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Articles

Sea Otters and Kelp Forests in Alaska: Generality and Variation in a Community Ecological Paradigm

James A. Estes and David O. Duggins

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.

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