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Author(s): James A. Estes and David O. Duggins

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SEA OTTERS AND KELP FORESTS IN ALASKA: GENERALITY AND VARIATION IN A COMMUNITY ECOLOGICAL PARADIGM¹

JAMES A. ESTES

*National Biological Survey, Institute of Marine Sciences, University of California,
Santa Cruz, California 95064 USA*

DAVID O. DUGGINS

Friday Harbor Laboratories, University of Washington, Friday Harbor, Washington 98250 USA

Abstract. Multiscale patterns of spatial and temporal variation in density and population structure were used to evaluate the generality of a three-trophic-level cascade among sea otters (*Enhydra lutris*), invertebrate herbivores, and macroalgae in Alaska. The paradigm holds that where sea otters occur herbivores are rare and plants are abundant, whereas when sea otters are absent herbivores are relatively common and plants are rare. Spatial patterns were based on 20 randomly placed quadrats at 153 randomly selected sites distributed among five locations with and four locations without sea otters. Both sea urchin and kelp abundance differed significantly among locations with vs. without sea otters in the Aleutian Islands and southeast Alaska. There was little (Aleutian Islands) or no (southeast Alaska) overlap between sites with and without sea otters, in plots of kelp density against urchin biomass. Despite intersite variation in the abundance of kelps and herbivores, these analyses demonstrate that sea otter predation has a predictable and broadly generalizable influence on the structure of Alaskan kelp forests. The percent cover of algal turf and suspension feeder assemblages also differed significantly (although less dramatically) between locations with and without sea otters.

Temporal variation in community structure was assessed over periods of from 3 to 15 yr at sites in the Aleutian Islands and southeast Alaska where sea otters were 1) continuously present, 2) continuously absent, or 3) becoming reestablished because of natural range expansion. Kelp and sea urchin abundance remained largely unchanged at most sites where sea otters were continuously present or absent, the one exception being at Torch Bay (southeast Alaska), where kelp abundance varied significantly through time and urchin abundance varied significantly among sites because of episodic and patchy disturbances. In contrast, kelp and sea urchin abundances changed significantly, and in the expected directions, at sites that were being recolonized by sea otters. Sea urchin biomass declined by 50% in the Aleutian Islands and by nearly 100% in southeast Alaska following the spread of sea otters into previously unoccupied habitats. In response to these different rates and magnitudes of urchin reduction by sea otter predation, increases in kelp abundance were abrupt and highly significant in southeast Alaska but much smaller and slower over similar time periods in the Aleutian Islands.

The different kelp colonization rates between southeast Alaska and the Aleutian Islands appear to be caused by large-scale differences in echinoid recruitment coupled with size-selective predation by sea otters for larger urchins. The length of urchin jaws (correlated with test diameter, $r^2 = 0.968$) in sea otter scats indicates that sea urchins <15–20 mm test diameter are rarely eaten by foraging sea otters. Sea urchin populations in the Aleutian Islands included high densities of small individuals (<20 mm test diameter) at all sites and during all years sampled, whereas in southeast Alaska similarly sized urchins were absent from most populations during most years. Small (<30–35 mm test diameter) tetracycline-marked urchins in the Aleutian Islands grew at a maximum rate of ≈ 10 mm/yr; thus the population must have significant recruitment annually, or at least every several years. In contrast, echinoid recruitment in southeast Alaska was more episodic, with many years to perhaps decades separating significant events. Our findings help explain regional differences in recovery rates of kelp forests following recolonization by sea otters.

Key words: *Aleutian Islands; bottom-up forces; community structure; growth; herbivory; random sampling; recruitment; scale; size-selective predation; southeast Alaska; top-down forces.*

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TABLE 1. Summary of prior field study results on sea otter–herbivore–kelp interactions in the North Pacific Ocean.

| Literature source | Study area | Study period | Conclusions* |
|---------------------------|--------------------|--------------|--------------|
| Benech 1977 | Central California | 1975–1976 | A |
| Bowlby et al. 1988 | Washington | 1987 | A |
| Breen et al. 1982 | Vancouver Island | 1979 | B |
| Cowen et al. 1982 | Central California | 1977–1979 | D |
| Duggins 1980 | Southeast Alaska | 1975–1979 | B |
| Duggins et al. 1989 | Aleutian Islands | 1985–1987 | B |
| Ebeling et al. 1985 | Central California | 1979–1983 | C |
| Ebert 1968b | Central California | 1967 | A |
| Estes et al. 1978 | Aleutian Islands | 1970–1972 | B |
| Estes and Palmisano 1974 | Aleutian Islands | 1970–1972 | B |
| Kvitek et al. 1989 | Washington | 1987 | A |
| Kvitek et al. 1992 | Kodiak Island | 1986–1988 | A |
| Kvitek and Oliver 1992 | Southeast Alaska | 1988–1990 | A |
| Laur et al. 1988 | Central California | 1976–1981 | B |
| Lowry and Pearse 1973 | Central California | 1973 | A |
| McLean 1962 | Central California | 1959–1961 | B |
| Oshurkov et al. 1988 | Commander Islands | 1972–1986 | B |
| Ostfeld 1982 | Central California | 1977–1979 | A |
| Pearse and Hines 1979 | Central California | 1972–1977 | C |
| Simenstad et al. 1978 | Aleutian Islands | 1976–1977 | B |
| Watanabe and Harrold 1991 | Central California | 1984–1988 | C |
| Watson 1993 | Vancouver Island | 1986–1991 | B |
| Wild and Ames 1974 | Central California | 1965–1972 | A |

* Key to conclusions: A = sea otter predation greatly reduced sea urchin populations (but no consideration of effect on algae); B = sea otter predation on urchins greatly increased algal abundance (or biomass); C = changes in urchin populations, due to reasons other than otter predation, caused changes in algal abundance (or biomass); D = sea urchin effect on algae overshadowed by effect of physical disturbance.

INTRODUCTION

Ecological field studies have provided definitive evidence for the population- and community-level influences of many biotic and abiotic processes. Rarely, however, has variation in these results been assessed over large areas or long periods of time. Moreover, the experimental units (i.e., field plots) to which treatments are applied in manipulative, natural, or mesurative experiments (sensu Hurlbert 1984) often are purposely selected in field ecological studies so as to reduce natural variation. The tendency to design field experiments around small areas, short time periods, and homogeneous experimental units has the desirable effects of increasing both logistical feasibility and the power of hypothesis testing. However, the cost of these benefits is an inability to rigorously generalize results for larger areas or longer intervals. The problem is illustrated in the largely unresolved and often contested status of broad conceptual issues, such as the importance of competition (Roughgarden 1983), top-down vs. bottom-up forces in biologically structured food webs (Hunter and Price 1992, Matson and Hunter 1992, Menge 1992), and forces acting on larval vs. adult life history stages (Underwood and Denley 1984, Roughgarden et al. 1988), as well as species- or guild-specific paradigms such as sea star predation in mussel beds (Foster 1990, Paine 1992), fish and crustacean predation on tropical gastropods (Palmer 1979, Ortega 1986), and plant benefits from herbivory (McNaughton 1983, Belsky 1986), among many. Thus, one of the most daunting challenges and contentious issues in

ecology concerns increasing the extent to which patterns and processes are general.

The generality of sea otter predation as a top-down force in structuring North Pacific kelp forests is a case in point. Several short term studies, conducted over relatively small spatial scales, describe a three-level trophic interaction among sea otters (*Enhydra lutris*), sea urchins (*Strongylocentrotus* spp.), and macroalgae (Estes and Palmisano 1974, Estes et al. 1978, Duggins 1980, Breen et al. 1982, Laur et al. 1988; see Table 1). The evidence is mainly comparative, contrasting nearby sites with and without sea otters that exist because of the fragmentation of a once continuously distributed population across the North Pacific rim. Another approach used in one published account (Laur et al. 1988), which controls for spatial variation not attributable to sea otter predation, has been to measure community structure at specific sites before, during, and after the reestablishment of sea otters. These spatial and temporal comparisons provide the evidence for a well-known ecological paradigm which holds that sea otter predation limits herbivorous invertebrate populations, unlimited herbivore populations limit kelp and other macroalgal populations, and thus, areas inhabited by sea otters support kelp forests whereas areas lacking sea otters are deforested by sea urchin grazing (VanBlaricom and Estes 1988). This paradigm was criticized by Foster and Schiel (1988) and Foster (1990). These authors contended that kelp forest communities in California (and perhaps in the larger North Pacific Ocean region) are organized by numerous biotic and

abiotic processes, and that the role of sea otter predation has been overemphasized and overgeneralized. Strong (1992: 749) also questioned the paradigm stating "there is a distinct possibility that this is a donor-controlled system, without effective carnivore suppression of the herbivore."

Published studies, while individually providing unequivocal small-scale evidence for the sea otter paradigm, must be used cautiously to evaluate its generality because in each case study sites were purposefully selected and the number and geographical range of sites is small. Conversely, the large number of studies (Table 1), their extensive collective geographical range, and the near-unanimity of their conclusions argues for the paradigm.

The role of otters in California is particularly controversial (Foster and Schiel 1988, Foster 1990). While the critics agree that otters have important effects on kelp forest community structure, they also argue that these effects are overshadowed in most places by other, more important factors, such as physical disturbance. The controversy concerns the role of herbivores in limiting algal assemblages rather than the role of sea otters in limiting herbivore populations. There is ample evidence from California studies that otters rapidly and predictably decimate grazer (particularly urchin) populations (McLean 1962, Ebert 1968*a, b*, Lowry and Pearse 1973, Wild and Ames 1974, Gotshall et al. 1976, Benech 1977, Laurent and Benech 1977, Pearse and Hines 1979, Ostfeld 1982, Laur et al. 1988).

One purpose of our paper is to provide a more rigorous and detailed account of generality in the sea otter paradigm for kelp forests in Alaska. As with previously published studies, our approach was to compare the abundance and population structure of kelp forest plants (kelps and other macroalgae) and their principal herbivores (sea urchins) across space or through time where the abundance and status of sea otter populations varied naturally. However, our data were taken from randomly selected plots at numerous randomly selected sites in two widely separate regions, thus permitting the analysis of variation over small (<100 m), intermediate (<100 km), and large (>1000 km) spatial scales. As such, our study is the first truly rigorous census of areas differing in sea otter influence.

A second purpose of our paper is to examine temporal variation in the structure of kelp-dominated and urchin-dominated communities. By following a given site over relatively long periods (≤ 15 yr), three issues were addressed. (1) Time-course data, gathered during periods of sea otter recolonization, provided another rigorous test of the otter-kelp paradigm. (2) Rates of transition between urchin- and kelp-dominated communities following sea otter recolonization were compared among regions. Regional differences were discovered and we examined their causes and consequences. (3) Long-term observation of both the urchin- and otter (kelp)-dominated communities pro-

vides an opportunity to evaluate the "persistence stability" (sensu Oriens 1975: 141) of these purported equilibria (Simenstad et al. 1978).

We propose that the effects of sea otter predation on sea urchins and kelps can be generalized to large areas. We further propose that kelp- and urchin-dominated assemblages exist as stable equilibria, define the "domains of attraction" (Holling 1973: 4) for each, and describe patterns of temporal variation within and between these domains. Our findings show that although kelp forests and urchin-dominated deforested habitats define two locally stable domains of attraction in Alaskan rocky-reef habitats, the trajectories of change between these domains following the recolonization of sea otters differ markedly among geographic regions. Two ecological processes—size-selective predation by sea otters on sea urchins, and large-scale variation in sea urchin recruitment—appear responsible for these different trajectories. We propose a model based on 1) variation in the intensity and predictability of sea urchin recruitment and 2) the dynamics of plant production and herbivory, to explain differences between the Aleutian Islands and southeast Alaska in recovery rates of kelp forests following the reestablishment of sea otters.

HISTORY AND STATUS OF SEA OTTER POPULATIONS IN STUDY REGIONS

Sea otters, once distributed across the Pacific Rim from northern Japan to central Baja California and numbering in the hundreds of thousands of individuals, were hunted to near-extinction during the 18th and 19th centuries (Kenyon 1969). By the early 1900s about a dozen colonies containing ≤ 1000 sea otters remained (Lensink 1962). Remnant colonies survived in the Rat and Andreanof island groups of the western and central Aleutian archipelago (Fig. 1). Following their protection in the early 1900s, these colonies increased at rates of 17–20%/yr (Chapman 1981, Estes 1990) until resources (food or space) apparently became limiting. The population at Amchitka Island (Rat Island group) contained an estimated 5500–8500 sea otters during the time our study was conducted (Estes 1990). The population at Adak Island (Andreanof Island group), although more poorly known, is roughly comparable in history, size, and density to the Amchitka population (J. A. Estes, *unpublished data*). Both populations have existed at or near equilibrium density for the past 20–40 yr (Kenyon 1969).

