Sea Mammals: Resources and Population

*Carl E. Abegglen**
U. S. Fish and Wildlife Service, Division of Wildlife Research, Anchorage, Alaska

The marine mammal resources near Amchitka Island consist of sea otters, harbor seals, and Steller sea lions as permanent residents, northern fur seals that migrate through Aleutian passes, and whales and porpoises in the surrounding seas. Archaeological and historic data on animal populations indicate that the species present then were the same as those present today and demonstrate the continued importance that sea mammals have played in the island's history. Sea otter observations and surveys made from 1935 to 1974 document the recovery of this species from near extinction at the start of the twentieth century. Conservation measures, national and international, have been many, some even having been started in Russian times. The crucial and finally successful ones are the Fur Seal Treaty of 1911 and the Executive Order of 1913, which established what is now known as the Aleutian Islands National Wildlife Refuge. The marine mammal populations (whales excluded) around Amchitka and in the western Aleutian Islands are in good condition.

ARCHAEOLOGICAL INDICATIONS OF SEA MAMMALS

The prehistoric people of Amchitka, in common with the historic Aleuts, had a maritime economy and were dependent on the sea for the bulk of their existence. These people also applied their skills in ocean fishing to marine mammal hunting. They were expert seamen and traveled in groups or family units from one island to another without difficulty. The practices required for existence on Amchitka and in the Aleutians in general changed very little during several millenia of human occupation.

From their 1971 dig on Amchitka, Cook, Dixon, and Holmes (1972) report the recovery of numerous sea mammal bones, which were apparently used as awls, casting lance heads, picks, and for decoration. Among these were eight notched or grooved teeth, including four harbor seal canines, one sea lion postcanine tooth, and three harbor seal incisors. Desautels et al. (1970) recovered 25 grooved teeth from Amchitka excavations in 1969. One of these was perforated as well as grooved. Clark (1968, cited in Cook et al., 1972) did not report finding grooved sea mammal teeth on Kodiak; however, Spaulding (1962, cited in Cook et al., 1972) mentioned sea lion teeth that were grooved on one end from Agattu. Cook et al. suggest that these grooved teeth were used for personal decoration—as pendants for nose ornaments.

Desautels et al. unearthed fireplaces associated with large cut whale bones. The close association suggested to them that these may have been used as supporting beams for structures. None of these bones were found in an upright position.

The animal remains from the six sites dug by Desautels et al. in 1969 consisted of sea mammal, fish, and bird bones as well as shells of marine invertebrates. Site RAT 31 yielded more than 11,000 mammal bones. Except for some human elements, the remainder were from whales, pinnipeds, and sea otters. The few whale bones represented both large and small cetaceans. Species identified included sea otters, harbor seals, Steller sea lions, and a few northern fur seals. About 50% of the sea otter bones were from juveniles. From the material collected, it appears that whole sea otters were brought back to the village sites but pinnipeds were butchered elsewhere. Percentages of sea mammals found in site RAT 31 generally reflect historical records concerning Aleut food preferences. Desautels et al. report Hrdlička (1945) as having said that sea otters, which were available near the shore, were killed in large numbers and that the Aleuts also killed many young harbor seals. These statements are in general agreement with the numbers and species of the animal remains from site RAT 31. Far fewer sea lion bones were found compared with the number of

*Now retired, at Olympia, Washington.

sea otter and harbor seal bones. The small number of fur seal remains is consistent with that species being a migrant without established rookeries in the area. Desautels et al. found sea mammal bones and teeth made into harpoon and dart heads, fishhooks, wedges, flakers, awls, clubs, and ornaments.

EARLY HISTORY OF THE FUR TRADE

The history of the Aleutian Islands clearly emphasizes the importance of the sea otter. Elliott (1887, pp. 484-485) wrote:

> To the sea otter geographers owe their early knowledge of Russian—America; had it not been for the greed and covetousness excited in the minds of fur dealers by the beauty and costliness of its peltries which Altasov and his Tartars first secured, towards the close of the seventeenth century, on the Kamchatkan coast,—had it not been for this incentive the exciting, pushing, aggressive, indomitable search made by the Russian 'Promishlyneks' would never have been undertaken. Indeed, for that matter, much of the glory which old Titus [sic] Bering is enveloped with, as a discoverer, was not due to his love for geography or hydrography, but it was the direct stimulation of fur hunters for a rich return. They backed him; they fitted out his small, miserable vessels, which in light of the present hour, make his voyages fairly fabulous, when the rickety, 'ram-shackley' construction of his rough Amoor-built shallops is understood . . . .
>
> It was not, therefore, until the Russians opened up the trade, swiftly supplemented by the third voyage of Captain Cook and the aroused attention of the Hudson Bay Company, which speedily began to search the coasts of British Columbia and Oregon in those early days—it was not until this action was taken, toward the close of the seventeenth century and the beginning of the eighteenth, that the sea-otter became known, first to the courts and then to the nobility of the civilized world . . . .
>
> During the first few years after discovery the numbers of sea-otters taken all along the Aleutian chain, and down along the whole northwest coast as far as the southern boundary of Oregon, were very great, and, compared with what are now captured, seem perfectly fabulous. For instance, we are told when the Pribylov Islands were first discovered, two sailors, Lukannov and Keikov, killed at St. Paul's Island during the first year's occupation, 5,000, but the next year they secured less than 1,000 and six years after not a single sea-otter reappeared, and none have been there since.
>
> When Shellikov's party first visited Cook's Inlet they secured 3,000; during the second year 2,000; in the third season only 800, and in the succeeding year they obtained 600, and finally, in 1812, less than 100, and since then not one-tenth of that number, although I am told, at the date of this writing, that during the past two years more than 500 sea otters annually have been taken on the coasts of Cook's Inlet . . . .

Eighteenth Century explorations throughout the North Pacific area opened up new regions to colonization and exploitation. Sea otters and other valuable fur-bearing animals served as the catalyst for this exploration. A Russian vessel is reported to have sailed to the Arctic Ocean from Kamchatka through the Bering Strait in 1648. In 1728 an expedition under Vitus Bering sailing northeasterly from Kamchatka discovered St. Lawrence Island and passed through the strait later named for him. Another Russian naval expedition sailed in 1733 but met with misfortune. There are no further accounts of explorations from 1733 to 1741 (Golder, 1914).

A second expedition led by Bering in 1741 made landings along the northwest coast of North America and in the Shumagin Islands. Several of the Aleutian Islands were seen during this voyage. Bering's ship was finally shipwrecked on one of the Commander Islands, and Bering died on the island that now bears his name. The return of his lieutenant, Chirikov, from the same area was of particular importance in turning attention to those shores. Chirikov's crew brought back many valuable furs, including the skins of 900 sea otters. Rumors of the richness of this newly discovered country kindled a spirit of enterprise in the merchants of Siberia. Tales of Bering's companions and crew, when they returned in 1741, did even more to increase the desire of merchants to profit from trade in sea otter skins, and, during the remaining years of the eighteenth century, merchants and adventurers made numerous voyages eastward from Russia.

The first fur hunter to undertake the daring sea voyage in search of sea otters was Emilian Basov, a Cossack sergeant from Kamchatka. He made four voyages but only reached Bering and Copper Islands. Later trips by others led to the discovery of new islands and to surveys of the Alaska mainland.

In 1763 Shelikhov, a prominent Siberian merchant, led an expedition to Bering Island, Unalaska, and Kodiak. He spent 4 years on these islands and established his own trading company, which later formed the nucleus of the Russian—American Company. In 1790 Shelikhov employed Alexander Andreevich Baranof to organize and manage the affairs of his company. Baranof used his talents to develop and increase hunting and trading throughout the Aleutian Islands and mainland Alaska.

Foreign ships also visited these shores. Berkh (1823, translated in Ricks, 1963, p. 38) says that Shelikhov complained in 1787 to Governor Jacobi about foreigners on American shores belonging to Russia:

> In August of last year during my sojourn in Petropavlovsk Harbor, I learned from William Peters of the [British East] Indian Company that a ship of their

company had visited our boundaries in Latitude 30° on the Northwestern Coast of America in 1785 for trading purposes. I do not know whether or not they had permission from the Russian government. They themselves stated that they bartered more than 800 sea otters and a considerable number of fur-bearing land animals in a short time. It follows from the above stated facts that the great profits which should belong to the Russian citizen are being usurped by people of other nations who do not own the adjoining land and have no rights in this sea.

In 1799 the Russian–American Company was granted a monopoly on hunting in the Aleutian Islands area. In 1811 the Russians, under Baranof, established themselves on the California coast. Baranof was relieved of his post as manager of the North American colonies in 1818. After that Russia's fortunes in the New World began to decline. Sickness, mismanagement, and competition from the Hudson Bay Company were primary factors in the decreasing income derived from the fur trade.

