

Aleuts, Sea Otters, and Alternate Stable-State Communities

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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 in-

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-

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.

fluence 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

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).

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Since cessation of large-scale fur hunting in 1911, the sea otter has reestablished its Aleutian populations throughout most of the archipelago, and in these regions, the nearshore community is characterized by sparse populations of sea urchins and abundant beds of macroalgae. Aboriginal Aleuts arrived in the western Aleutian Islands about 2500 years ago, although today they are extinct in that area.

The Aleut

Faunal remains in Aleut and pre-Aleut kitchen middens excavated in the Aleutians probably are the best indication of nearshore community structure during prehistoric times (20-24). But Dall (20) and his successors have generally interpreted stratified faunal midden remains as different cultural periods, implying exploitation of a single stable community

in which diverse marine mammals, macroinvertebrates, and fishes were equally available for harvest. This interpretation no doubt comes from investigations showing that the Aleuts in the eastern Aleutians depended more on seasonally abundant migratory food resources than their neighbors did in the western Aleutians (24). Even these excavations, however, indicate disruption of the more stationary component of the eastern Aleuts' food resources by overuse.

The homogeneous composition and stratified position of prominent faunal components (Fig. 2) have suggested to us another possibility, namely, that one or more shifts in the food subsistence base for aboriginal populations occurred during Aleut occupation before intrusion of Western man. We have used the previous data and have reexamined faunal material from a prehistoric Aleut midden (49 Rat 31) (25) that was excavated on the Pacific coast of Amchitka Island in

1969 (23). The strata and their major faunal components are described in Fig. 3 (26). These faunal data include the minimum number of sea otters and harbor seals (*Phoca vitulina*) (27) and the gram dry weights of fish bones, sea urchin spines and tests, and limpet shells per centimeter of deposition. Minor components such as mussel and chiton shell, and bones of northern fur seals (*Callorhinus ursinus*) and Steller's sea lions (*Eumetopias jubata*) (28), are not numerous enough to include graphically. Although the faunal remains are graphed by stratum, these strata are not discrete, equal time periods but are the archeologists' designations of layers dominated by remains of certain organisms—for example, stratum E is the lens of sea urchin spines and tests seen in Fig. 2. The scale is a measurement of depth from the surface. Carbon dates at several depths indicate a uniform rate of deposition (about 1 centimeter per 10 years), and

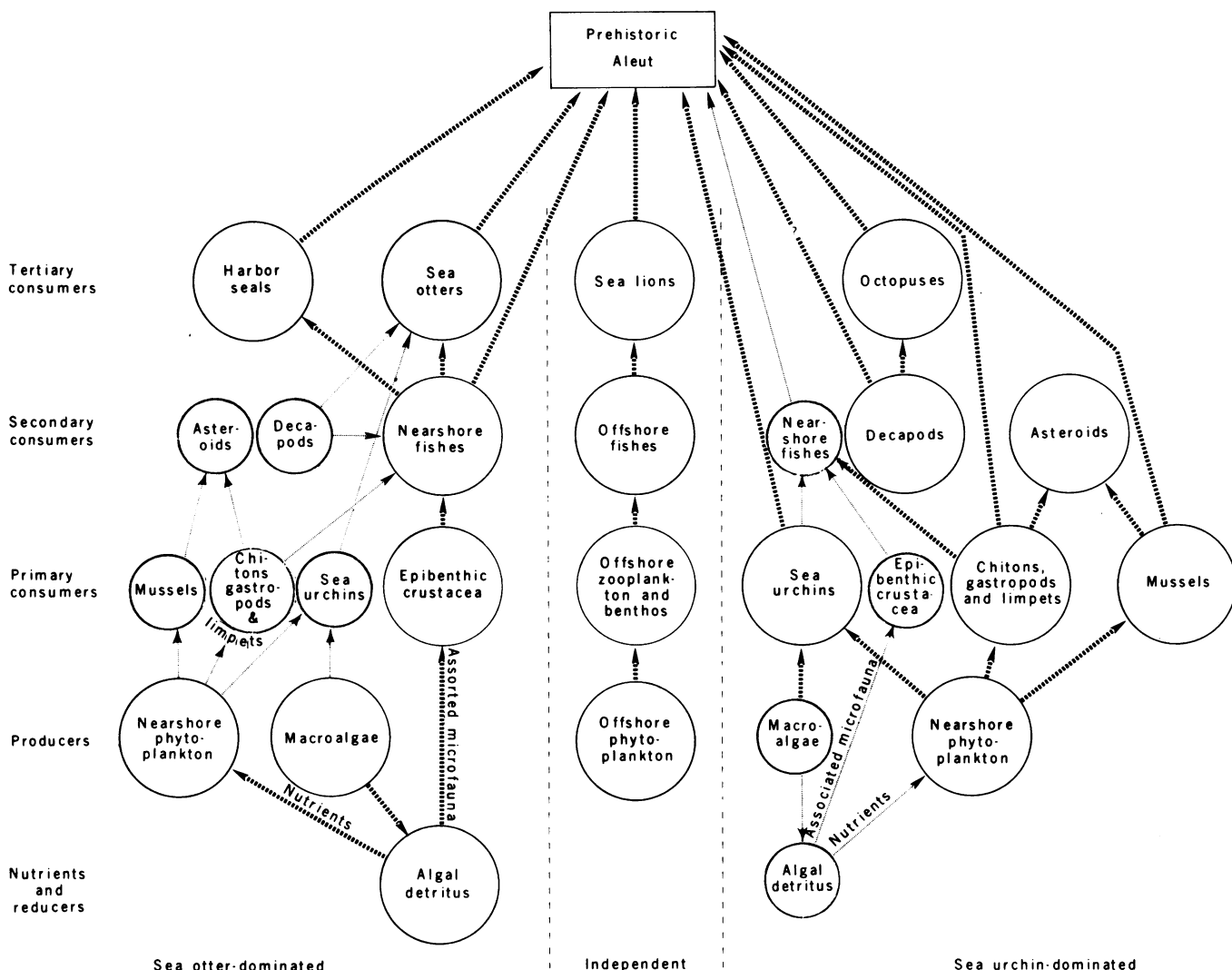


Fig. 1. Generalized food web in the western Aleutian Islands emphasizing the effect of aboriginal Aleuts on the principal components of the nearshore community. The sizes of circles indicate relative differences in standing crop between various components of the community in the two alternate states of community organization. Arrows indicate the direction of biomass or energy flow; heavy arrows indicate importance or magnitude of an interaction compared with the alternate community.

therefore a moderately even time scale, over the past 2500 years.