Sea otters were exterminated from the Near Islands, westernmost of the Aleutian archipelago, although records from the fur trade indicate they once were abundant in the area (Lensink 1962). Broad, deep passes separating the Near Islands from the Rat Islands to the east and the Commander Islands to the west apparently prevented recolonization until the mid-1960s, at which time R. D. Jones (1965) counted 13 sea otters at Attu Island. The population at Attu increased rapidly thereafter, and when last surveyed in 1991 it had spread around the entire perimeter of the island and contained

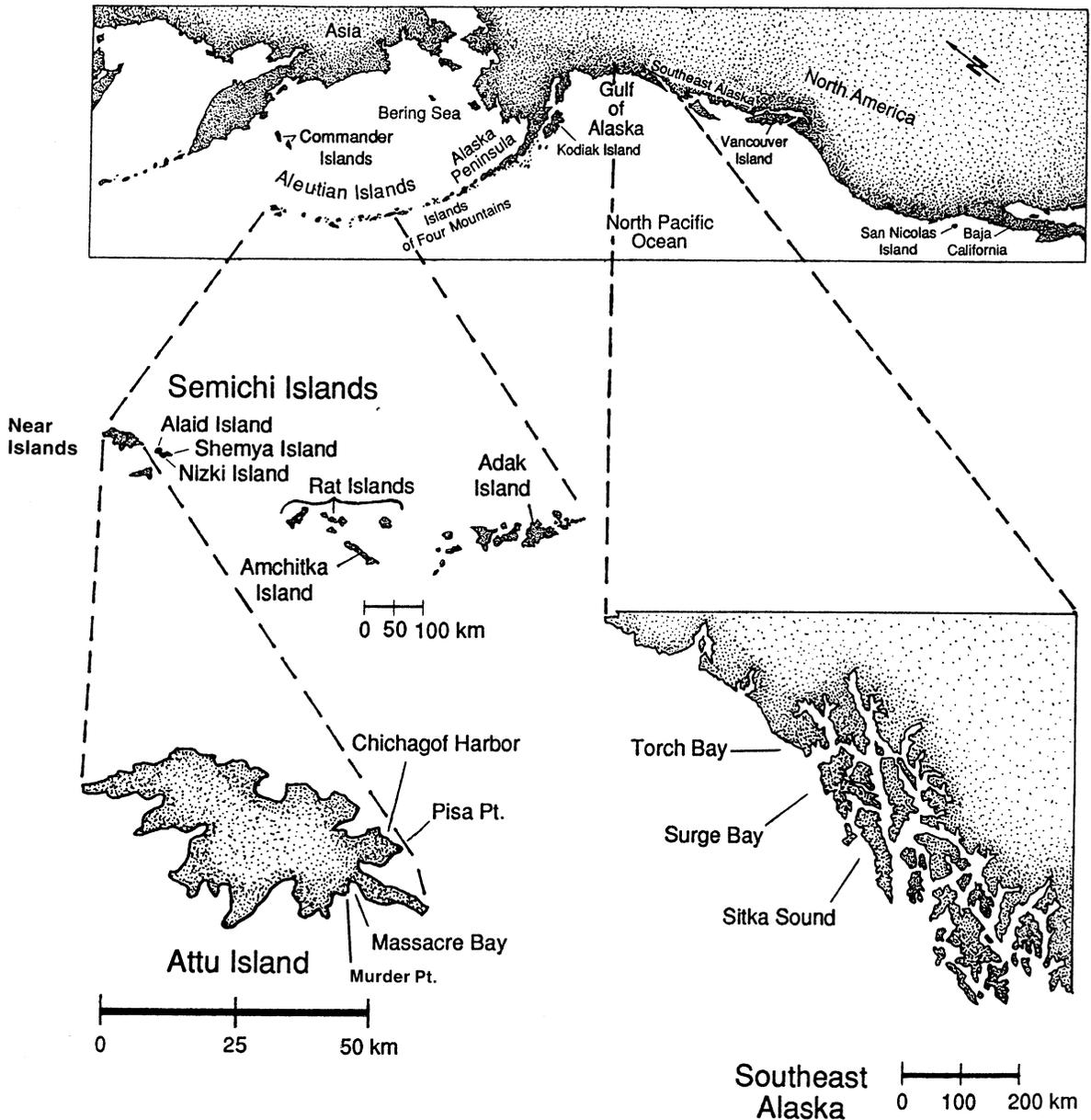


FIG. 1. Map of North Pacific Ocean showing study locations, sample sites, and place names referred to in the text.

an estimated 3000–4000 individuals (J. Estes and A. DeGange, *unpublished data*). The spreading population first appeared at our study sites on the west side of Massacre Bay in the mid-1980s (Estes 1990). Two sites at Chichagof Harbor were occupied by sea otters before benthic sampling was begun in 1976. Although there have been occasional sea otter sightings east of Attu in the Semichi Islands (Alaid, Nizke, and Shemya islands), these animals apparently were transients and the Semichi Islands remained uninhabited by otters through the time of our studies there (1987).

In 1968–1971, the Alaska Department of Fish and Game relocated 411 otters (Jameson et al. 1982) from

Prince William Sound to southeast Alaska (Fig. 1). The relocated population had expanded into Surge Bay (on the west coast of Yakobi Island) by the early to mid-1970s and several hundred individuals occurred there in 1978 when we first surveyed the benthic habitat (Duggins 1980). Otters spread into Torch Bay in 1985 (Vequist 1987).

METHODS

Spatial patterns of community structure

To assess spatial variation in the structure and composition of rocky-reef communities with and without

TABLE 2. Summary statistics from habitat surveys at islands with and without sea otters in the western and central Aleutian Islands.*

| Parameter | Location | | | | | | Statistics | | |
|--|--------------------|--------------------|---------------------|--------------------|--------------------|--------------------|------------|--------|---------|
| | Alaid Is.† | Nizki Is.† | Shemya Is.† | Attu Is.‡ | Amchitka Is.§ | Adak Is.§ | F | df | P |
| Understory kelp density (inds./0.25 m ²) | 0.23 ^C | 0.79 ^C | 0.27 ^C | 1.46 ^{BC} | 3.87 ^{AB} | 6.56 ^A | 10.07 | 5, 128 | <0.0001 |
| Surface canopy kelp density (inds./0.25 m ²) | 0.35 | 0.14 | 0.37 | 0.65 | 0.81 | 0.85 | 1.90 | 5, 128 | 0.098 |
| Turf cover (%) | 16.3 ^C | 12.8 ^C | 18.1 ^C | 26.3 ^C | 98.0 ^A | 50.4 ^B | 39.74 | 5, 128 | <0.0001 |
| Suspension feeder cover (%) | 31.6 ^{CD} | 16.0 ^D | 21.7 ^{CD} | 64.8 ^A | 50.3 ^{BC} | 88.2 ^{AB} | 9.40 | 5, 128 | <0.0001 |
| Sea urchin density (inds./0.25 m ²) | 28.5 | 26.3 | 29.6 | 39.8 | 24.6 | 25.4 | 0.98 | 5, 124 | 0.4315 |
| Sea urchin biomass (g/0.25 m ²) | 336.4 ^B | 471.4 ^A | 434.7 ^{AB} | 208.6 ^C | 38.8 ^D | 38.4 ^D | 28.00 | 5, 124 | <0.0001 |
| Sea urchin max. size (test diameter, mm) | 66.4 ^B | 71.4 ^A | 77.3 ^A | 40.5 ^C | 26.9 ^D | 26.7 ^D | 295.87 | 5, 125 | <0.0001 |

* Similarities among locations tested with 1-way ANOVA using locations as treatments and site means within locations as replicates. When H_0 was rejected, selected treatment comparisons were done with Duncan's multiple range test ($\alpha = 0.05$). Means with the same letter could not be shown to differ significantly. Analysis of percent cover data done on arcsine-transformed values.

† Sea otters absent.

‡ Sea otters recently reestablished; population < equilibrium.

§ Sea otters long established; population at or near equilibrium.

sea otters, we conducted extensive surveys in the Aleutian Archipelago and southeast Alaska. Henceforth we refer to the Aleutian Islands and southeast Alaska as "regions," islands or place name locations within regions as "locations," study areas within locations as "sites," and sample points within sites as "quadrats."

To assess the generality of the otter-kelp paradigm in Alaska, we sampled 153 randomly selected sites from seven locations at which the history and status of sea otter populations were known: four locations with otters (Amchitka and Adak islands, Torch and Surge bays), two without otters (the Semichi Islands, including Alaid, Nizki, and Shemya islands, and Sitka Sound), and one in transition (Attu Island; Fig. 1, Tables 2 and 3). The Aleutian Islands were sampled in July 1987, Torch and Surge bays in May 1988, and Sitka Sound in July 1988. At each location we first delineated a 10–20 km stretch of coast as the study area, determined by the maximal distances we could travel safely from the bases of operation in a small

boat. A grid pattern was then superimposed over a navigational chart of the study area and the grid intersections with shore marked and numbered as potential sites. The sites we sampled were selected at random from among these with no prior knowledge of the benthic flora or fauna. At each location our sample of sites included a broad range of conditions, from the exposed outer coast to protected bays. The substratum was typically consolidated rock or large, stable boulders at all of our sample sites in the Aleutian Islands and southeast Alaska. Cryptic habitats capable of harboring small sea urchins were rare or absent.

Sampling at each site was conducted in the following way. A scuba diver placed 20 0.25-m² quadrats on the sea floor along the 6–7 m (shallow) and 12–13 m (deep) depth contours. Distances between quadrat placements were determined by a prearranged, random number of kicks. We counted individuals of each kelp and sea urchin species and estimated percent cover of fleshy red algae and suspension feeding invertebrates in the

TABLE 3. Summary statistics from habitat surveys at locations with and without sea otters in southeastern Alaska. Explanations as for Table 2.

| Parameter | Location | | | Statistics | | |
|--|-------------------|-------------------|--------------------|------------|-------|---------|
| | Surge Bay* | Torch Bay† | Sitka Sound‡ | F | df | P |
| Understory kelp density (inds./0.25 m ²) | 9.12 ^A | 6.43 ^A | 0.01 ^B | 18.25 | 2, 59 | <0.0001 |
| Surface canopy kelp density (inds./0.25 m ²) | 0.63 ^B | 2.03 ^A | 0.00 ^B | 7.07 | 2, 59 | <0.0001 |
| Turf cover (%) | 60.6 ^A | 8.0 ^B | 4.3 ^B | 52.52 | 2, 59 | <0.0001 |
| Suspension feeder cover (%) | 5.0 ^A | 0.9 ^B | 0.3 ^B | 6.95 | 2, 59 | 0.0019 |
| Sea urchin density (inds./0.25 m ²) | 0.01 ^B | 0.02 ^B | 1.52 ^A | 35.38 | 2, 55 | <0.0001 |
| Sea urchin biomass (g/0.25 m ²) | 0.2 ^B | 0.1 ^B | 369.9 ^A | 65.23 | 2, 55 | <0.0001 |

* Sea otters long established.

† Sea otters recently reestablished.

‡ Sea otters absent.

quadrats. Although the latter two groups contain numerous species (see Lebednick and Palmisano 1977 and O. Clair 1977 for species lists of marine algae and invertebrates at Amchitka Island) we did not identify these in the field samples because of 1) the time required to do so; 2) difficulties with in situ species identifications; and 3) varying levels of skill and training among the numerous observers.

Percent cover was visually estimated as 1 of 6 categories (i.e., 1 = 0–5%, 2 = 6–25%, 3 = 26–50%, 4 = 51–75%, 5 = 76–95%, 6 = 96–100%) and the site means calculated from the midpoints. Visual estimates can be used quickly and effectively underwater and have been shown to provide measures that are both unbiased and consistent among observers in littoral assemblages (Dethier 1984, Dethier et al. 1993; but see Foster et al. 1991). Although we did not rigorously analyze for inter-observer variation, we doubt that it contributed significantly to areal or regional patterns because our sampling procedures purposefully confounded possible inter-observer biases nearly equally among areas and we (J. Estes and D. Duggins) together gathered much of the data from the Aleutian Islands and most of the data from southeast Alaska.

We identified a single species of sea urchin (*S. polyacanthus*, the green urchin) in our samples from the Aleutian Islands and 3 species (*S. franciscanus*, *S. droebachiensis*, and *S. purpuratus*; the red, green, and purple urchins, respectively) in southeast Alaska. Densities and size distributions of sea urchin populations were estimated by collecting and measuring animals from randomly placed 0.25-m² quadrats at each of the 153 sites described above. Sampling was terminated at each site after obtaining 200 animals or sampling 20 quadrats. These plots were searched carefully, and individuals ≤ 2 –3 mm test diameter, when present, were easily seen and collected. Sea urchin biomass per 0.25 m² was estimated for each site from that site's urchin density, size distribution, and a regression function of live mass vs. test diameter.

Temporal patterns of community structure

The persistence of deforested or kelp-dominated communities was evaluated at four locations over periods of time ranging from 3 to 15 yr during which the status of otter populations remained unchanged. The categories of data are not entirely consistent among regions or times because the information was obtained from two independent research programs in which we employed different methodologies.

Locations lacking sea otters.—Three sites at Torch Bay were sampled during the late summers of 1976, 1977, and 1978. Two sites at Shemya Island were sampled during the summers of 1972 and 1987.

Locations with sea otters.—Five sites were sampled at Surge Bay during the summers of 1978 and 1988. Four sites at Amchitka Island were sampled in the summers of 1972 and 1987.

The extent and rate of change in benthic community structure following sea otter recolonizations were determined by comparing census data from benthic communities at Attu Island and Torch Bay both before and after otters arrived. Nine sites at Attu were sampled in the summers of 1976, 1977, 1979, 1981, 1983, 1986, 1987, and 1990, during which time the growing sea otter population spread into these sites. At Torch Bay, four sites were sampled in 1978 before sea otters became reestablished, and again in May 1988, ≈ 2 yr after their reestablishment.

Sea urchin growth and recruitment

A common feature of sea urchin populations in the western Aleutian Islands was that they contained large numbers of small individuals (< 15 mm test diameter). In contrast, populations in southeast Alaska contained few small animals. Because it was unclear whether these small animals in the Aleutian Islands represented frequent recruitment or slow growth, we used tetracycline markers (following the methods of Kobayashi and Taki 1969, Ebert 1975, 1980, 1982, Pearse and Pearse 1975, and Russell 1987) to measure their growth rates in situ. This was done by injecting tetracycline hydrochloride (1 mg/100 mL seawater) through the peristomial membrane. Dosages varied with test diameter as follows: < 16 mm, 0.02 mL; 17–22 mm, 0.05 mL; 23–28 mm, 0.10 mL; 29–32 mm, 0.15 mL; 33+ mm, 0.20 mL; as recommended by Kobayashi and Taki (1969) and Pearse and Pearse (1975).