In 1864 delegates of the Russian government began to negotiate with the United States for the sale of Russia's possessions in North America. Congress approved the treaty, transferring the territory in 1867, and the next year appropriated the $7,200,000, which was Russia's price for Alaska.

When the Russians reached the Aleutians in the 1740s, practically every island was inhabited. Agattu was reported to have had 31 villages and Unalaska 24, with numerous settlements on other large islands. By 1831 there were only 10 villages on Unalaska. Only 15 of the other islands were inhabited, and the total population is estimated to have been less than 2000.

Aleut villages were on the seacoast; the interiors of the islands were completely unoccupied and seldom visited. No people were more dependent on the sea than the Aleuts. The land provided only a few of their needs—stones for knives and other implements, grass for weaving, and a few plants for food. Everything else came from the sea. For most of their food they depended on sea mammals, fish, sea birds, sea urchins, and mollusks. Their clothing was made from the skins of the sea mammals and birds and their boats from driftwood and skin. Implements, weapons, and household utensils were made of bone or driftwood, and material for their houses was driftwood and whale bones (McCartney, Chap. 5, this volume).

The Aleuts were skillful sea hunters. In their single- or double-hatched bidarkas (light skin boats), they made long coastal voyages and often ventured far from shore in pursuit of sea otters, seals, sea lions, and even whales. Their weapons were light darts and spears cast with a throwing board. Sea otter hunting was a cooperative activity requiring from 4 to 20 bidarkas, each carrying one or two hunters. The boats would start out in a wide semicircle, keeping 50 to 100 yards apart. The sea otter comes to the surface to breathe at least every 5 min; his head sometimes remains visible only a few seconds. When an otter came up within casting distance of one of the hunters, he would throw his dart. The otter was not likely to be killed outright by the small bone point of the dart, but its movements were impeded by the dart, and it was soon dispatched (Veniaminov, 1840, Vol. II, pp. 342-344).

Whales were hunted in an entirely different manner. Instead of being surrounded, they were killed with poison lances. Hunters approached whales carefully from the rear, cast their spears, and rapidly retreated. The lance head with its poison blade became detached from the shaft and remained in the whale's flesh, causing the whale to die after about 3 days. If the hunter was fortunate, the whale would drift ashore (Veniaminov, 1840, Vol. II, pp. 132-134).

SEA MAMMAL RESOURCES

Sea Otter (*Enhydra lutris*)

The only immediate government action after the cession of Alaska to the United States in 1867 was to establish a contract with the Alaska Commercial Company for the regulated exploitation of fur seals. It was only 17 years later that a local government was established in Alaska, and there was essentially no regulation of fur hunting and trading in the Aleutian Islands. As a result, by the time of the Fur Seal Treaty of 1911, it seemed that the sea otter population had been exterminated and the fur seal population was in danger of extermination. The treaty devotes only 1 section out of 27 to the sea otter; all the rest, including the very title of the treaty, are concerned with fur seals.

The beginnings of contemporary sea otter studies by Americans were informal. There were intermittent almost casual published references to sea otters between the 1911 treaty and 1935; these were primarily notations that a few sea otter skins had been confiscated or surrendered and subsequently sold at public auction.

Surveys. *1935.* The persistence of reports of sea otter observations sent to the Bureau of Fisheries ultimately had its effect. Three memoranda in the files of the Anchorage office of the U. S. Fish and Wildlife Service (FWS) are worthy of mention. The first was prepared June 21, 1935, by Lieutenant Howard B. Hutchinson, U. S. Navy,

for the Commander, Aleutian Islands Survey Expedition. Entitled "A Report on the Existence of Sea Otter in the Rat Islands," it says:

> 1. The Biological Survey of the Department of the Interior [Agriculture] requested the Navy Department in 1932 to have the Alaskan Survey Expedition of that year investigate and verify the existence of the sea otter *(Enhydra lutris)* which was reported to exist in the western islands of the Aleutian group. The animal was not identified in that year by any member of the expedition, either at Attu or Kiska, although the chief of the Attu Natives assured the commander of the expedition that there were a few at Agattu, which would soon be gone because the Japanese came frequently to take them. 2. On May 1933 [1935?] it was determined definitely that the sea otter does exist in the Rat Island group. On that date, the reporting officer [Hutchinson] while ashore on the northwestern end of Amchitka Island at the survey station, BIRD, saw eight (8) adult animals and three (3) of the young or pups moving about in the kelp beds which surround the station. With the aid of good binoculars, two animals were watched at play in the clear water under the sheer bluff of the station. From this favorable point of vantage it was seen that the animals were sea otter and not seals nor sea lion. There is no doubt that the animal in question is a sea otter.