Several assumptions are vital to interpretation of the midden faunal remains, the most important being that these remains represent the availability of dominant food organisms for Aleut harvest from the nearshore community. Overall, skeletal, calcareous, and shell remains of food organisms are well preserved. The most notable exception is the lack of bones from Pacific salmon (*Oncorhynchus* spp.), Dolly Varden (*Salvelinus malma*), and the smooth lump sucker (*Aptocyclus ventricosus*), which we know to have been harvested commonly throughout the Aleutians (20, 24, 29). These fish bones and macrocrustacean exoskeletons apparently were too fragile or not calcified enough to be preserved. Soft-bodied mollusks such as cephalopods are not represented in the faunal remains for a similar reason. We further assume that the Aleut harvested food in proportion to availability, so that major shifts in harvesting strategies were imposed by changes in the availability of harvestable organisms. Correspondingly, we assume that the remains of different food organisms were not discarded in different areas, and that faunal remains in the vertical profiles through the middens represent changes in the composition of food exploited by the Aleuts through time (30).

The data in Fig. 3 indicate a strong negative relationship between the harvest of sea otters, fish, and harbor seals, on the one hand, and the harvest of sea urchins and limpets on the other. We interpret this as evidence that (i) the availability of prey items preferred by Aleuts changed greatly during the time Aleuts occupied Amchitka and (ii) this change was caused largely by Aleuts overharvesting or harassing sea otters, with the consequence that during at least the past 2500 years the nearshore community at Amchitka shifted between one dominated by sea otters to one characterized by few sea otters and an abundance of large invertebrate herbivores. That the Aleut was technically capable of locally reducing or eliminating sea otters during prehistoric times is supported by the near elimination of sea otters from the North Pacific Ocean after the enslavement of Aleut hunters by Russian fur traders (31, 32).

The effect of Aleut exploitation was therefore twofold: (i) By overexploiting sea otters, Aleuts limited the availability of this prey, forcing a change in harvesting strategy to increasingly more available organisms such as sea urchins and limpets; and (ii) in limiting the sea otter,

Aleuts induced a shift in the nearshore community toward an alternate structure as populations of invertebrates that were once limited by sea otters expanded with the sea otter's decline. Many of the sea otter's principal prey are herbivores, and these populations probably grew because of an abundance of algae and the release from intense predation. These herbivores invaded the sublittoral fringe and littoral zones where they became available for harvest by Aleuts. Eventually an alternate state of community organization was attained.

Sea Urchin Size Frequencies

Stratigraphic variation in the abundance of midden faunal remains, together with prehistoric and present size class distributions of sea urchins, provides evidence for the general pattern of spatial and temporal changes in nearshore community organization at Amchitka Island during the past 2500 years. The inverse relationship between abundance of sea otters and grazing invertebrates (Fig.

3) suggests superficially that dominant components of the community shifted from marine mammals and fish to herbivorous invertebrates, then back to marine mammals and fish. Since there is no obvious historical or biological explanation for the second shift, these data might be interpreted as evidence for cultural changes in Aleut use of temporally uniform food resources, or perhaps as cyclic overuse of both marine mammals and herbivorous invertebrates. In the absence of additional information, a convincing argument could not be made for these, or perhaps other, alternative explanations.

Comparison of the size and distribution of sea urchins between prehistoric and present communities clarifies the situation. The size of sea urchin remains in middens cannot be measured directly, owing to fragmentation of the tests; however, a conspicuous feature of these remains at Amchitka is the large size of calcareous parts of the oral apparatus, or Aristotle's Lantern, which are found intact amid the broken tests and spines. *Strongylocentrotus polyacanthus* is the

Table 1. Comparative status of nearshore communities in Rat Islands and Near Islands, western Aleutian Islands, Alaska.

Species (sources)	Rat Islands (Amchitka Island) (48)	Near Islands (Shemya and Attu islands)
Sea otters (31, 49)	Abundant for at least last several decades; current estimated population greater than 6000	Sparse; first sighting in late 1960's after extermination by fur traders; current population on Attu about 350; none at Shemya
Macroalgae (7, 10)	Abundant; diverse epibenthic canopy (principally four species of <i>Laminaria</i> , <i>Agarum cribrosum</i> , Rhodophyta spp.) and a dense surface canopy (<i>Alaria fistulosa</i>); competitive interactions predominate	Rare; restricted to a few species isolated in sublittoral fringe and sublittoral patches
Sea urchins, <i>S. polyacanthus</i> (7)	Rare; maximum test diameter < 32 mm; increasing density and size with depth	Dense; maximum test diameter > 100 mm; highest density and greatest individual size at sublittoral fringe
Limpets (11), <i>C. pelta</i> (50)	Density 8 m ⁻² and maximum length 51 mm	Density 82 to 356 m ⁻² and maximum length 67 mm
Chitons, <i>K. tunnicata</i> , <i>C. stelleri</i> (7)	Rare; density < 1 m ⁻²	Common; density 32 m ⁻²
Mussels, <i>Mytilus edulis</i> , <i>Modiolus</i> sp. (7)	Rare and small; density 3.8 m ⁻²	Common and large; density 722 m ⁻²
Barnacles, <i>Balanus glandula</i> , <i>B. cariosus</i> (7)	Rare and small; density 4.9 m ⁻²	Common and large; density 1215 m ⁻² , dominating upper littoral zone
Nearshore fish (18, 51)	Abundant, diverse fauna; high standing crop supported by algae detritus-based food web	Sparse fauna outside littoral zone except for deepwater demersal and neritic forms and populations associated with sparse, isolated patches of macroalgae
Harbor seal, <i>P. vitulina</i> (52)	Estimated density, 8.1 per kilometer of coastline; frequently observed in groups larger than 50 animals	Estimated density 1.5 to 2.1 per kilometer of coastline; seldom observed in groups larger than ten animals