We marked sea urchins (*S. polyacanthus*) at Attu Island in isolated tide pools near the sublittoral fringe to increase the likelihood of recovering the same animals 1 yr later. Growth rates of animals in these habitats probably were as high or higher than those in sublittoral habitats because 1) algal drift from the littoral zones and sublittoral fringe frequently washes into such pools, thus increasing food availability and growth rates (Vadas 1977), and 2) urchins with the largest gonads and test diameters that we have found in the western Aleutian Islands occurred in tide pools (Mayer 1980). We marked every sea urchin found in each of two tide pools on the west side of Murder Point on 23 July 1986 and collected them on 14 July 1987. The sea urchins in two additional tide pools on Pisa Point were similarly marked on 18 July 1986 and collected on 15 July 1987. In total, 486 animals were marked and 496 collected (there was some recruitment or immigration into the pool); 274 of the collected animals had recognizable tetracycline marks. At the time of collection, the test diameter of each animal was measured and its Aristotle's lantern (a calcified feeding structure) removed. Later we dissolved the remaining soft tissue from Aristotle's lantern in bleach (a dilute NaOCl solution), removed the jaws, and examined them under ultraviolet light through a dissecting microscope with an ocular micrometer. Regions of the jaw in which tetracycline had been incorporated fluoresced. When

such marks were present, we measured the growth increments between their proximal margins and the respective ends of the jaw. Jaw length when marked was estimated by subtracting these increments from jaw length at the time of collection. Since jaw length and test diameter are well correlated ($r^2 = 0.968$, Simenstad et al. 1978), we estimated test diameter from jaw length at the time of marking. Jaw length at the time an animal was marked was plotted against growth increment at the time it was collected. However, the Richards variable growth functions (Ebert 1980a) could not be parameterized so as to produce realistic growth rates for animals < 5 mm or > 45 mm test diameter at the time they were marked. Therefore average growth rates were estimated for 5 mm intervals in test diameter (i.e., 1– <5 , 5– <10 mm, etc.) and the size–age relation determined by assuming the urchins settled at 1 mm test diameter and adding the appropriate growth increments at 0.1-yr intervals.

The frequency and intensity of urchin recruitment was assessed from population size distributions. While size is not a precise indicator of age in urchins, the virtual absence of small size classes at several locations was taken as an indicator of infrequent recruitment.

Size selective foraging by sea otters

Prior studies of sea urchin populations from Aleutian Islands with and without sea otters demonstrated that 1) large sea urchins (>35 – 40 mm test diameter) were absent from exploited populations and disappeared rapidly (<1 – 2 yr) in the wake of expanding sea otter populations, 2) sea urchins >60 mm test diameter were common in unexploited populations, and 3) even areas with sea otter populations at or near equilibrium density supported sea urchin populations with high densities of small individuals (<35 – 40 mm test diameter) (Estes 1978, Simenstad et al. 1978, this study). These observations, together with the common presumption that sea otters, like many other predators, forage so as to maximize net rate of energy intake (Krebs 1978), led us to hypothesize that otters preferentially consumed the largest available sea urchins. We tested this idea by collecting sea otter scats from Attu and Amchitka islands. The scats were softened in warm water, sea urchin remains separated from organic debris and the remains of other species, and the length of all jaws measured under a dissecting microscope. Size distributions of sea urchins eaten by sea otters were estimated from these data and compared with size distributions of living populations from the same areas.

RESULTS

Spatial variation in community structure

Kelp density.—Understory and surface-canopy kelp species (e.g., Dayton 1975, Duggins 1980) were analyzed separately because of their structural and ecological differences. Understory species seldom grow

TABLE 4. Relative abundance (%) of species in kelp assemblages of the western Aleutian Islands and southeast Alaska. Calculations based on total plants counted from all quadrats sampled at each location.

| Kelp species | Location | | | |
|----------------------------------|------------------|----------|------------------|-------|
| | Aleutian Islands | | Southeast Alaska | |
| | Adak | Amchitka | Surge | Torch |
| <i>Agarum cribrosum</i> | 3.3 | 21.3 | 2.6 | 0.0 |
| <i>Alaria fistulosa</i> | 12.0 | 16.1 | 0.0 | 2.9 |
| <i>A. marginata</i> | a* | a | 6.0 | 14.5 |
| <i>Costaria costata</i> | a | a | 0.7 | 1.5 |
| <i>Cymathera triplicata</i> | 0.2 | 0.9 | 1.2 | 0.9 |
| <i>Laminaria</i> spp. | 83.9 | 58.0 | 75.5 | 61.5 |
| <i>L. yezoensis</i> | 0.0 | 2.4 | 5.4 | 2.4 |
| <i>Macrocystis integrifolia</i> | a | a | 0.2 | 0.0 |
| <i>Nereocystis leutkeana</i> | a | a | 0.7 | 6.9 |
| <i>Pleurophycus gardneri</i> | a | a | 7.6 | 9.4 |
| <i>Thalassiophyllum clathrus</i> | 0.6 | 1.4 | a | a |

* a = absent (outside geographic range of species).

>2 m above the substratum whereas the surface-canopy species may grow from >30 m depth and often accumulate most of their biomass at the ocean surface. The understory kelps are typically competitive dominants over surface-canopy species in both the western Aleutian Islands (Dayton 1975) and southeast Alaska (Duggins 1980). Common species are listed in Table 4. *Laminaria* spp. composed most of the biomass and individuals in habitats that were shallow ($<$ about 10 m depth) or exposed to moderate to heavy wave-generated surge in both regions. *Agarum* spp. (and *T. clathrus* in the Aleutian Islands) were more common in deeper and more protected habitats (Dayton 1975, Estes et al. 1978), especially where there was moderate grazing by sea urchins. The surface canopy was formed by a single species (*Alaria fistulosa*) in the Aleutian Islands and by three species (*A. fistulosa*, *Nereocystis leutkeana*, and rarely *Macrocystis integrifolia*) in southeast Alaska.

Understory kelp density in southeast Alaska varied strikingly between locations with and without sea otters (Fig. 2, Table 3). Understory kelp densities did not vary significantly between Surge and Torch bays (Table 3) even though sea otters had occupied these locations for 1–2 (Torch) and ≈ 20 yr (Surge). This suggests that kelp assemblages in southeast Alaska proliferate quickly following sea otter recolonization, progress rapidly through a successional sequence ending in the dominance of understory species, and remain largely unchanged thereafter.

Patterns of variation in understory kelp abundance between locations in the Aleutian Islands with and without sea otters were similar to those measured in southeast Alaska (Fig. 2). The abundance of understory kelps among quadrats sampled at Attu Island (Fig. 2) was intermediate to and significantly different from those measured at Alaid-Nizki-Shemya islands and

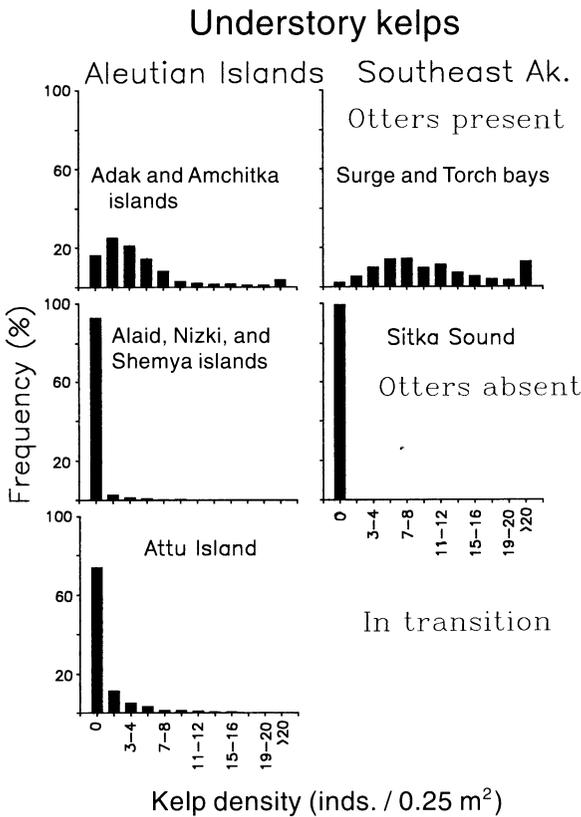


FIG. 2. Frequency distributions of understory kelp densities (inds./0.25 m²) from random samples taken at A) Torch and Surge bays; B) Sitka Sound; C) Adak and Amchitka islands; D) Alaid, Nizki, and Shemya islands; and E) Attu Island.

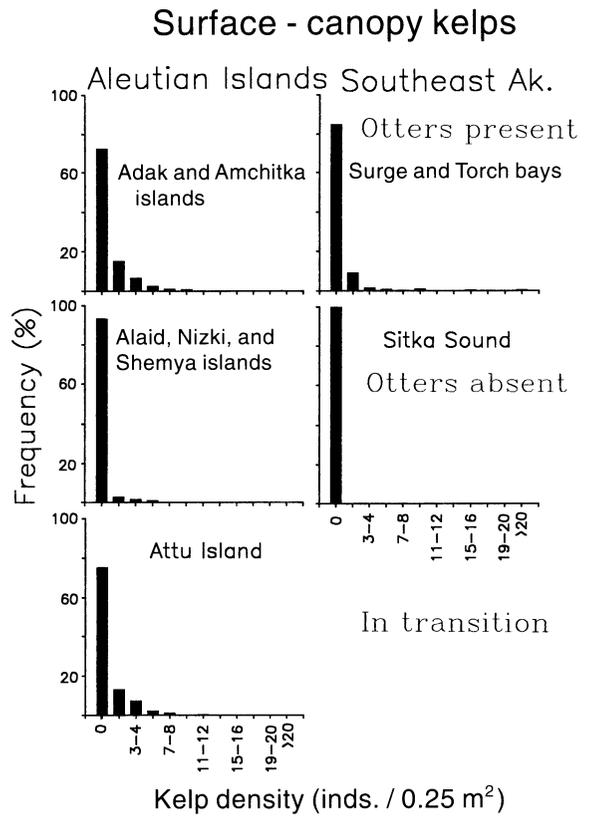


FIG. 3. Frequency distributions of surface-canopy forming kelps (inds./0.25 m²) from random samples taken at A) Torch and Surge bays; B) Sitka Sound; C) Adak and Amchitka islands; D) Alaid, Nizki, and Shemya islands; and E) Attu Island.

Adak-Amchitka islands (Table 2), thus suggesting that kelp recovery following sea otter recolonizations occurs more slowly in the western Aleutian Islands than in southeast Alaska.

Less extreme differences were measured for densities of surface-canopy-forming kelp between locations with and without sea otters in southeast Alaska and the Aleutian Islands (Fig. 3). These differences probably resulted from competitive dominance (and exclusion) of surface canopy kelps by understory species and the longer time this interaction had been occurring in Surge Bay.

Urchin density and biomass.—Sea otters had predictable though different effects on sea urchin populations in southeast Alaska and the Aleutian Islands. In southeast Alaska, sites without sea otters (Torch Bay 1976–1978 and Sitka Sound 1988) supported dense urchin populations (Tables 3 and 6). We observed numerous broken urchin tests in Surge Bay in 1978 and Torch Bay in 1988, and urchins were nearly absent from all sites at otter-dominated locations in southeast Alaska (Torch Bay 1988, Surge Bay 1978 and 1988) (Tables 3 and 6).

In contrast, both sites with and without sea otters in

the Aleutian Islands supported dense urchin populations (Tables 2 and 5) of various size distributions. At sites lacking otters, urchin density and biomass was greatest just below the sublittoral fringe, whereas these measures increased with depth at sites with otters (Fig. 4). Sea urchin density was greater at Attu Island than it was at either Adak-Amchitka or Alaid-Nizki-Shemya islands. However, sea urchin biomass at Attu was intermediate. This discrepancy resulted from the fact that foraging sea otters selectively removed the largest urchins (at sites following section on size-selective predation), thus eliminating the major contributors to biomass and perhaps releasing the population from intraspecific competition, which in turn may have caused the number of small individuals to increase.

Sea urchin size structure.—The size distributions of sea urchin populations in the Aleutian Islands differed between locations with and without sea otters (Fig. 5). Maximum test diameter ranged from 45–85 mm among the 42 sites (297 quadrats, 6915 individuals) sampled at Alaid, Nizki, and Shemya islands and all but one of these sites contained individuals >56 mm. In contrast, the largest animal from 75 sites (483 quadrats, 7505

TABLE 5. Abundance and population characteristics of kelps and sea urchins at Amchitka and Shemya islands in 1972 and 1987 (shown as means ± 1 SE, across sites). The same four sites at Amchitka and two sites at Shemya were sampled in both years*. Sea otters were continuously abundant at Amchitka and absent from Shemya during the 15-yr period.

| | Amchitka Island | | Shemya Island | |
|---|-----------------|-------------|---------------|--------------|
| | 1972 | 1987 | 1972 | 1987 |
| Kelp species (inds./0.25 m ²) | | | | |
| <i>Alaria fistulosa</i> | 1.6 ± 1.30 | 0.3 ± 0.22 | 0 | 0.5 |
| <i>Laminaria</i> spp. | 2.3 ± 0.49 | 3.9 ± 0.95 | 0 | 0 |
| <i>Agarum cribrosum</i> | 1.2 ± 0.61 | 0.5 ± 0.42 | 0 | 0 |
| <i>Thalassiophyllum clathrus</i> | 0.1 | 0 | 0 | 0 |
| Total kelps | 5.1 ± 0.66 | 4.7 ± 1.15 | 0 | 0.5 |
| Sea urchins | | | | |
| Maximum test diameter (mm) | 30.5 ± 1.34 | 27.3 ± 3.24 | 72.5 ± 0.71 | 70.5 ± 4.95 |
| Biomass (g/0.25 m ²) | 45.1 ± 16.9 | 36.7 ± 15.0 | 368.2 ± 151.7 | 369.3 ± 14.3 |
| Density (inds./0.25 m ²) | 27.9 ± 14.5 | 23.4 ± 7.5 | 50.0 ± 14.6 | 38.6 ± 1.4 |

* The 1972 data were obtained from 10 haphazardly placed 0.25-m² quadrats/site, the 1987 data from 20 randomly placed 0.25-m² quadrats/site.

individuals) sampled at Adak and Amchitka islands was 39 mm and most (>99%) were <30 mm.

