggest that it will be appropriate to reexamine Ebert's (1968) thesis when the sea otter reoccupies this community. Dayton (1975*b*) recently has drawn an analogy between the "keystone disturbance role" of sea urchins in rocky intertidal communities and fire in many terrestrial communities. He argued that both sea urchins and fire serve as disturbances, prevent monopolization of resources by competitively superior species, and allow fugitive species to occupy niches from which they otherwise would be competitively excluded. We do not question the validity of this analogy; however, we suggest that the relative importance of sea urchins in this capacity probably was much less dramatic in the coevolution of those communities that contained sea otters.

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