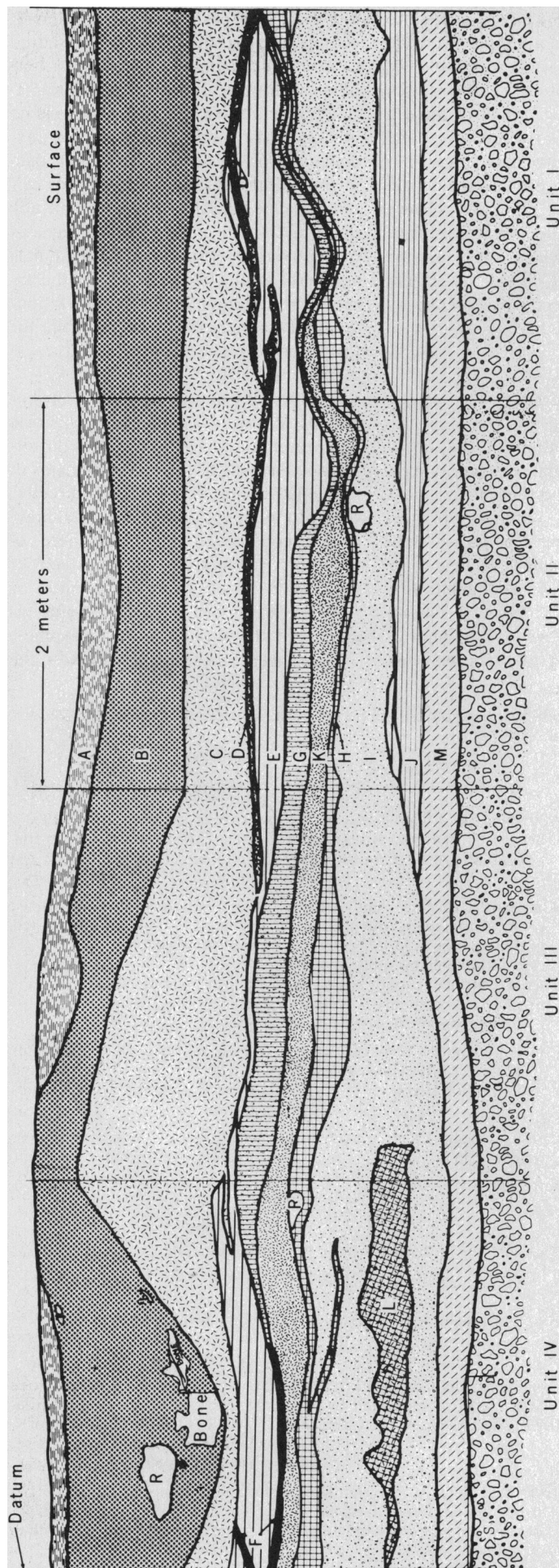


Fig. 2. Stratigraphic profile (front face of excavation units) of midden site 49 Rat 31, Amchitka Island. ■, ^{14}C sample locations. The figure (with minor relabeling) and the following legend are reproduced from Desautels *et al.* (23, figure 15): A, Dark brown highly organic humus (root zone), mixed with sand and overriding a thin lens of dark clay. B, Dark brown-colored midden and sea urchin mixture with a low and sporadic content of sand and black clay. C, Light brown sea urchin and midden mixture with light-colored sea urchin lenses and sand. D, Dark brown sea urchin and midden mixture with a high concentration of inter-mixed sand and clay; constitutes a basement layer of C. E, Light yellowish-white colored sea urchin and limpet mixture. F, Pure fish bone. G, Dark brown sea urchin, sand, and midden mixture. K, Light brown sea urchin and midden mixture with deposits of pure sea urchin; becomes discolored and in spots more compact towards the base of the stratum. H, Dark black greasy, highly organic, with a high concentration of fish bone. I, Dark brown sea urchin and midden mixture with an increased amount of sand; contains thin inter-mixed lenses of (i) black organic materials and (ii) light sea urchin lenses. J, Pure brown sand; scattered fish and mammal bone. M, Yellowish-brown sand; oxide layer appearing at base. S, Indicates sterile; starting with a pure clay lens and continuing down into a light brownish-gray sand layer.

only species of sea urchin known to have inhabited the western Aleutians during the Recent epoch. Therefore we suspected that some parts of Aristotle's Lantern in the midden remains might indicate the size of Aleut-harvested urchins. The demipyramids, which are the thickest and most robust parts of Aristotle's Lantern, were chosen as the most likely indicator, since they are not prone to wear and regeneration from grazing.

The correlation between sea urchin diameter and demipyramid length was determined from living specimens collected at Amchitka and Shemya Islands (Table 2). We found that linear regressions of test diameter and demipyramid length were not significantly different between Amchitka and Shemya ($F_{2,212} = 3.61$, $P > .05$), and that the common regression function

$$y_1 = -5.9484 + 5.1732 x_1$$

where y_1 equals test diameter and x_1 equals demipyramid length, was extremely precise ($r = .9838$).

The high correlation between urchin diameter and demipyramid length has allowed us to estimate accurately and precisely the size of sea urchins harvested by Aleuts at Amchitka. Figure 4 illustrates size frequency histograms by stratum for sea urchins deposited in the Amchitka midden, together with comparable data from recent collections from the littoral and shallow sublittoral zones at Amchitka (12) and Attu Islands (15). These data demonstrate that the size-frequency distributions of sea urchins gathered by Aleuts occupying the midden were virtually constant throughout the period of Aleut occupancy. Only "M stratum," representing the earliest period of occupation of this site, provides no record of sea urchins. Most important, these size-frequency distributions typify present-day communities devoid of sea otters, as shown by the data from Casco Point [see also (7)] which is outside the range of the small population of sea otters now occupying that island (33). In contrast, these distributions contain larger sea urchins than we found either at Pisa Point (34), which now is in the center of the sea otters' range on Attu, or at Amchitka where sea otters are currently abundant (35). Furthermore, whereas sea otters have been abundant at Amchitka for at least several decades, in contrast with the small, recently established population at Attu, the size-frequency distributions of sea urchins at Pisa Point on Attu and those from Amchitka are nearly identical. From these observations and data we conclude that even a sea otter population at low den-

sity rather quickly causes a noticeable shift in the size-frequency distribution of sea urchins toward smaller individuals.