Sea urchins as small as 2–3 mm test diameter occurred at all six locations sampled in the Aleutian Islands, and individuals <10 mm comprised 11–31% of the total (Fig. 6). Minimum size could not be shown to vary significantly (one-way ANOVA, $F_{5, 125} = 1.79$, $P = 0.12$) among sites within or among locations (Fig. 5).

Small sea urchins were sparse or absent at deforested sites in southeast Alaska (Fig. 5). Urchin size distributions were not determined at otter-dominated sites in southeast Alaska because they were virtually absent.

Kelp density vs. sea urchin biomass.—There was little (Aleutian Islands) or no (southeast Alaska) overlap in the distributions of kelp density vs. sea urchin biomass between locations with and without sea otters (Fig. 7). Kelp density was high and variable whereas sea urchin biomass was consistently low among sites with sea otters. In contrast, sites lacking sea otters had comparatively low and invariable kelp densities with high and variable sea urchin biomass (Tables 2 and 3).

Different distributions of kelp density vs. urchin bio-

mass are evident between the Aleutian Islands and southeast Alaska. The most obvious of these was that sea urchin biomass was higher at sites where otters were present in the Aleutian Islands than at similar sites in southeast Alaska (Tables 2 and 3). Significant differences could not be demonstrated between Adak and Amchitka islands or Torch and Surge bays.

Algal turfs.—This group, which is comprised largely of red algae, contains numerous undescribed taxa in western Alaska, and field identification of many of the described taxa is difficult. Consequently, we have not differentiated the members of this assemblage. Except for crustose forms and erect coralline algae, all functional groups (sensu Littler and Littler 1980, Steneck and Watling 1982, Steneck and Dethier 1994) were included.

Patterns of algal turf abundance between locations with and without sea otters (Fig. 8) were similar to but less extreme than those for understory kelps. Mean turf cover differed significantly between Sitka Sound vs. Surge and Torch bays (one-way ANOVA on arcsine-transformed data, $P < 0.0005$). Similar patterns occurred in the Aleutian Islands (Fig. 8). Mean turf cover

TABLE 6. Abundance and population characteristics of kelps and sea urchins at Torch Bay (1976–1978) and Surge Bay (1978 and 1988) shown as means ± 1 SE, across sites. Sea otters were continuously absent at Torch Bay and present at Surge Bay during these time periods.

| | Torch Bay | | | Surge Bay | |
|-------------------------------------|------------|------------|-------------|-------------|-------------|
| | 1976 | 1977 | 1978 | 1978 | 1988 |
| Kelps (inds./m ²) | | | | | |
| Annuals* | 2.1 ± 1.39 | 0.2 ± 0.25 | 11.6 ± 6.69 | 2.1 ± 0.45 | 3.7 ± 2.34 |
| Perennials† | 0.1 ± 0.11 | 0 | 0.9 ± 1.14 | 48.4 ± 6.33 | 50.3 ± 7.46 |
| Total 2.2 | 2.2 | 0.2 | 12.5 ± 5.56 | 50.5 ± 6.43 | 54.0 ± 9.33 |
| Sea urchins (inds./m ²) | | | | | |
| <i>S. franciscanus</i> | 3.6 ± 3.05 | 3.8 ± 2.55 | 4.9 ± 3.71 | 0 | 0 |
| <i>S. purpuratus</i> | 1.0 ± 0.75 | 2.3 ± 2.52 | 0.3 ± 0.41 | 0 | 0 |
| <i>S. droebachensis</i> | 3.4 ± 2.24 | 1.5 ± 0.95 | 0.2 ± 0.18 | 0.02 | 0.04 |
| Total | 8.0 ± 4.56 | 7.6 ± 5.78 | 5.4 ± 4.27 | 0.02 | 0.04 |

* Primarily *Alaria fistulosa* and *Nereocystis leutkeana*.

† Primarily *Laminaria groenlandica*.

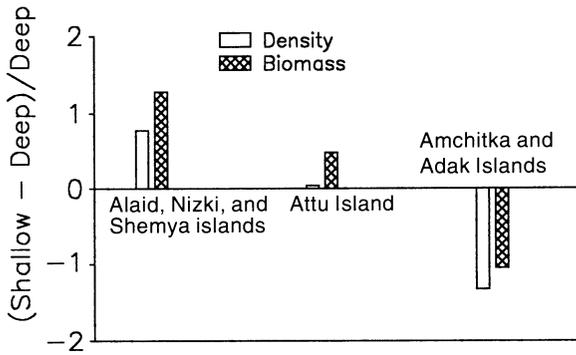


FIG. 4. Relative differences in sea urchin density and biomass between shallow (6–7-m depth) and deep (13–15-m depth) sites at locations where the population status of sea otters differed. Deep water values were arbitrarily chosen as standards for comparison (e.g., a quotient of +1 indicates a 2× greater value in shallow water, a quotient of –2 indicates a value 3× lower in shallow water, etc.). Alaid, Nizki, and Shemya islands (otters absent); Attu Island (otters recently reestablished); Adak and Amchitka islands (otters long established, at or near population equilibria).

at Attu Island (10.8%) and the frequency distribution of estimated turf cover among quadrats (Fig. 8) were intermediate between those measured at Adak-Amchitka and Alaid-Nizki-Shemya, although they were more similar to the latter. Mean turf cover differed significantly between Adak-Amchitka and Alaid-Nizki-Shemya islands; turf cover at Attu Island also differed significantly from similar measures at Adak-Amchitka but did not differ significantly from those at Alaid-Nizki-Shemya (Table 2).

Suspension feeders.—Suspension feeders comprise a taxonomically diverse group of organisms including bivalves, barnacles, holothurians, cnidarians, bryozoans, sponges, and tunicates. Members of these taxa consume particulate matter derived directly or indirectly from kelp and other macroalgae (Duggins et al. 1989), are consumed by foraging sea urchins (Vance 1979), and thus might be expected to differ between locations with and without sea otters. Alternatively, suspension feeders may compete with algae for space, an interaction that would decrease their abundance at locations with sea otters.

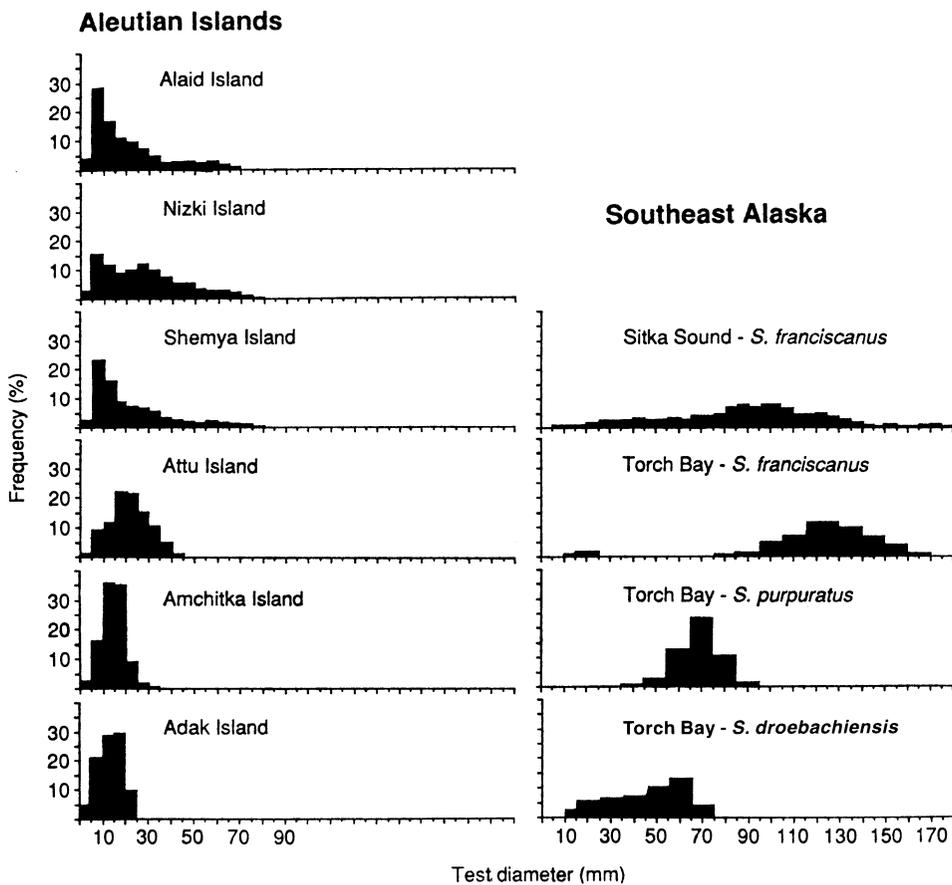


FIG. 5. Size–frequency distributions in sea urchin populations from study locations in the Aleutian Islands and southeast Alaska. Data from the Aleutian Islands are for the green urchin, *Strongylocentrotus polyacanthus*, and were obtained in 1987. Data from Torch Bay were obtained in 1978 and from Sitka Sound in 1988. Frequency distributions were obtained by pooling samples taken over all sites at the respective locations.

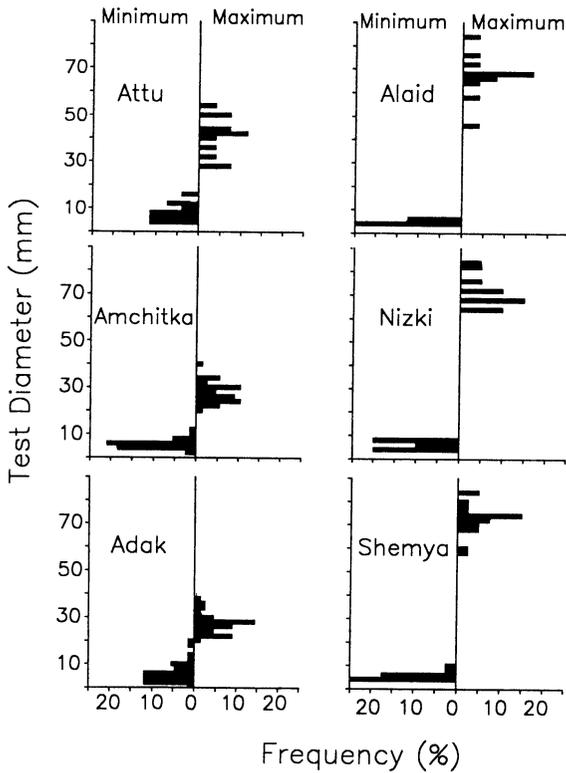


FIG. 6. Frequency distributions of the maximum and minimum sizes of sea urchins (*S. polyacanthus*) among sites sampled across study locations in the Aleutian Islands. The population status of sea otters at each study location is noted in Fig. 4 legend.

Differences in the percent cover of suspension feeders between locations with and without sea otters were apparent but not striking (Fig. 9). Mean percent cover of suspension feeders was greater, although not statistically significant (one-way ANOVA on arcsine-transformed data, $P = 0.075$) in Surge and Torch bays than in Sitka Sound. Similar patterns occurred in the Aleutians, although differences between locations with and without sea otters were larger and highly significant ($P < 0.0001$). As was true for kelp abundance and algal turf cover, the percent cover of suspension feeders at Attu was intermediate between Alaid-Nizki-Shemya islands and Adak-Amchitka islands (Fig. 9).

Temporal patterns in community structure

Sites with no change in status of otters.—We surveyed varying numbers of sites at 2 locations in the Aleutian Islands (Amchitka and Shemya islands) and 2 locations in southeast Alaska (Surge and Torch bays) over periods ranging from 3 to 15 yrs. There was no change in the status of sea otters over the reported time periods at any of these locations; otters were continuously present at Amchitka Island and Surge Bay, and continuously absent at Shemya Island and Torch Bay.

The two locations with sea otters (Amchitka Island,

Table 5; and Surge Bay, Table 6) were remarkably consistent among years for all taxa surveyed. Kelp density at Amchitka Island could not be shown to vary significantly among sites or among years (two-way ANOVA, $P = 0.70$ for sites and 0.69 for years). Urchin density, biomass, and maximum test diameter were also similar among years and sites (Density: $P = 0.79$ for sites and 0.75 for years; Biomass: $P = 0.67$ for sites and 0.65 for years; maximum test diameter: $P = 0.41$ for sites and 0.22 for years). In 1978, only one sea urchin was found in 80 1-m² quadrats sampled over the five sites at Surge Bay, and in 1988 only two urchins occurred in 100 0.25-m² quadrats sampled at each of the same five sites. Kelp abundance also did not vary significantly among sites ($P = 0.17$) or over time ($P = 0.70$, two-way ANOVA).

