Aleuts, Sea Otters, and Alternate Stable-State Communities

Charles A. Simenstad, James A. Estes, Karl W. Kenyon

Summary. Reexamination of stratified faunal components of a prehistoric Aleut midden excavated on Amchitka Island, Alaska, indicates that Aleut prey items changed dramatically during 2500 years of aboriginal occupation. Recent ecological studies in the Aleutian Islands have shown the concurrent existence of two alternate stable nearshore communities, one dominated by macroalgae, the other by epibenthic herbivores, which are respectively maintained by the presence or absence of dense sea otter populations. Thus, rather than cultural shifts in food preference, the changes in Aleut prey were probably the result of local overexploitation of sea otters by aboriginal Aleuts.

Interpretations of paleoecological evidence in the Aleutian Islands have been made with the assumption that aboriginal Aleuts exploited and maintained a stable and uniform resource base (*1, 2*). Laughlin (*2*) supposed the ecological role of aboriginal Aleuts to be "a moderating influence on population fluctuations in the other resident species" such as sea otters (*Enhydra lutris*) and their principal prey. These interpretations presume that aboriginal man arrived in the New World as a "prudent predator" (*3*) and survived as a wise manager of the natural resources he exploited. These interpretations also are consistent with the popular hypothesis that paleoecological changes, such as Pleistocene extinctions of New World megafauna, were caused directly by rapid environmental change—climatic and geological phenomena producing high rates of extinction and speciation. There are, however, alternative hypotheses, such as that proposed by Martin and Wright (*4*), positing that aboriginal man reduced or eliminated various large vertebrates upon arriving in the New World. Results of recent ecological and archeological investigations in the Aleutian Islands have prompted us to consider the Martin-Wright hypothesis specifically for aboriginal Aleuts.

Predation is important to the structure and organization of many natural communities (*5*). The "keystone predator's" role (*6*) of sea otters is particularly dramatic in that two alternate nearshore community structures are maintained by the presence or absence of sea otters in the Aleutian Islands (*7*), supporting Sutherland's (*8*) evidence that multiple stable-state communities can occur in one environment. Our intent here is to integrate this understanding of sea otter–induced alternate communities with a reinterpretation of the faunal remains in Aleut middens to propose that (i) multiple stable-state communities can be found historically and presently in the Aleutian Archipelago and that (ii) aboriginal man, the Aleut in this case, was instrumental in driving the community from one stable state to another (Fig. 1). To our knowledge this article is the first amalgamation of two theories, treating aboriginal man as an important predator through his influence on the nearshore community.

Alternate Communities

Through intense predation, the sea otter profoundly influences the organization of nearshore communities in the North Pacific Ocean (*7, 9, 10*). We have identified some of the more visible consequences of sea otter predation by comparing islands in the western Aleutian Archipelago with and without sea otters (*7, 11–13*). Differences between these two insular communities (Table 1) are dramatic even to the casual observer. Dense sea otter populations reduce herbivorous epibenthic macroinvertebrates such as sea urchins (*Strongylocentrotus polyacanthus*) (*14*), limpets (*Collisella pelta*), and chitons (*Katharina tunicata*, *Cryptochiton stelleri*) to sparse populations of small individuals. This interaction in turn allows an abundant association of macroalgae to flourish on the rocky substrate of the broad littoral benches and shallow (0 to 20 meters) sublittoral zones (*7, 10*). In contrast, islands with few or no sea otters support dense populations of large herbivorous invertebrates which, by overgrazing, virtually exclude the association of fleshy macroalgae. These islands are characterized by bare rocky substrates covered by a dense carpet of sea urchins and, in some areas, abundant bivalves (*Modiolus rectus*), colonial tube worms (*Potamilla reniformis*), predaceous asteroids (*Leptasterias alaskensis*, *Crossaster papposus*, *Solaster stimpsoni* and a number of species yet to be identified), epibenthic macrocrustaceans (*Telmessus cheiragonus*, *Erimacrus isenbecki*, and *Elassochirus tenuimanus*), and octopus (*Octopus dofleini*) (*15*).

The association of macroalgae is the major source of marine primary production in the western Aleutian Islands and other north temperate areas (*16*). Consequently, islands lacking sea otters (and thus the robust association of macroalgae) apparently are relatively unproductive compared with islands where sea otters are abundant (*7, 17*). This condition is further manifested both directly and indirectly in the composition and standing crop of nearshore fishes. Islands dominated by sea otters characteristically have high standing crops of species that depend on and use sublittoral macroalgae for protection and spawning substrate. A characteristic detritus-based food web supports most of these fishes through abundant populations of epibenthic crustaceans—mysids and amphipods—which are sustained by breakdown of macroalgae (*18, 19*). In contrast, islands without otters possess noticeably fewer nearshore fishes, and those present typically are species associated with the pelagic ecosystem and its food web. This condition apparently has more far-reaching effects on higher trophic forms, because islands without sea otters have a comparatively depauperate vertebrate fauna in terms of both number of species and abundance of individuals (*7*).

Charles Simenstad is on the staff of Fisheries Research Institute, College of Fisheries, University of Washington, Seattle 98195; James Estes is a biologist with the Anchorage Field Station of the National Fish and Wildlife Laboratory, U.S. Fish and Wildlife Service, and Affiliate Assistant Professor with the Center for Quantitative Science, University of Washington; Karl Kenyon is retired from the U.S. Fish and Wildlife Service.

0036-8075/78/0428-0403$02.00/0