The reconstructed size-class distributions of sea urchins (Fig. 4) therefore imply that a community lacking or nearly devoid of sea otters persisted (at least locally) throughout the time Aleuts occupied Amchitka. Aleuts probably selectively gathered the largest urchins available to them, and although such selective behavior would tend to mask minor changes in the size-frequency distribution of sea urchins over time, it could not account for the distributions observed in the midden strata if many sea otters were present (36).

The most reasonable interpretation of midden faunal remains is that there was some spatial disparity in Aleut hunting and gathering activities. We suggest that Aleuts gathered sea urchins and limpets near the villages—areas from which sea otters were harvested or harassed to near extinction. Later hunting (and perhaps fishing) activity was apparently directed toward more distant areas, perhaps even other islands. This explanation is most plausible because even sparse populations of sea otters cannot occur in the same place as sea urchins of the size gathered by Aleuts (37).

The Fish Assemblages

Abundance of fish in the various midden strata is correlated with the abundance of sea otters (Fig. 3). This pattern follows logically from our recent findings that the abundance of nearshore fishes is positively correlated with the abundance of macroalgae, and therefore with a high-density population of sea otters (38). However, although the relationship between aboriginal Aleuts, sea otters, and certain herbivorous macroinvertebrates seems fairly clear, the interpretation of coincident availability and harvest of specific nearshore fishes is more complicated. The relative abundance of principal fish species occurring in the midden strata is illustrated in Fig. 5. These data were derived from estimates of the minimum numbers of fish, based on the abundance of characteristic head bones (39).

Information concerning Amchitka's recent fish communities (18) suggests that the marine fish assemblage available to the Aleuts included two components, only one of which was directly tied to the structure of the nearshore community. One component includes species probably little affected by Aleut fishing pressure or by kelp abundance, such as offshore (> 40 m depth) demersal or epi-

Table 2. Sources of sea urchin, *S. polyacanthus*, used in correlation between urchin dimension and demipyramid (component of Aristotle's Lantern, mouth structure) size.

Location	Collection method	Depth range (m)	Sample size (N)	Urchin test diameter range (mm)
Amchitka Island	Bottom trawl	82 to 92	58	32 to 80
Amchitka Island	Scuba collection	6 to 31	62	5 to 52
Shemya Island	Scuba collection	3 to 23	96	6 to 74

benthic fishes, and several seasonal or transient inhabitants of nearshore communities such as Atka mackerel (*Pleurogrammus monopterygius*), Pacific halibut (*Hippoglossus stenolepis*), and rock sole (*Lepidopsetta bilineata*). These species are not directly dependent on nearshore communities for food or protection, although they may use these waters periodically for spawning and, as with the rock sole, their juveniles may

occupy the nearshore community as a nursery area. In the eastern Aleutians, where these fishes are generally more abundant, they constituted more significant food resources and contributed to seasonal patterns in resource exploitation by the Aleuts of that region (24).

The second component of the fish fauna includes species that are more permanent members of the nearshore fish assemblage, including rock greenling

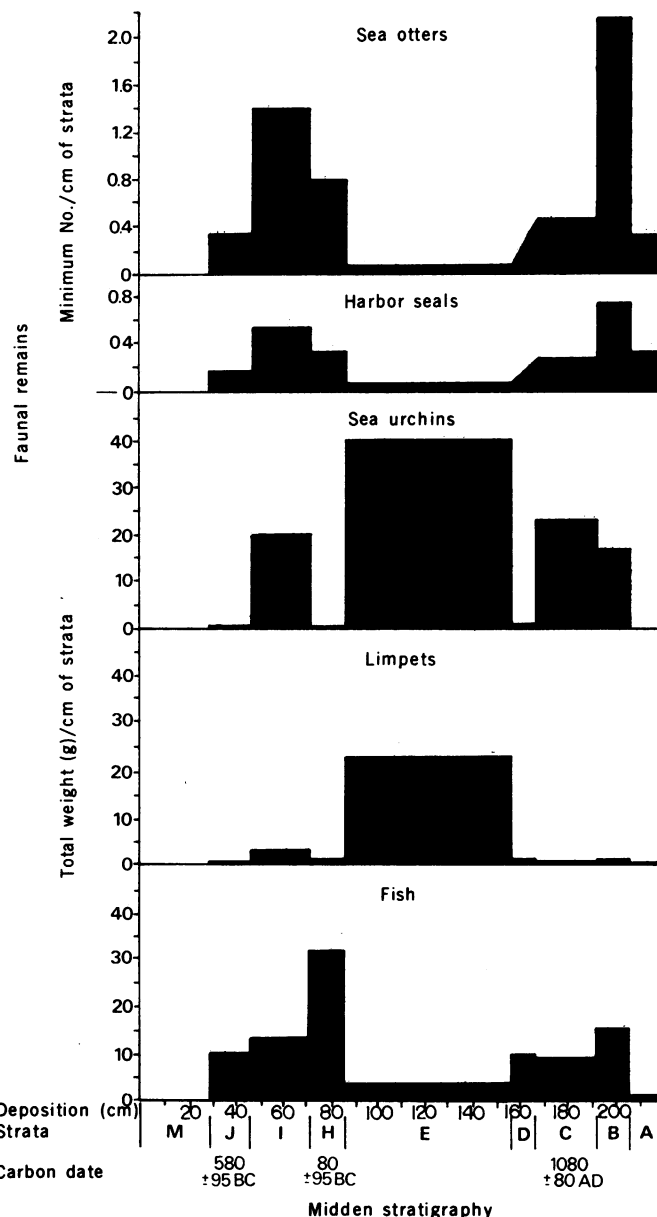


Fig. 3. Principal faunal remains in the strata of midden 49 Rat 31 at Amchitka Island. The strata were designated by Desautels *et al.* (23).