Patterns of variation were similar at the two locations without otters, with several notable exceptions. There was little temporal variation for any of the measured groups or taxa in the Aleutian Islands. Kelps were nearly absent in both 1972 and 1987 from the two sites at Shemya Island where we have data spanning the 15-yr period. Urchin densities, biomass, and maximum test diameter were consistently high at both sites in both

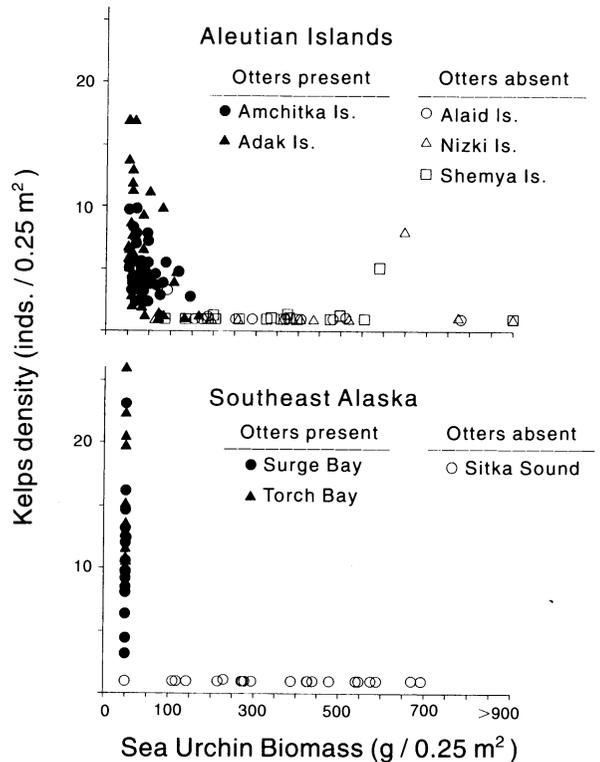


FIG. 7. Epibenthic kelp density (inds./0.25 m²) plotted against estimated sea urchin biomass (g/0.25 m²) for the Aleutian Islands and southeast Alaska. Points represent averages for sites within locations. Sea urchin biomass was estimated from samples of population density, size-frequency distribution, and the functional relation between test diameter and wet mass.

Red algae

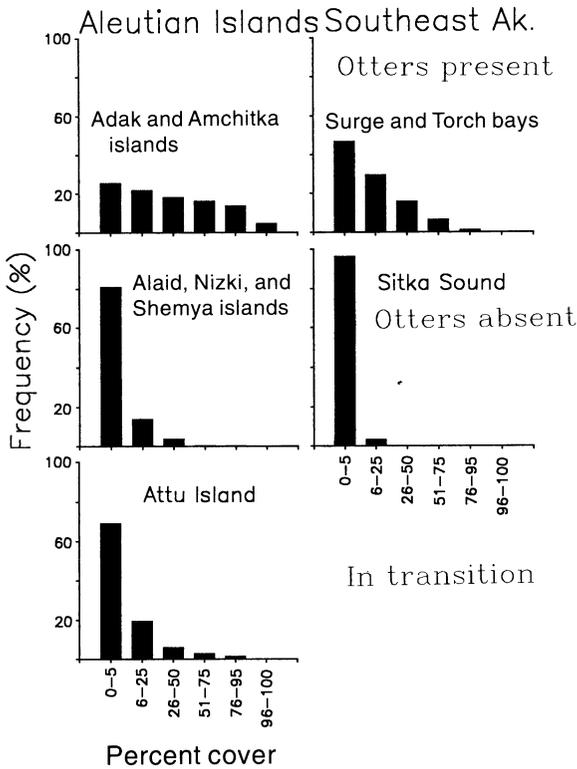


FIG. 8. Frequency distributions of estimated percent cover of red algal turf from random samples taken at A) Torch and Surge bays; B) Sitka Sound; C) Adak and Amchitka islands; D) Alaid, Nizki, and Shemya islands; and E) Attu Island.

Suspension feeders

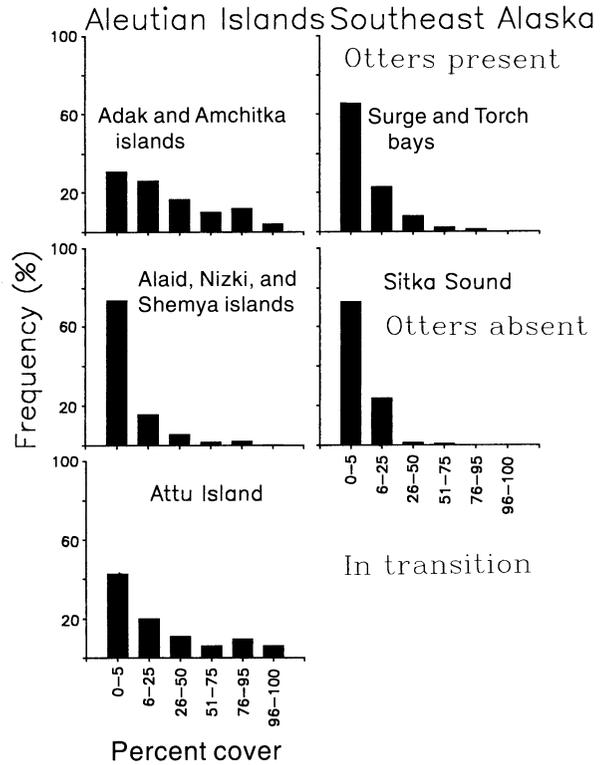


FIG. 9. Frequency distributions of estimated percent cover of suspension feeding invertebrates from random samples taken at A) Torch and Surge bays; B) Sitka Sound; C) Adak and Amchitka islands; D) Alaid, Nizki, and Shemya islands; and E) Attu Island.

years (Density: $P = 0.44$ for sites and 0.44 for years; Biomass: $P = 0.44$ for sites and 0.99 for years; maximum test diameter: $P = 0.56$ for sites and 0.25 for years).

A shorter time interval (1976–1978) is available for Torch Bay because otters had recolonized the location before we returned in 1988. However, the pattern over three consecutive years was considerably more variable than it was at any of the three locations described above. The patchiness of urchins in space, and the dynamic nature of these patches (Duggins 1983) led to high among-site and among-year variation (Table 6). Kelp density varied significantly among the three years ($F_{2,4} = 8.24$, $P = 0.038$) but not among sites ($F_{2,4} = 2.18$, $P = 0.23$). Urchin density varied significantly among sites ($F_{2,4} = 25.62$, $P = 0.005$) but not among years ($F_{2,4} = 1.10$, $P = 0.42$). In general, kelp density was low; however, annual species of kelp were abundant at two sites in 1978 because of anomalous physical and biological conditions (Duggins 1981). While kelp populations at Torch Bay in the absence of sea otters were unpredictable and variable (Table 6), the benthic community was nonetheless controlled by herbivory, as demonstrated by experimental urchin removals

(Duggins 1980) and by changes that followed the eventual recolonization of sea otters.

Changes following sea otter recolonization.—In contrast with the generally low spatial and temporal variation in populations of herbivores and benthic algae at otter-free locations, changes that followed sea otter recolonization at each location were striking. We surveyed benthic species before and after the arrival of sea otters from nine sites at Attu Island and four sites at Torch Bay. Only data on kelp and sea urchin abundance are presented here.

Kelp density and urchin biomass at the pre-otter Torch Bay sites (1978: Table 6) were similar to those measured at Sitka Sound in 1988 (Table 3, Figs. 2 and 7). In 1988, 2 yr after sea otters recolonized Torch Bay, kelp density had increased $85\times$ and urchin biomass had declined $>10\,000\times$. The post-otter kelp density and urchin biomass measured in Torch Bay were within the range of variation observed at other sites in southeast Alaska where sea otters were present (compare Figs. 7 and 10). Both kelp and urchin density at the post-otter sites in Torch Bay differed significantly from values obtained from these same sites before the arrival

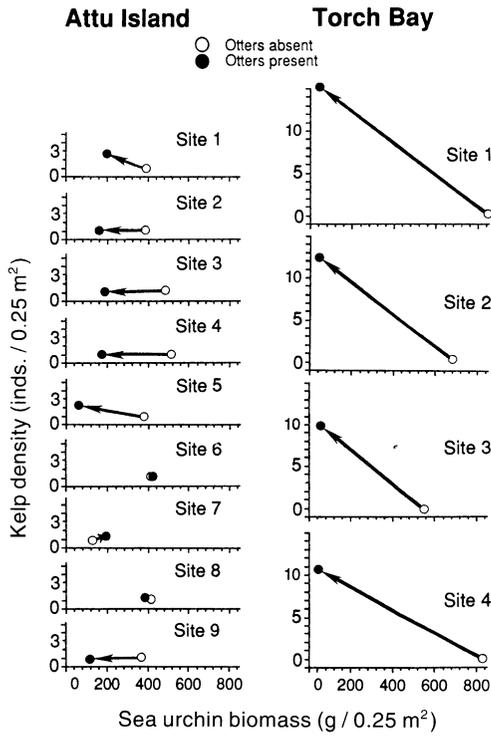


FIG. 10. Epibenthic kelp density (inds./0.25 m²) vs. estimated sea urchin biomass (g/0.25 m²) measured before and after the recolonization of sea otters from nine sites at Attu Island (1983, otters absent; 1987, otters present) and four sites at Torch Bay (1978, otters absent; 1988, otters present). Note: sea otters recolonized the Torch Bay sites in 1985–1986 and the Attu Island sites in 1984–1985, so both locations were sampled about 2 yr after being recolonized by sea otters.

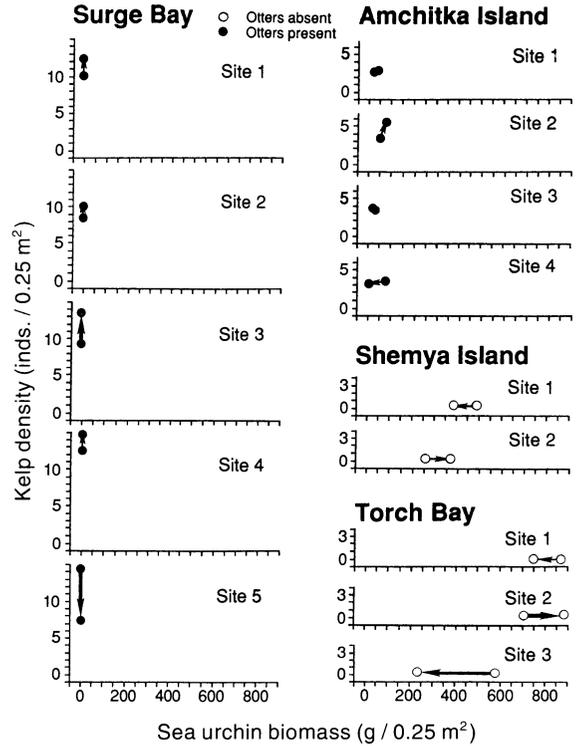


FIG. 11. Epibenthic kelp density (inds./0.25 m²) vs. estimated sea urchin biomass (g/0.25 m²) measured through time at locations where the status of sea otter populations did not change (Surge Bay 1978 and 1988, sea otters present; Amchitka Island 1972 and 1987, sea otters present; Shemya Island 1972 and 1987, sea otters absent; Torch Bay 1977 and 1979, sea otters absent).

of otters (paired *t* tests: kelp, $t_7 = 3.626$, $P = 0.036$; urchins, $t_7 = 3.256$, $P = 0.047$) as well as from sites sampled in Sitka Sound (Table 3). Neither differed significantly from sites sampled in Surge Bay where sea otters were present (see previous section, Table 3).

Samples taken from the five Surge Bay sites in 1978 and 1988 did not differ significantly in either kelp abundance or sea urchin biomass (Fig. 11; see previous section), thus indicating that the temporal changes observed at Torch Bay during this same time interval were caused by the arrival of sea otters rather than larger scale temporal changes in kelp forest community structure in southeast Alaska.

In southeast Alaska, sea urchin population changes in response to sea otter predation were rapid and extreme. Sea urchins were the most conspicuous macroinvertebrate in Torch Bay from 1975–1979, during which time population density and biomass averaged 4.5 individuals/0.25 m² and 1221 g/0.25 m², respectively (Table 6). By May 1988, ≈2 yr after sea otters had recolonized in Torch Bay, urchins were virtually absent from our four long-term sites as well as from 14 other sites sampled only in 1988. *Strongylocentrotus franciscanus* and *S. purpuratus* had disappeared from

the four long-term sites and the density and biomass of *S. droebachiensis* had declined >96% and >99%, respectively (Table 7). In Surge Bay during May 1988, sea urchin density and biomass remained near zero at the five long-term sites, as well as at 15 other sites sampled only in 1988.

The short-term changes in kelp density and sea urchin biomass at nine Attu Island sites following the arrival of sea otters differed from those seen in southeast Alaska (Fig. 10). Kelp density at Attu did not change significantly over time within sites (paired *t* test, $t_8 = 1.503$, $P = 0.17$). Changes in urchin biomass at Attu Island also were small compared with those that occurred in southeast Alaska (Fig. 10).

The broad patterns of community structure, their changes in response to sea otter predation, and the manner in which these changes differ between the Aleutian Islands and southeast Alaska are captured in a two-way ANOVA of kelp density and sea urchin biomass (Table 8). Both measures differed significantly between the Aleutian Islands and southeast Alaska, and although sea otter predation ultimately drove the configuration of sublittoral reef communities from deforested habitats to kelp forests at both locations, the highly sig-

TABLE 7. Density and biomass of sea urchin populations before and after reestablishment of sea otters via natural range expansion into Massacre Bay, Attu Island and into Torch Bay, southeast Alaska.

| Location/Species | Population density (inds./0.25 m ²) | | | Biomass (g/0.25 m ²) | | |
|--------------------------|---|-------|---------|----------------------------------|-------|---------|
| | Before | After | % diff. | Before | After | % diff. |
| Massacre Bay | | | | | | |
| <i>S. polyacanthus</i> | 31.5 | 39.6 | +25.7 | 374.9 | 180.7 | -51.8 |
| Torch Bay | | | | | | |
| <i>S. franciscanus</i> | 1.48 | 0.0 | -100 | 982.8 | 0.0 | -100 |
| <i>S. droebachiensis</i> | 1.22 | 0.0 | -100 | 161.5 | 0.0 | -100 |
| <i>S. purpuratus</i> | 1.45 | 0.05 | -96.6 | 76.3 | 0.3 | -99.6 |

nificant Region \times Time interaction reflects the much more rapid effect in southeast Alaska.