(*Hexagrammos lagocephalus*), red Irish lord (*Hemilepidotus hemilepidotus*), rockfish (*Sebastes* spp.) (40), great sculpin (*Myoxocephalus polyacanthocephalus*), and smooth lump sucker (*A. ventriosus*). Pacific cod (*Gadus macrocephalus*) represents a transitional species

which, although also found in deeper waters offshore, occupies the nearshore waters during much of the year. These species characterize the otter-dominated community at Amchitka, or once did (18, 31). By their reliance directly on the kelp community for protection and spawning

substrate, or indirectly on the detritus-based food web, they represent populations which (i) could have been overexploited and (ii) should have been reduced with expansion of the sea urchin population and declining kelp abundance.

Apparently the Aleut, by controlling the abundance of sea otters, indirectly influenced the concurrent abundance (Fig. 3) of these fishes. Data from the midden strata (Fig. 5), in conjunction with our recent collections at Amchitka and Attu, support this conclusion. Fishes of the exposed, rocky nearshore habitat were more abundant at Amchitka than at Attu (as much as 44 times the catch per unit effort), although percentage composition of species was not strikingly dissimilar. Rock greenling predominated in both communities and, when the small patches of kelp bed habitat persisting at Attu were sampled, catch per unit effort for this species was similar to that of Amchitka. Thus we believe that the availability of nearshore fishes is strongly correlated with the abundance of macroalgae.

Nearshore fish species (rock greenling, red Irish lord, and Pacific cod) typically were exploited more successfully than offshore species (Fig. 5). While the abundance of both components is correlated with patterns of sea otter/urchin abundance (Fig. 3), the nearshore component consistently predominates throughout all strata. This suggests that Aleut fishing was directed principally at nearshore areas and that offshore species were probably caught incidentally to the nearshore component. The predominance of nearshore fish remains in the midden also supports the argument that fluctuations in fish abundance (Figs. 3 and 5) were an effect of overexploitation of sea otters by Aleuts and the consequences to the nearshore community.

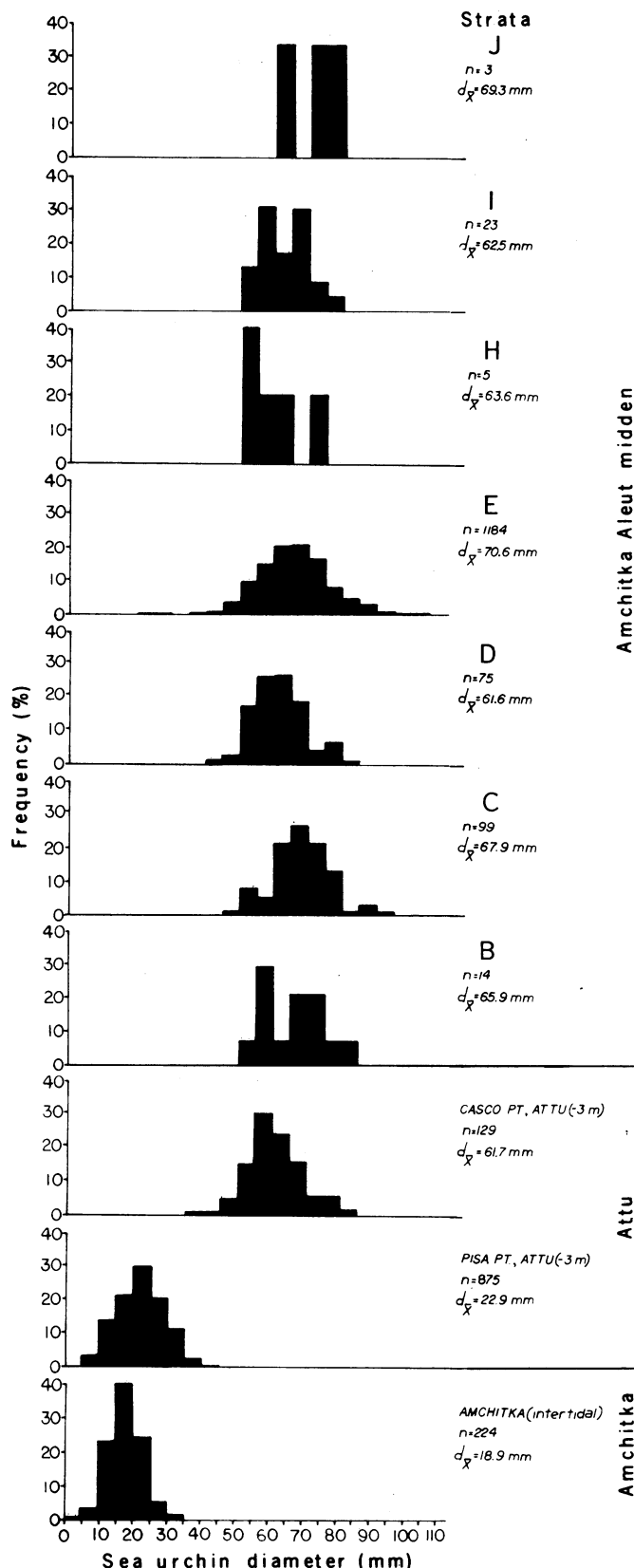


Fig. 4. Sea urchin size-frequency distributions from strata of midden 49 Rat 31 at Amchitka, and from present-day communities at Amchitka and Attu islands. An explanation of locations is given in the text. Strata levels correspond with those given in Fig. 3. Abbreviations: d_x = mean diameter; n = sample size.