Three main patterns in urchin demography and population structure are evident from our time series of data in the Aleutian Islands: (1) recruitment was frequent and broadly occurring; (2) population density and size structure were constant at locations where otter population status remained unchanged; and (3) population density and size structure changed at locations that were recolonized by otters.

Temporal variation in the Aleutian Islands in the rate and extent of response of sea urchin populations to sea otter predation is evident from samples taken during 1972–1990 at Attu Island. Two sites (Pisa Point, northeast coast, and Murder Point, southeast coast) were sampled intermittently during this period. Sea otters were present at Pisa Point in roughly constant numbers throughout the period. In contrast, otters were absent from Murder Point through the 1970s, began spreading into the area in the early 1980s, and were common at our study sites by the mid-1980s (Estes 1990).

Sea urchin size.—1. *Recruitment.*—Relatively large numbers of urchins with test diameters <10 mm were present in all sample years at both sites (Fig. 12), thus indicating either strong annual recruitment or very slow growth. In situ growth measures argue against the latter explanation (see following section). This finding and the prevalence of small animals over a broad spatial scale in 1987 (Figs. 3 and 5) indicate that sea urchins recruited heavily to most areas in the western and central Aleutian Islands during all or most of the nearly 20 yr of our study.

TABLE 8. Two-way ANOVA of the effects of location (Aleutian Islands vs. southeast Alaska) and the reestablishment of sea otters (before vs. 1–2 yr after) on kelp density and sea urchin biomass.

| Source | df | F | P |
|--------------------|-------|-------|--------|
| Kelp density | | | |
| Region | 1, 22 | 44.78 | 0.0001 |
| Time | 1, 22 | 82.91 | 0.0001 |
| R \times T | 1, 22 | 77.61 | 0.0001 |
| Sea urchin biomass | | | |
| Region | 1, 22 | 11.76 | 0.0024 |
| Time | 1, 22 | 32.23 | 0.0001 |
| R \times T | 1, 22 | 27.75 | 0.0001 |

2. *Size structure.*—Although the exact form of the sea urchin size-frequency distribution at Pisa Point varied among the six sample years (especially 1979 when individuals of test diameter 14–18 mm were relatively abundant), minimum and maximum sizes changed little (Fig. 12, Table 9). Maximum size declined from \approx 48 to 40 mm during this period, perhaps because of continuing or increased intensity of size-selective predation by sea otters. Overall, the size distributions of sea urchins at Pisa Point were more similar to those measured at Adak and Amchitka islands than they were to those measured at islands without otters (Table 9).

Maximum urchin size at Murder Point declined markedly following the spread of sea otters into this area (Table 9), and the size distribution eventually converged upon those measured at other locations in the Aleutian Islands with established sea otter populations (i.e., Pisa Point, Adak and Amchitka islands). In 1972 and 1976 respectively, prior to the arrival of otters in Massacre Bay, 26.2 and 21.9% of the urchins were >50 mm, and in both years individuals >80 mm were obtained. These population characteristics were similar to those from other areas lacking sea otters in the Aleutian Islands (i.e., Alaid, Nizki, and Shemya islands). A few otters had spread into Massacre Bay by 1983 (10 were counted in the west Massacre Bay–Murder Point survey areas in 1983 and seven more in areas to the west [Estes 1990]), and although some urchins with test diameters >80 mm still occurred at that time, those >50 mm had declined to comprise only 3.6% of the population. Sea otters were well established in the area by 1986 (29 were counted in the west Massacre Bay–Murder Point survey area in 1986 and an additional 485 were seen in areas to the west [Estes 1990]). Sea urchins with test diameters >80 mm had disappeared from our study sites by 1986 and 1987, and only 0.2 and 0.05% of the individuals sampled were >50 mm during these respective years. The sea otter population at Attu continued to increase through the late 1980s, and in 1990 39 animals were counted in the west Massacre Bay–Murder Point survey area with an additional 649 seen in areas to the west (J. Estes, unpublished data). By 1990 the size structure of sea urchins at Murder Point had become similar to that of other exploited populations in the western and central Aleutian Islands

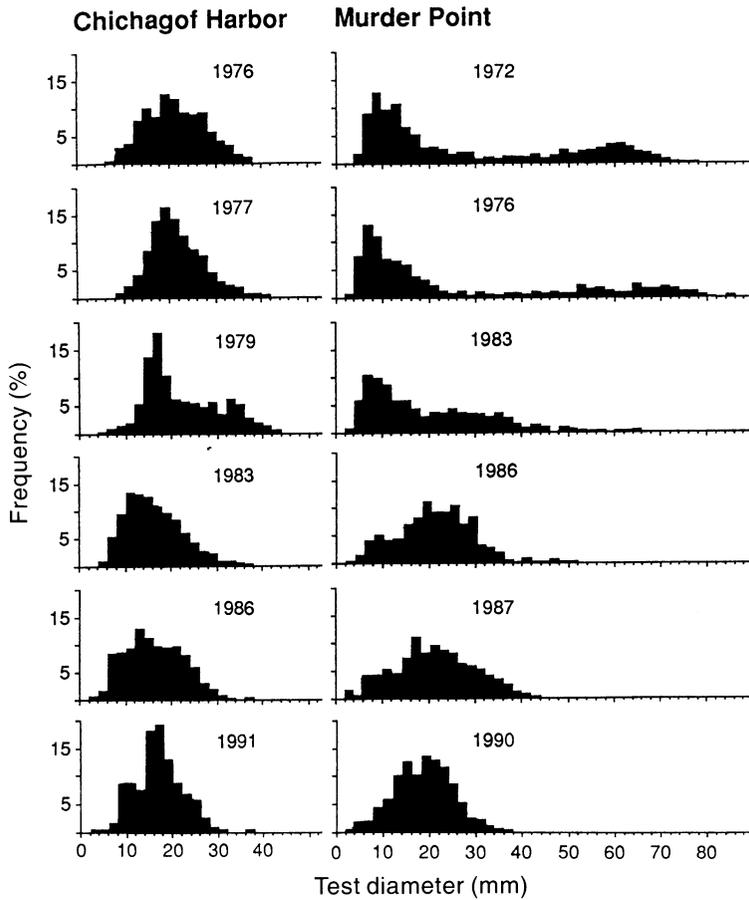


FIG. 12. Sea urchin (*S. polyacanthus*) size–frequency distributions from Attu Island (two sites at Chichagof Harbor and two sites at Murder Point) sampled at various times between 1972 and 1991. Sea otters were continuously present at Chichagof Harbor during the years shown; they recolonized the Murder Point area in the early 1980s.

(e.g., Pisa Point, Amchitka Island, Adak Island; Fig. 10 and Table 8).

The progressive loss of large individuals from the sea urchin population at Murder Point closely coincided with otters spreading into the area and preying on sea urchins in a size-selective fashion. Changes in urchin population structure between 1972–1976 and 1986–1987 reflect the nature and rate of this transition. Urchin biomass at Attu declined about 50% and density actually increased about 25% during this time (Table 7). These data contrast with our time series on sea urchin populations from Torch Bay (i.e., 1978 vs. 1988), where density declined by 99% and biomass by $\geq 99\%$ following the recolonization of sea otters.

Sea urchin growth

Sea urchin abundance and size distribution were similar in the tidepool populations marked with tetracycline for growth measurements between July 1986 (marked) and June 1987 (collected) at Attu Island. The total number of animals found in the four pools was 2% greater in 1987 than in 1986 (496 vs. 486 urchins),

the smallest animals from each pool had test diameters of < 10 mm in both years, and in both years the largest animals in pools at Pisa Point had test diameters of 40–50 mm whereas those in the Murder Point pools had test diameters of 60–70 mm.

Slopes of the linear regressions of \ln test diameter vs. \ln jaw length did not vary significantly among the four pools ($F_{3, 496} = 2.357$), and since size-specific growth increments also appeared similar, the data were pooled (Fig. 13). Two hundred and seventy-four urchins had distinctive tetracycline marks, among which the estimated annual increase in test diameter ranged from 0 to 13.08 mm. Although highly variable among individuals, the average growth rate increased with size up to the 15– < 20 mm diameter size class, declined somewhat for animals 20– < 30 mm, and declined more abruptly for animals > 30 mm (Table 11). Together with the size–frequency distributions of sea urchins (Figs. 5, 6, and 12), these data indicate that significant recruitment events occur at least every 2–3 yr. Despite the fact that we marked numerous individuals with test diameters > 50 mm, few marked animals were recov-

TABLE 9. Characteristics of sea urchin populations in the western and central Aleutian Islands, contrasting areas with and without sea otters, and temporal changes at particular sites following the growth and spreading of otter populations into these sites.

| Location and Date | Test diameter (mm) | | Percentage of population | | |
|-------------------------|--------------------|-------|--------------------------|--------|--------|
| | Mini- | Maxi- | >30 mm | >40 mm | >50 mm |
| | mum | mum | | | |
| Alaid Island* | | | | | |
| 1987 | 3 | 83 | 23.9 | 21.1 | 14.7 |
| Nizki Island* | | | | | |
| 1987 | 3 | 84 | 42.1 | 25.1 | 14.7 |
| Shemya Island* | | | | | |
| 1987 | 3 | 84 | 30.6 | 19.7 | 12.9 |
| Adak Island‡ | | | | | |
| 1987 | 2 | 38 | 0.4 | 0 | 0 |
| Amchitka Island‡ | | | | | |
| 1987 | 2 | 39 | 0.5 | 0 | 0 |
| Attu Island | | | | | |
| Chichagof Harbor | | | | | |
| 1976† | 5 | 44 | 10.5 | 0.2 | 0 |
| 1977† | 5 | 48 | 7.8 | 0.2 | 0 |
| 1979† | 5 | 44 | 21.1 | 2.1 | 0 |
| 1983† | 4 | 44 | 2.9 | 0.1 | 0 |
| 1986† | 2 | 40 | 1.5 | 0 | 0 |
| Murder Point | | | | | |
| 1972* | 4 | 86 | 28.5 | 26.9 | 21.9 |
| 1983† | 4 | 86 | 23.7 | 9.1 | 3.6 |
| 1986† | 4 | 52 | 10.3 | 1.9 | 0.2 |
| 1987† | 3 | 54 | 17.6 | 1.4 | 0.1 |
| 1990† | 3 | 39 | 3.6 | 0 | 0 |

* Sea otters absent.
† Sea otters present but below equilibrium density.
‡ Sea otters at equilibrium density.

TABLE 10. Percentage of total change in sea urchin biomass and kelp density following the arrival of sea otters to long-unoccupied sites in the Aleutian Islands and southeast Alaska.*

| | Percentage of total change | |
|-------------------------|----------------------------|-------------------|
| | Aleutian Islands | Southeast Alaska† |
| Sea urchin biomass | 50% decline | 100% decline |
| Epibenthic kelp density | 1% increase | 103% increase |

* Total change was estimated from measurements at sites with and without sea otters. Data are from Tables 2 and 3.
† Data from area occupied by equilibrium-density sea otter population not available for southeast Alaska. However, data from Surge Bay sites assumed to represent equilibrium situation, based on data in Fig. 2.

ered in this size range thus preventing us from reliably making age estimates of the larger sea urchins. A number of these larger animals appeared to have dim tetracycline marks at the terminal ends of their jaws, thus indicating that they had been marked but accrued little or no net growth in the ensuing year. These observations, together with the negative relationship between size and growth rate for animals of test diameter >20–30 mm, indicate that the large individuals (> about 50–60 mm test diameter and which characterize nearly all sea urchin populations in the western Aleutian Islands that are unexploited by sea otters) are several to many decades old (Fig. 14).

Size-selective predation

Urchin size distributions, estimated from jaw lengths in otter scats collected during 1986 and 1987 from Amchitka and Attu islands, demonstrated that otters selectively consumed the largest available prey (Fig. 15). An alternate interpretation is that the jaws of small urchins either were not consumed or, because of their relative fragility, were selective destroyed between

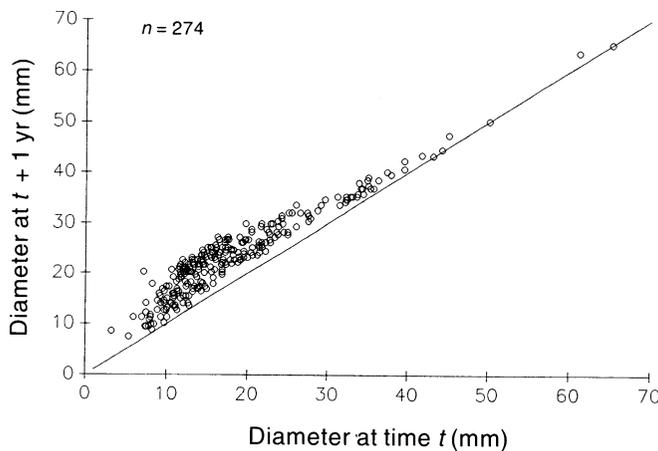


FIG. 13. Size-specific annual growth increments in test diameter (corrected to 365 d) for tetracycline-marked sea urchins (*S. polyacanthus*) from four tide pools at Attu Island. The solid line represents zero growth. Each point (O) represents the annual growth increment of one sea urchin.