Harbor Seals

The distribution of harbor seal bones through the midden strata suggests a pattern of availability and exploitation similar to that of the sea otter (Fig. 3). Harbor seals may have been harvested opportunistically during periods when Aleuts hunted marine mammals. If marine mammal hunting was more intense during those prehistoric periods when sea otters were abundant, then the observed pattern of use of harbor seals would be expected, even if the abundance of seals remained nearly constant. Harbor seals probably are closely linked with the nearshore detritus-based food

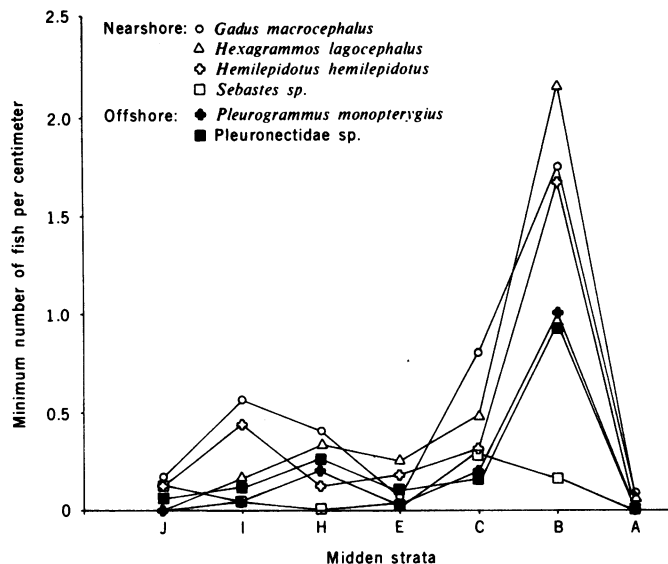
web through their consumption of near-shore fishes (41). Therefore, a relatively high abundance of harbor seals is a predictable consequence of abundant sea otters in the community, and this increased availability of harbor seals would explain their increased use during times when, or in areas where, sea otters were abundant. There is some support for this hypothesis from our observation that harbor seals appear to be more abundant on Amchitka than on Attu (Table 1) (7).

Discussion

Natural communities can exist at multiple stable points in space or time (8)—a stable point being characterized by a specific structural and functional assemblage of species in a community which is persistent through time and recognizably different from other assemblages that can occur in the same space. This definition charges us to examine communities and to interpret community changes with appropriate reference to time and space. Because several important predatory species in the western Aleutian Islands are highly motile (for example, Aleuts and sea otters), the appropriate space may be as large as islands or island groups. The appropriate time may be decades or centuries, considering the life histories of the communities' "foundation species" (42) such as Aleuts, sea otters, sea urchins, and various perennial brown algae. Indeed, the communities described in this article have been sufficiently persistent through time and space so that there can be little doubt they are locally stable in this context.

The question thus becomes, Why is a particular stable state observed at a particular point in time and space? Sutherland (8) argued that the explanation often is found through examination of specific historical events and the consequent understanding of how these events may have led to the presence or absence of key consumers in the community. History in this instance has provided us insight into the relationship between the arrival of aboriginal man to the Aleutian Islands and the initiation of shifts in the structure of the nearshore marine community to alternate stable states. The mechanism for this change is the removal of a keystone predator, which, by definition, preferentially feeds on prey that are capable of excluding subordinate species through competition for a requisite resource such as food or space. The sea otter is clearly such a predator: its foraging activities prevent sea urchins from dominating food and space re-

Fig. 5. Abundance (minimum number per centimeter of strata) of dominant marine fish species in strata of midden 49 Rat 31. Strata levels correspond with those given in Fig. 3; no fish data were available from D stratum.



sources. Therefore, the presence or absence of sea otters in the nearshore community is a driving force toward either one of two alternate stable points.

We envision that evolution in the western Aleutian nearshore community proceeded under a suite of selective forces which were associated closely with the presence of sea otters as a keystone predator. Most of the larger Aleutian Islands were extensively glaciated during the Pleistocene (43). Precursors to the contemporary communities in this area probably existed in refuges associated with the Asian and North American continents where they persisted and evolved with the predecessors of modern-day sea otters (*Enhydra*) since about the Pliocene (44).

The community probably evolved toward a relatively stable state in the sense that it apparently was resilient to minor perturbations and that it did not undergo major oscillations through time. We base this conclusion on the high longevity of many of the foundation species in the present-day community, together with the observation that populations of these species are not known to fluctuate greatly under natural circumstances. Selective forces controlling the evolution of these patterns apparently were centered on the control of herbivores by sea otters and the consequent development of a macroalgal association that served as a requisite resource to many other species of animals in the community.

As Dayton (10) pointed out, such hypothetical speculation concerning evolutionary adaptation is frequently complicated by unknown interactions involving recently extinct species—in this case Steller's sea cow (*Hydrodamalis gigas*). Sea cows are known to have inhabited Amchitka Island until the

Pleistocene (45), and they were common in the Commander Islands until shortly after G. W. Steller first observed them in 1741 (46). They apparently fed on the surface canopy (47), and their role as herbivores in the nearshore community was no doubt an important one.

Despite these uncertainties, it is evident that the arrival of the Aleut served as a driving force toward the alternate stable community state by effectively removing the sea otter as a keystone predator and replacing it at a higher trophic level. Indications are that this change dramatically effected a new structure, composition, and organization in the nearshore community.

Conclusion

Contrary to popular opinion, it is likely that aboriginal man directly caused the extinction of certain New World megafauna during the Pleistocene (4). Evidence for this conclusion generally has been in the form of temporal-spatial correlations between the extinction of species and arrival of aboriginal man. In this article we have employed a somewhat different approach by treating aboriginal Aleuts as key predators and assuming that, as such, their activities are revealed by characteristic biotic assemblages that can be interpreted in the light of a contemporary understanding of community dynamics.

The ecological interaction critical to our interpretation of the activities of aboriginal Aleuts is that dense populations of sea otters in the western Aleutian Islands limit sea urchins to sparse populations of small individuals. In turn, this interaction is important to the maintenance of robust kelp beds and a rich

associated fauna of fish, birds, and marine mammals. Midden remains suggest that aboriginal Aleuts locally disturbed this system by overexploiting the sea otter, thus minimizing or eliminating its keystone maintenance role in the community. Consistent with predictions based on observations of communities with and without sea otters, the abundance of sea otter bones through the midden strata is directly related to the abundance of marine fish and seals, and inversely related to the abundance of sea urchins and limpets.