TABLE 11. Size-specific growth increments from tetracycline-marked sea urchins at Attu Island, Alaska. ND = no data.

| Size range (mm) | n | Diameter growth (mm/yr) | |
|-----------------|----|-------------------------|------|
| | | \bar{X} | SD |
| 0-<5 | 1 | 5.41 | ... |
| 5-<10 | 30 | 4.39 | 2.73 |
| 10-<15 | 93 | 6.39 | 2.70 |
| 15-<20 | 63 | 6.72 | 2.27 |
| 20-<25 | 35 | 5.02 | 1.74 |
| 25-<30 | 19 | 5.25 | 1.67 |
| 30-<35 | 9 | 3.40 | 1.22 |
| 35-<40 | 14 | 2.43 | 0.91 |
| 40-<45 | 6 | 1.93 | 0.79 |
| 45-<50 | 3 | 0.95 | 1.23 |
| 50-<55 | 0 | ND | ... |
| 55-<60 | 0 | ND | ... |
| 60-<65 | 0 | ND | ... |
| 65-<70 | 1 | 2.48 | ... |

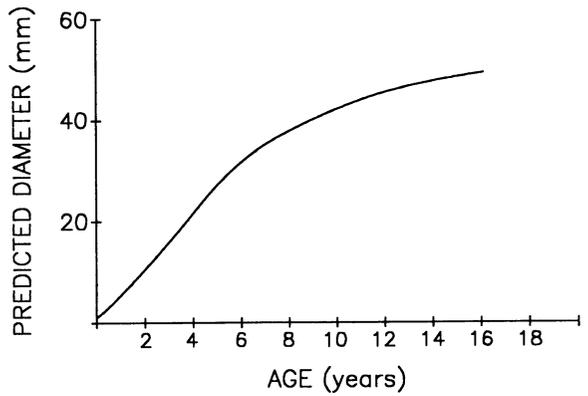


FIG. 14. Estimated size (test diameter) vs. age relations for sea urchins (*S. polyacanthus*) from Attu Island. Estimates are based on average growth rates for 5-mm size increments (Table 11).

consumption and excretion. These possibilities are unlikely. First, sea otters tend to consume small urchins in their entirety whereas the tests and other calcareous tissues of the larger ones are discarded. Second, larger calcified structures, simply by virtue of their comparatively large surface area, may be more prone to inadvertent damage by the grinding motion of an otter's heavy molars. In fact, our subjective impression was that many of the larger jaws extracted from scats were partially fractured whereas the smaller ones were less frequently damaged. In any case, because of their highly conserved form, it was easy to estimate lengths of most partially fractured jaws.

The mean respective urchin sizes (test diameter) available to and consumed by sea otters at Attu (based on otter scats and living populations sampled near Murder Point) were 21.9 and 26.7 mm. Similarly, mean respective urchin sizes available to and consumed by sea otters on the northeast coast of Amchitka Island were 14.9 and 19.0 mm. Size distributions of animals eaten differed significantly from those in living populations in both instances (Attu, $\chi^2 = 31.65$, $df = 17$, $P = 0.017$; Amchitka Island, $\chi^2 = 34.52$, $df = 13$, $P = 0.001$).

Sea otters did not eat the smallest available sea urchins in Aleutian Island populations. Only 0.3% of the animals consumed at Attu were <10 mm whereas about 11% of the available population was <10 mm; 1.9% of the urchins consumed at Amchitka Island were <10 mm whereas about 19% of the population were <10 mm. These data indicate that the smallest sea urchins in the Aleutian Islands have a refuge in size from sea otter predation and further imply an increased risk of predation with increased size.

Although we have no comparable data on the sizes of sea urchins consumed by otters in southeast Alaska, those sizes that appear to offer a refuge from sea otter predation in the Aleutian Islands (i.e., <30 mm) were

sparse (red and green urchins) or absent (purple urchins) in southeast Alaska.

DISCUSSION

Ecological communities, and the processes that structure them, typically vary in space and time (Dayton and Tegner 1984, Wiens 1986). Furthermore, such variation exists at a broad range of scales (Powell 1989). Therefore, the ability to generalize ecological patterns and processes depends on the magnitude and scale of spatial and temporal variation in nature. This

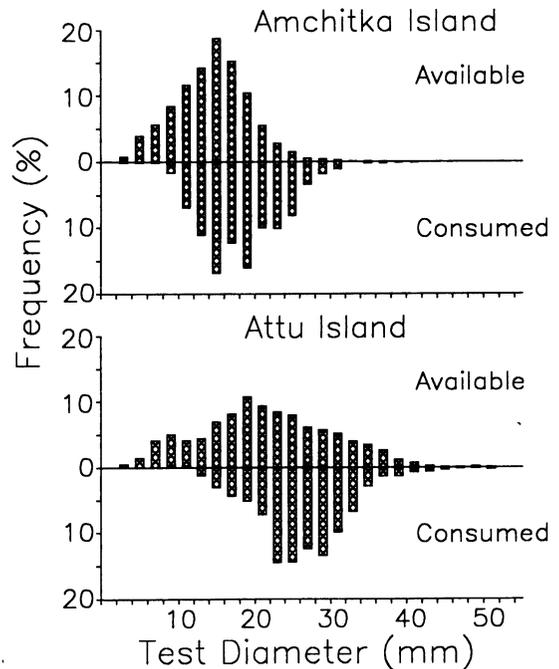


FIG. 15. Size-frequency distributions of sea urchins (*S. polyacanthus*) in natural populations (available) and those consumed by sea otters at Amchitka and Attu islands.

point is substantiated by a rapidly growing list of published studies (Sutherland 1981, Williams 1983, Dayton and Tegner 1984, Hay 1984, Schneider and Piatt 1986, Wiens 1986, Wiens et al. 1986, Dethier and Duggins 1988, Paine 1988, Powell 1989, Foster 1990, Rose and Leggett 1990, Angel 1991, Witman and Sebens 1992).

Our study is perhaps the first rigorous attempt to define the generality and variation of a community ecological paradigm—in this case the claim that sea otter predation on sea urchin populations reduces intensity of herbivory, thereby enhancing abundance and production of kelps and other macroalgae. A number of previous studies (see Table 1) have provided evidence that the interactions exist, and there is reasonably strong evidence for a range of indirect consequences as well (Trapp 1979, Estes et al. 1982, Irons et al. 1986, Duggins et al. 1989, Estes et al. 1989). However, claims have also been made that these interactions occur under a limited range of circumstances, that previous studies were done under these limited circumstances or in habitats chosen to support the paradigm's predicted outcomes, and thus that the paradigm is of more limited importance than published studies imply (Foster and Schiel 1988, Foster 1990).

A rigorous evaluation of the extent to which any character or process is general requires that (1) the sample space or population of interest be defined, (2) sample units be appropriately defined, (3) a process for selecting those sample units be chosen that will provide unbiased (or at least representative) estimates of the character or process, and (4) a sufficiently large number of sample units be selected to provide reasonably precise estimates. These fundamental principles of probability sampling (Cochran 1963) raise problematic questions for community ecology. In contrast with many statistical populations (i.e., sample spaces, Hoel 1971), spatial and temporal boundaries of biological communities are usually either difficult to define or nonexistent. At a minimum it is necessary to know the geographical ranges of component species to properly define community boundaries, characteristics that often are poorly understood. This problem is exacerbated by the likelihood that species ranges vary discordantly (Curtis and McIntosh 1950, Whittaker 1975), making the precise spatiotemporal definition of a community necessarily arbitrary. Furthermore, in contrast with many biological populations for which individuals are the obvious sample units (those comprising clonal organisms are exceptions), the appropriate sample units in community ecological studies are unclear and usually arbitrarily selected. Because many natural populations vary extensively on small spatial and temporal scales, the structure of natural communities, however they are defined and measured, may vary at least as much, and on the same scales, as the populations that comprise them. The sources of such variation must be understood and accounted for in defining the sample

space, which is probably possible only if large numbers of units can be sampled to provide a sufficiently robust generalization. It is for these reasons that rigorous attempts to generalize even the most well known and important of community ecological paradigms are rarely, if ever, done, and consequently, why community ecological paradigms, as they become popular or well known, often become contentious.

*Generality and variation in Alaskan
sea otter–kelp forest systems*

We do not claim to have met all of the above stated requirements for evaluating the generality of a community ecological paradigm, although we were able to meet two of the more important ones. That is, our evaluation was based on rigorous probability sampling of sites within locations and plots within sites, thus providing unbiased estimates of the parameters we measured. Furthermore, our sample sizes were large. This helped assure that our measurements captured the range of natural variation, thus permitting realistic measurements of statistical confidence in the estimates. We believe these accomplishments are unprecedented in prior community ecological studies in which specific a priori hypotheses have been at issue.

Our findings showed that the influence of sea otter predation on kelp forest community structure is consistent in some ways and variable in others. For instance, the distributions of kelp density vs. sea urchin biomass among sites with and without sea otters (Fig. 6) were largely non-overlapping in the western Aleutian Islands and mutually exclusive in southeast Alaska, thus indicating that, based on these measurements, a random sample of 20 0.25-m² plots from a given site is sufficient to predict, with a high level of confidence, the presence or absence of sea otters in Alaskan kelp forest communities. This is not to say that the configurations of these systems are describable as precise point estimates. In communities lacking sea otters, urchin biomass was high and variable whereas kelp density was low and relatively invariant. In contrast, communities with sea otters had kelp densities that were relatively high and variable whereas sea urchin biomass was low and invariant. These patterns indicate that abundances of autotrophs and herbivores in this system both are precisely set when directly limited by top-down control. This precision declines when direct top-down control is relaxed, perhaps because a broader array of limiting processes (e.g., competition, physical disturbance) come into play. Thus, neither sea urchin biomass nor kelp density alone was a good predictor of the influence of sea otter predation although together they provided a predictable measure of the presence or absence of sea otters.

The most reliable indicator of the presence or absence of sea otters was the maximum size of sea urchins. In the Aleutian Islands, the frequency distributions of this measure did not overlap between islands

lacking sea otters and those where otters were at or near equilibrium density (Fig. 5). Data from Attu Island indicate that the larger sea urchins (i.e., >35–40 mm test diameter) were consumed within 1–2 yr of otter recolonization. The speed of this change and the virtual population uniformity thereafter probably resulted from the size-selective nature of sea otter predation and the slow growth rate of sea urchins in the western Aleutian Islands. This pattern was not seen in southeast Alaska because sea urchin populations there were effectively eliminated by sea otters shortly following recolonization.

The abundance of red algae and benthic suspension feeders varied less between areas with and without sea otters than did the abundance of sea urchins and kelps. The abundance of red algae was greater at sites with sea otters than at sites without them, and although this difference was statistically significant, the abundance of fleshy red algae was not a predictable measure of the presence or absence of sea otters at any given site. The abundance of suspension feeders was an even poorer predictor of the presence or absence of sea otters, even though growth rates of several suspension feeding species are enhanced significantly by particulate organic carbon derived from kelp and other macrophytes (Duggins et al. 1989). The failure of these guilds of organisms to covary as strongly as urchins and kelp with the presence and absence of sea otters probably results from both positive and negative influences imposed on these groups in both ecological settings. For instance, the presence of sea otters should enhance the red algal turf via reduced herbivory and inhibit it via increased competition for light or space with the kelp overstory. Suspension feeding invertebrates should be subject to similar opposing forces, in this case enhancement from algal-derived detritus and reduced grazing and inhibition by competition with kelp and red algae.

Foster (1990) and Foster and Schiel (1988) argued that the importance of sea otters as a structuring element in California kelp forests has been greatly exaggerated, and that other factors, such as physical disturbance, are primarily responsible for patterns of kelp species abundance and distribution within the otter's current range. Foster's arguments are based upon the observation that outside the range of otters, sea urchin and kelp are highly variable in their abundance, with a relatively small proportion ($\approx 20\%$) of benthic habitats qualifying as deforested areas. Unfortunately, no corresponding data are provided by Foster regarding kelp or urchin distribution within the sea otter's range. Such variation is in fact typical of habitats without otters at virtually all sites with which we are familiar along the northeast Pacific coast. Even in the Aleutian Islands, where expansive deforested undersea areas are ubiquitous, microhabitats exist where urchins are either ineffective or rare; especially at wave exposed, shallow sites where extreme turbulence creates conditions in

which urchins cannot forage (Dayton et al. 1984, 1992). Particularly striking is how little variation there is in kelp and urchin abundance within the present range of otters (including sites in California) and how different measures of these parameters are from sites without otters.

The preponderance of observations and experimental studies in California (Table 1) support the sea otter paradigm. Additionally, in the only long term (historical) analysis of changes in kelp abundance following otter reintroduction in California, VanBlaricom (1984) presented compelling observations supporting the importance of otters. His pre-otter vs. post-otter comparisons suffer (as do most such comparisons) from the fact that only two points in time are compared. Kelp surface canopies (e.g., *Macrocystis*) are temporally variable in extent regardless of whether otters are present, and two-point comparisons must be viewed with caution given the number of co-variables which could contribute to kelp variation. However, VanBlaricom's observations came from three sites, with pre-otter assessments made in two years (1911 and 1912), and post-otter assessments (all of which showed dramatic increase in surface canopy cover) made at three different times spanning ≈ 40 yr.

If differences in the structure of kelp forests do exist between California and other regions, two life-history attributes may be responsible. In California, physical disturbance may be particularly important in that the competitively dominant kelp is a long-lived, surface-canopy species. Not only are these surface canopies more susceptible to damage by storm turbulence, but their removal has broad ramifications to other algal species. North of northern California, surface canopies are composed of competitively inferior annual species that exert little influence on other benthic plants. Additionally, in California (as in the Aleutian Islands), urchin recruitment may be considerably less variable than to the north. If our proposal for the interactive importance of urchin recruitment and size-selective predation by sea otters is correct, we would expect that California kelp forests would respond more slowly to otter reintroduction than their counterparts in Washington, British Columbia, and southeast Alaska.

While we agree completely with Foster and Schiel that sea otters are not the only important factor regulating kelp-dominated communities, we believe that it is unlikely that California represents a substantial exception to the sea otter paradigm. Even if rates of change in kelp forests following otter reintroduction were significantly slower in California, the end results (a highly significant increase in algal abundance, biomass, and distribution) are likely to be similar to those documented farther north.