Specific life history adaptations and interactions among species in this community probably evolved, to a large extent, either directly or indirectly in response to the keystone disturbance role of sea otters. This role probably was constant and persistent over relatively long time periods because sea otter populations probably were seldom, if ever, subjected to disruptive disturbances from predation or climatic-geological catastrophes. For these reasons we conclude that the nearshore community had little inertia against predation of sea otters by aboriginal Aleuts. Changes in the community that followed this disturbance consequently were for the most part dramatic and not preadapted for.

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- Although quantitative data are still lacking, kelp bed communities of the north Pacific appear to be analogous to eelgrass communities in their support of a food web based on detritus and associated microfauna.
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- The midden site 49 Rat 31 is located on the Pacific Ocean side of Amchitka Island on a bluff fronting a small bay. A large stream drains into the bay adjacent to the midden site and a broad expanse of intertidal bench characterizes the coastline to the east. Extensive kelp beds presently exist immediately offshore. A more detailed description of the site and its excavation and artifacts is given in (23).
- Faunal remains were sifted in 1/8-inch screen sieves (23).
- Identification and extrapolation of minimum number of sea otter and seal remains per stratum were originally made by J. S. Aigner, University of Connecticut, Storrs.
- The paucity of sea lion bones in 49 Rat 31 is surprising in view of the abundant sea lion remains reported from middens in the eastern Aleutian Islands. Presently, there are relatively few sea lions at Amchitka despite the fact that they have not been exploited for years, and it may simply be that there never were many sea lions at Amchitka for Aleuts to harvest.
- W. Jochelson, *History, Ethnology and Anthropology of the Aleut* (Publ. 432, Carnegie Institution of Washington, Washington, D.C., 1933).
- This assumption is supported by evidence in (23, pp. 36-37) showing that the vertical distribution of strata is roughly uniform horizontally and in consistent temporal sequence through the profile of midden 49 Rat 31. Several minor strata are horizontally discontinuous, hence the omission of strata F, G, K, and L from Fig. 3, and D, F, and G from Fig. 5.
- K. W. Kenyon, *The Sea Otter in the Eastern Pacific Ocean* (Government Printing Office, Washington, D.C., 1969).
- The hunting technology of Aleuts under enslavement by Russian fur traders remained unchanged from aboriginal methods, except that large ships were used to transport Aleuts to the most favorable hunting grounds [W. R. Hunt, *Arctic Passage—The Turbulent History of the Land and People of the Bering Sea, 1697-1975* (Scribner, New York, 1975)].
- Sea otters inhabited Attu about 1965. The population now appears to be well established on the northeast end of the island and is highly productive. During summer 1976 we saw 344 sea otters in the course of surveys, 33 percent of which were pups still associated with females.
- Data from samples collected at only the 0 to 3-m depth during summer 1976 are presented here because this depth range probably represents the area—the littoral bench and sublittoral fringe—from which aboriginal Aleuts gathered sea urchins. Some variation in the size frequency distribution of sea urchins is related to such factors as exposure and depth; however, this variation is small compared with the magnitude of the difference depicted between Casco Point and Pisa Point in Fig. 4, which are generally representative of those two areas. Sea urchins about equal in size to those we observed at Shemya and Attu were collected from 90- to 100-m depth at Amchitka in a bottom trawl by the M.V. Commander (University of Washington charter research vessel). There is no evidence, however, to suggest that Aleuts harvested sea urchins from these depths.
- The sea otter population at Amchitka Island currently is near carrying capacity and was recently estimated to contain more than 6000 animals (11, 49).
- Otters and large sea urchins could coexist in a more intimate spatial association if there were refuges, such as substrate crevices, in which urchins could escape predation by otters (9). However, the rocky sublittoral substrate of the western Aleutian Islands is essentially flat or of broad relief in all areas that we have examined. This substrate is covered by a smooth, continuously flat pavement of encrusting coralline algae (*Clathromorphum* spp.). Apparently the only refuge sea urchins have from predation by sea otters is in deep (> 100 m) offshore water beyond the otter's effective diving depth.
- Besides the Aleut preclusion of sea otters, three alternative hypotheses, stated below, might be advanced to explain the patterns of faunal distribution through the midden strata that are seen in Fig. 3. Although each of these may be to some extent true, we have rejected them as principal explanations for the reasons stated with the hypotheses:
 - 1) Fluctuations in faunal abundance through the midden reflect cultural changes by Aleuts. Perhaps the strongest support for this hypothesis lies in the second peak in otter abundance (strata C and B, Fig. 3). Although the Aleut culture certainly must have changed during the 2500 years that they occupied this Amchitka Island midden, we reject this as an alternative to the otter preclusion hypothesis on the basis of sea urchin size class distributions shown in Fig. 4. If the cultural change hypothesis is correct, it would predict (as the result of sea otters being abundant in the community) smaller sized sea urchins than we observed through the midden strata.
 - 2) Fluctuations in faunal abundance through the middens reflect natural changes in the community. We rejected this hypothesis for two reasons. There is no evidence that sea otter populations fluctuate greatly under natural circumstances. Even if otters did fluctuate in abundance from time to time, it is difficult to believe that the population would have declined to such low numbers and remained depressed for nearly 2500 years as the data in Fig. 4 would predict under this hypothesis.
 - 3) Aboriginal Aleuts overexploited otters but replaced the ecological role of otters as keystone predators in the nearshore community. This hypothesis is rejected based on the sea urchin size frequency distributions in Fig. 4. If Aleuts replaced the otters' ecological role, we would predict an absence of larger size frequency distributions of sea urchins through the midden strata than we found.
- This interpretation assumes that fishing was not restricted to those areas from which sea otters were eliminated. If fishing activities were as widespread as marine mammal hunting, then the ecological model presented in this article predicts that access to sea otters is positively correlated with access to nearshore fish.
- The notable exception is the surprising absence of readily identifiable head bones from Pacific halibut. Some of the numerous vertebrae, however, may have belonged to this species. The literature documents this fish as a major food source of the Aleut in historic times (21, 29). This suggests that either (i) the halibut was harvested in prehistoric periods but was not treated by the Aleut in the same manner as other fish, or (ii) halibut were not available or sought during this era. More extensive dissection of the midden stratigraphy and more thorough examination of the fish faunal remains perhaps would