Mechanisms of persistence and change in plant-herbivore interactions

The results of this study show that rocky reef communities in Alaska tend to persist as either kelp-dom-

inated or deforested assemblages, and that intermediates between these community configurations are both rare and highly transitory. Two sources of information from our study support this conclusion. First, the bivariate plots of sea urchin biomass vs. kelp density (Fig. 7) were strongly hyperbolic in both the western Aleutian Islands and southeast Alaska. If the community was not characterized by 2 domains of attraction separated by unstable intermediates, one would expect herbivore biomass and plant density to be either uncorrelated or more nearly correlated as a first-order function. Second, the transition from deforested to algal-dominated communities in response to the reestablishment and growth of sea otter populations occurs rapidly. In southeast Alaska, this transition occurred soon after sea otters had expanded into previously unoccupied habitats whereas in the western Aleutian Islands it was often delayed for years or decades. Nonetheless, the shift to a kelp-dominated community probably occurs abruptly in the latter region because we have seen no evidence for the gradual recovery of kelp forests at Attu in >20 yr of observation. Abrupt transitions between forested and deforested communities have been reported in kelp forests worldwide, especially in the northern hemisphere (Harrold and Pearse 1989). Furthermore, Steneck (1993) also reported a strongly hyperbolic pattern of association between the abundances of sea urchins (*Diadema antillarum*) and macroalgae on a Caribbean reef, thus suggesting that alternative stable equilibria in plant-herbivore interactions occur broadly in benthic marine systems.

Since algal-dominated or deforested communities in Alaska appear to be determined in large part by the presence or absence of sea otters, they are more properly characterized as boundary points (Lewontin 1969) than as alternate stable communities (Holling 1973, Sutherland 1974, 1981). The mechanisms responsible for maintaining these points are complex and varied, and the temporal patterns of change differ remarkably between the western Aleutian Islands and southeast Alaska. Our findings, together with those of other workers, suggest that three processes—sea urchin recruitment, size-selective predation, and the dynamical properties of plant production and herbivore consumption—are important to the stability of and rates of transition between these community configurations.

Sea urchin recruitment.—The most striking difference in sea urchin population structure between the Aleutian Islands and southeast Alaska was that small animals (<15 – 20 mm test diameter) were abundant in the former region and virtually absent in the latter (Fig. 5). High densities of small sea urchins characterized most of the numerous locations we sampled in the central and western Aleutian Islands, and observations made during a cruise through the Aleutian archipelago in 1987 indicate that this situation persists eastward to

at least the Islands of Four Mountains (Fig. 1; J. Estes, unpublished data).

Small sea urchins were also consistently abundant through time in Aleutian Islands populations. We found similar size–frequency distributions of sea urchins at Amchitka Island in the late 1960s and early 1970s (Estes et al. 1978) and again in 1986 and 1987 (this paper). Small individuals occurred at all sites sampled at Attu Island in 1975–1981, 1983, 1986, 1987, 1990, and 1991. These patterns could only be maintained by persistent recruitment or slow growth.

The relative importance of growth vs. recruitment to the abundance of small individuals in Aleutian Islands sea urchin populations is somewhat equivocal because growth was indeed slow and we have no direct evidence for settlement. Nonetheless, given an average growth rate for tetracycline-marked animals of ≈ 5 mm/yr, major settlement events must have occurred at least every 2–3 yr to produce the observed patterns. In addition, such settlement patterns must be broadly occurring as we have yet to discover an urchin population in the Aleutian Islands that lacked small individuals. Whatever the exact cause, its main consequence is that echinoid populations throughout the Aleutian Islands contain numerous individuals in the size range of 5–35 mm test diameter.

Although our records are less extensive for southeast Alaska, settlement there was episodic and apparently did not occur in most areas during most years. For instance, our samples of sea urchin populations (mostly red urchins) from 21 sites in Sitka Sound generally lacked individuals $<$ about 35 mm test diameter, an often recurrent pattern for red and purple sea urchins from southeast Alaska to central California (Ebert 1983, Paine 1986, Harrold and Pearse 1987, Pearse and Hines 1987, Sloan et al. 1987). In 5 yr of study at Torch Bay, we observed a single settlement event for red urchins at one study site, and none for purple urchins. The main consequence of this recruitment pattern is that urchin populations in southeast Alaska contain few or no individuals between the sizes of 5–35 mm test diameter.

Processes responsible for this difference in echinoid population structure between the Aleutian Islands and southeast Alaska are uncertain. Biological differences among echinoid species represent one possible explanation. A second possibility is that small sea urchins in southeast Alaska occurred in cryptic habitats and entered the observable population only upon becoming larger. Third, comparable rates of urchin recruitment may have occurred in southeast Alaska and the Aleutian Islands, but with the small recruits lost to some other predator unique to southeast Alaska. The sunflower star, *Pycnopodia helianthoides*, an urchin predator, is in fact abundant in southeast Alaska and rare or absent in the central and western Aleutian Islands. These and other predators are known to influence the distribution and abundance of sea urchin populations.

However, this species is not known to selectively exploit small sea urchins. The fact that a single strong recruitment pulse of red urchins, and periodic weak recruitment by green sea urchins, did occur during the time of our studies in southeast Alaska, argues against all these possibilities, especially the latter two. A final possibility is that physical oceanographic processes responsible for transporting larvae differ between the Aleutian Islands and southeast Alaska. Even in regions where recruitment is generally more predictable (e.g., California and Oregon, Ebert and Russell 1989) it is patchy at meso-scales, probably because of offshore larval transport. Recent studies have demonstrated that meso-scale patterns of larval and spore transport influence adult populations of many marine organisms including fish (Cowen 1985), invertebrates (Gaines and Roughgarden 1985, Roughgarden et al. 1988, Ebert and Russell 1989), and kelps (Reed et al. 1988). Little is known at present about meso-scale current patterns and larval transport in the Aleutian Islands, although presently available evidence makes us favor this last explanation.

Size-selective predation.—Sea otters selectively exploited the largest available sea urchins from populations in the Aleutian Islands, avoiding prey <15–20 mm test diameter almost entirely (Fig. 15). The likely reason for such selective feeding is that the differential costs of locating, capturing, and consuming different sized sea urchins are probably negligible whereas nutritional benefits, which scale as a cubic function of test diameter, are obtained from larger prey. Because of frequent recruitment coupled with slow growth rates, sea urchin populations in the Aleutian Islands contain numerous individuals that apparently are too small to be eaten profitably. Thus, the largest sea urchins are selectively eaten and eliminated by expanding sea otter populations in the Aleutian Islands whereas individuals below the optimal to minimal sizes consumed by otters are reproductively mature and sufficiently abundant to prevent the recovery of kelp populations. Consequently, deforested habitats persisted in the Aleutian Islands. Although we have no data on either growth rates or the sizes of sea urchins consumed by predators in southeast Alaska, there is no reason to expect that the size-specific costs and benefits to foraging on sea urchins should differ between the regions. Thus, even the smallest sea urchins available in typical southeast Alaska populations probably are readily captured and consumed by sea otters, leaving no size refuge from predation. Consequently, abundant sea urchins disappeared and kelp forests developed quickly following the reestablishment of sea otters in southeastern Alaska.

A dynamical model for plant–herbivore interactions

A conceptual model is used to help envision how the processes discussed above might act to preserve or dis-

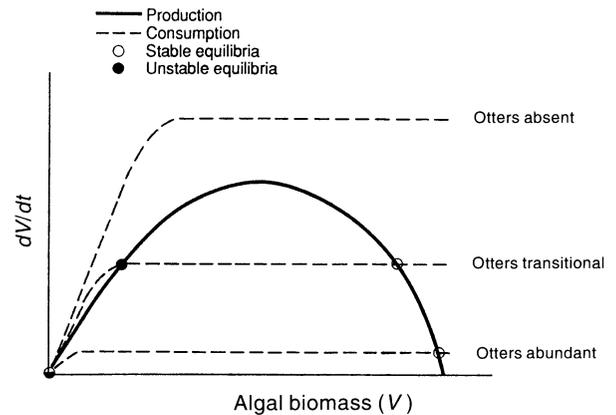


FIG. 16. Graphical model for the maintenance of stable equilibria between the production and consumption of kelp as a function of sea otter population status in the Aleutian Islands. Note that the equilibrium where algal biomass = 0 is stable when sea otters are absent or transitional but unstable when otters are abundant. This discrepancy is an arbitrary consequence of the way we have drawn the satiation curves.

rupt a stable equilibrium between plant growth and herbivore consumption in the face of recovering sea otter populations. Several of the model's features require clarification. First, we do not present it as a strict portrayal of empirical reality in our systems, but rather as a heuristic aid for discussing how dynamical properties and natural histories of those systems and their key players might be linked to explain observed patterns. Second, although rates of net production and consumption are characterized as independent functions of plant biomass, these processes in fact may interact. Finally, our system probably is atypical in that extremely high herbivore abundance is somehow maintained even after their fleshy macroalgal food resources have been eliminated. Whether the maintenance of high herbivore abundance results because of a unique ability by sea urchins to persist under starvation conditions or because food resources are subsidized from elsewhere is uncertain.

The existence of two stable equilibria in a plant–herbivore system, one with low plant biomass and the other with plant biomass near the maximum attainable, is a recurrent feature of kelp forest and some other natural communities (Noy-Mier 1975, May 1977, Walker et al. 1980). The proposed explanation for these alternate stable equilibria stems from several assumptions about the dynamical interaction between biomass-dependent plant production and herbivore consumption. The first assumption is that biomass-dependent plant production (dV/dt) is a standard yield curve in which net production rate is zero when plant biomass (V) is both zero and maximum, and maximum at some intermediate value (Fig. 16). A second assumption is that herbivores satiate with increased food availability. Equilibria occur at values of plant biomass where net production and consumption rates coincide. These

equilibria are stable within the contiguous range of low plant abundances for which production exceeds consumption (thus driving plant abundance upward toward the equilibrium point) and the contiguous range of high plant abundances for which consumption exceeds production (thus driving plant abundance downward toward the equilibrium point). The equilibria are unstable when the opposite conditions apply. Plant biomasses that define stable equilibria depend on the shapes of the yield curve and the herbivore consumption rate at satiation. Although the forms of these curves are unmeasured in kelp forests, stable equilibria should occur near V_0 and V_{\max} under many realistic circumstances. Algal-herbivore dynamics in kelp forest communities frequently conform to the predictions of this model. That is, fleshy algal stands typically are either deforested or largely ungrazed (Harrold and Pearse 1987), organizational states that we suggest represent the two stable equilibria. Intermediate conditions usually are transitory, and we suggest these correspond with transition intervals or unstable equilibria depicted in Fig. 16.

When these general conditions apply, changes in the abundance of sea otters (i.e., intensity of predation on sea urchins) drives the herbivore satiation plateau (i.e., consumption rate vs. algal biomass) upward or downward. For systems lacking sea otters, herbivore consumption exceeds net algal production at all values of algal biomass except V_0 which thus defines a single stable equilibrium. Similarly, for systems in which sea otters are at or near equilibrium density, production exceeds consumption for all values of V_x except V_{\max} . V_0 is unstable and the system has a single stable equilibrium at V_{\max} . Hence the system supports dense algal stands. These extreme conditions appear to pertain in the Aleutian Islands and southeast Alaska. That is, we found communities lacking sea otters to be generally deforested, and those with otter populations at or near equilibrium density generally to support dense algal stands with little evidence of grazing damage. However, the reestablishment of low density otter populations has profoundly different short-term effects between the Aleutian Islands and southeast Alaska, apparently in large measure due to the otter's size-selective foraging behavior and the presence or absence of high densities of sea urchins smaller than the otter's size preference threshold. Thus, the plateau of the herbivore consumption curve in southeast Alaska is driven effectively to zero by recolonizing sea otters whereas in the Aleutian Islands a similar intensity of otter predation has less of a depressing influence on the consumption rate plateau. The magnitude of reduction in herbivore consumption may be further compromised in the Aleutian Islands by an increased density of small sea urchins in response to the selective removal by sea otters of large individuals (Fig. 4, Tables 7 and 10), the result being that herbivore consumption rate in the Aleutian Islands is only modestly influenced in the

short term by the recolonization of an area by sea otters. Similar in situ kelp consumption rates and survival rates of whole kelp plants (J. Estes, *unpublished data*) in deforested habitats with and without sea otters at Attu Island support these conclusions.

CONCLUSIONS

The findings of this study leave little doubt that Alaskan kelp forests are broadly dependent on sea otter predation for protection against destructive grazing. That is, the predicted outcomes of sea otter predation are broadly recurrent, which is not to say they occur invariably, but rather that they occur at most times, places, and under most natural circumstances. This notwithstanding, the patterns of variation are also intriguing and broadly relevant. On relatively small spatial scales (metres to kilometres), sampling variation and the variation among sites within locations help define the "domains of attraction" (Holling 1973: 4) between stable boundary points of community organization. The fact that these points were essentially non-overlapping indicates that the proposed equilibrium states are mutually exclusive and that transitional or intermediate states of community organization are rare events. Nonetheless, the extent to which small-scale (among site) measurements varied in space and time indicate that both kelp- and urchin-dominated communities are highly dynamic, and thus variable, within their respective domains of attraction.

Variation at the regional scale was both significant and informative, in particular the vastly different frequencies and intensities of urchin recruitment between the Aleutian Islands and southeast Alaska. This finding provides insight into the coupling of meso-scale oceanographic processes that influence larval life history stages and microscale processes that influence adult life history stages. In the context of adult life history phases, Alaskan kelp forests are dominated by top-down forces, i.e., carnivores limit herbivores, and when carnivores are absent, herbivores limit plants. However, in the broader context of larval life histories, interregional comparisons between the Aleutian Islands and southeast Alaska indicate subtle but important donor-controlled or bottom-up forces, namely the supply of planktotrophic larvae to the rocky benthos. The coupling of scales (micro and meso), systems (rocky reefs and demersal), and life history stages (propagule and adult), when interfaced with a strongly connected food web and an understanding of the natural history of consumer choice, provides the conceptual elements that are both necessary and sufficient to explain strikingly different interregional rates of transition between deforested conditions and the development of kelp forests with the reintroduction of sea otters.

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