- serve to determine which explanation is true.
40. There are presently eight species of rockfish (*Sebastes* spp. and *Sebastolobus* spp.) which have been reported from the Aleutian Islands, only two of which (*Sebastes ciliatus* Tilesius and *S. polyspinus*) are abundant nearshore. *Sebastes ciliatus*, by its prevalence and higher abundance in today's communities (18), is probably the species occurring in the midden remains.
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48. Nearshore community structure at Adak Island in the Andreanof Islands is similar to that at Amchitka Island in many respects (12, 13). Sea otters are near carrying capacity at Adak (K. B. Schneider, personal communication).
49. J. A. Estes, in *Environment of Amchitka Island, Alaska*, M. L. Merritt and R. G. Fuller, Eds. (TID-26712, Energy Research and Development Administration, Oak Ridge, Tenn., 1977), p. 511.
50. The black oyster catcher (*Haematopus bachmani*), which also preys on limpets, is common in the Rat Islands but absent from the Near Islands. The presence of oyster catchers in the Rat Islands complements the effect of sea otter predation on limpets to some unknown extent.
51. C. A. Simenstad, unpublished data.
52. K. W. Kenyon and J. G. King, "Aerial survey of sea otters, other marine mammals and birds, Alaska Peninsula and Aleutian Islands, 19 April to 9 May 1965," Bureau of Sport Fisheries and Wildlife Report, on file at the Fish and Wildlife Service, Department of Interior, Anchorage (1965); J. A. Estes, unpublished data. Population estimates of seals are uncertain because seals are readily observable only when hauled out, and their hauling out behavior is poorly understood.
53. We thank R. Desautels for access to unpublished data and specimen material from 49 Rat 31; E. J. Dixon and the University of Alaska museum for providing additional material from 49 Rat 31; and R. Burgner, P. Dayton, D. Eggers, C. Fowler, C. Harris, P. Martin, R. Nakatani, R. Paine, J. Palmisano, and C. E. Ray for criticizing earlier drafts of the manuscript. J. McMahon and S. Nancy Steinfert assisted with laboratory analysis. The Aleutian Islands National Wildlife Refuge, and particularly the R.V. *Aleutian Tern*, provided essential logistic support on Attu during the 1976 field season. This work was supported as a research project of the National Fish and Wildlife Laboratory and by U.S. Fish and Wildlife Service, contract 14-16-0008-2043, to the University of Washington. Contribution No. 482, College of Fisheries, University of Washington, Seattle 98195.

NEWS AND COMMENT

Guillemin and Schally: The Three-Lap Race to Stockholm

The discovery made by Guillemin's team on the eve of the January 1969 conference in Tucson was a small step forward in one sense, a major advance in another. After processing some 270,000 sheep hypothalami they had obtained a 1-milligram sample of thyrotropin-releasing factor (TRF), the hormone with which the brain directs the pituitary's control of the thyroid gland. Their sample was pure enough to allow two conclusions to be drawn. First, the sheep TRF molecule consisted of three amino acids, glutamate, histidine, and proline—the same trio that Schally had found in 1966 in his preparation of pig TRF.

Schally had had chemists at the pharmaceutical house of Merck Sharp & Dohme synthesize the six possible combinations in which the three amino acids could be arranged. (He declined to share the samples with Guillemin on the grounds, says Guillemin, that "the FDA did not allow such transfers across state lines.") But all six tripeptides were biologically inert. Schally had therefore concluded that the biologically active part of the hormone must reside in the other two thirds of the molecule, with which he could make no headway.

The second conclusion which Guillemin was able to draw was that the other two thirds didn't exist—it was just an impurity, the three amino acids being essentially the whole of the molecule.

But now came a hard decision. The

three amino acids were evidently not joined together in any simple way or Schally would have solved the structure with one of his synthetic tripeptides in 1966. If the new composition were announced at the Tucson conference, the prize of deciphering the structure would be up for grabs by any chemist in the world, with the Guillemin team having only a 3-week start.

A Photo Finish Race for TRF

Guillemin took the gamble and announced the composition. In the event, his start was more than abolished. Schally, who had temporarily abandoned the TRF problem, instantly perceived how close his rival was to the coup of being first with a chemical structure for a brain hormone. At the conference site he joined forces with an eminent structural chemist, Karl Folkers of the University of Texas at Austin, and arranged for the synthetic tripeptides to be transferred—across several state boundaries—to Folkers' laboratory. Guillemin, also in a call made from the conference, asked Hoffman-La Roche to synthesize the six tripeptides which Schally would not share.

From January through the fall of 1969 there ensued a furious race to solve the structure of TRF. The finish was so close and confused that to this day both teams claim priority, although on the Schally side with some internal difference of em-

phasis. Schally seems content to concede a draw, having written that the credit for solving the TRF project "had to be shared with Burgus and Guillemin, who elucidated the structure of ovine TRH* about the same time." Folkers, on the other hand, says flatly that "We were working totally independently of Guillemin and his team and we got it before they did."

The TRF molecule did not respond to

This is the second of three articles on the history of the pursuit of the brain's hormones by Roger Guillemin and Andrew Schally. Last week's article described how the two scientists had spent 7 fruitless years in search of the putative hormone known as CRF and a further 6 years in quest of TRF. To decide whether to continue supporting research in the field, the National Institutes of Health convened a conference in Tucson, Arizona, in January 1969. Three weeks before the conference began, averting an otherwise almost certain cutoff of funds, Guillemin obtained a result of critical significance.

the established chemical tests for identifying the ends of peptides, so evidently nature had blocked the ends in some

*The two teams naturally have different nomenclatures for the hypothalamic hormones or factors. Schally now calls them hormones, which indeed they are; Guillemin prefers the term factor to distinguish them from all the other hormones. The term factor was first used by Saffran and Schally in the name CRF. There are different versions as to who coined the term. In their respective contributions to *Pioneers in Endocrinology*, vol. 2, a forthcoming volume of memoirs edited by Joseph Meites, Saffran says that "we" coined the word CRF, Schally that "I" did, and Guillemin that credit belongs to R. A. Cleghorn, another member of their department.

Aleuts, Sea Otters, and Alternate Stable-State Communities

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

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