The memorandum continues with numbers of animals seen and finally an estimate that the sea otter population around Amchitka numbers 1000 adults and 500 pups.

The second memorandum was prepared by Ward T. Bower, Chief, Division of Alaska Fisheries, for a Mr. Jackson on Aug. 19, 1935. It told of a recent telegram from the Commander of the Bering Sea Patrol Force of the Coast Guard and gave an estimate of 1000 to 6000 sea otters around Amchitka Island and indicated that they were spreading to other nearby islands. Bower emphasized the necessity of protective measures so that this gain and reestablishment of sea otters could be maintained and expanded. Bower suggested a conference to be attended by representatives of the Coast Guard, the Navy, the Bureau of Biological Survey, and the Coast and Geodetic Survey to meet during the winter to determine the best means of conserving and protecting the Aleutian Islands' sea otter herd and to formulate plans that could be put into effect for the next season.

The third memorandum was prepared by Ward T. Bower and sent to Commissioner Bell of the Bureau of Fisheries. Bower's memorandum says in part:

> This morning Captain B. L. Canaga, Room 2058, Navy Department, Telephone Branch 214, called at this office and said that a confidential report had been received from an officer attached to the Navy Expedition to the Aleutian Islands this summer in regard to sea otters in that region. Captain Canaga permitted me to read the report and then took it away with him. He said it was planned in due course to send a copy to this Bureau for appropriate consideration. As I remember, the report showed that about 600 sea otters were observed at Amchitka Island this summer. Captain Canaga said that another report, a copy of which he also had planned to have sent to this office, referred to about 1,000 sea otters at another place. Captain Canaga expressed apprehension lest Japanese might capture numbers of these valuable animals for their pelts. He suggested need of adequate protective measures. I suggested to Captain Canaga that the Navy Department might be able to cooperate in this work in connection with expeditions to the region. I further suggested that as a feature of such cooperative effort, the Navy Department might consider the establishment of a radio station in the region and thus, in addition to the Bureau of Fisheries employees, there would be the radio station personnel.

1936. O. J. Murie and C. S. Williams were assigned to make an inventory of resources in the Aleutian Islands Wildlife Reservation, as it was then called. This inventory was initiated primarily because of the government's responsibilities relating to the blue fox industry in the Aleutians and not from concern for sea otters. Murie (1959, p. 285) says:

> In spite of occasional poaching, in 1936 we found substantial sea otter populations in several places throughout the Aleutian chain, and we made a conservative estimate of 2,000. Most heartening of all, they were extending their range, not only in the Aleutians, but also along the Alaska Peninsula. However on our last visit to Sanak Islands, the sea otters had not reappeared, although at one time this area was one of the best sea otter hunting territories (since our visit, five sea otters have been seen).

The data obtained in 1936 indicated that there were still a few otters remaining about isolated islands, and infrequently they visited bays of the North Pacific. The most southeasterly point at which they were reported was Montague Island in Prince William Sound. To the east, trappers and local residents said sea otters were present near Shuyak Island and Latax Rocks, just north of Afognak Island in the Kodiak group. From Sutwik Island near the lane of Alaskan shipping, they were also reported. Eleven sea otters were seen off Simeonof Island in the Shumagins. The rocky Sanak group was reported to harbor a few, whereas information obtained from Mr. Homer Jewell, Alaskan Game Warden, indicated that they occurred on the Alaskan Gulf side of the Alaskan peninsula at Aiugnak columns, the southeast portion of Cape Kumlik, and at Kujulik Bay.

In the Aleutian Islands proper, natives said that otters occurred occasionally about the following islands: Seguam, Little Tanaga, Kanaga, Kiska, Semichi, Agattu, and Attu. The survey party visited all these islands except Semichi and Agattu but observed no sea otters. However, the party did

encounter the animals at Umak, Ulak, Kavalga, Ogliuga, Amchitka, and Tanaga Islands.

At most of these islands, only a few sea otters were seen, the greatest number at any one island being 48. Nowhere were they abundant, 10 per mile representing the greatest concentration observed. The islands of Amchitka, Ogliuga, and Tanaga appeared to be the most productive; a most liberal estimate of the number of otters occurring about the three being 700. The small concentrations near other islands might raise the total number of sea otters in North America to 2000. To add a note of contrast, in the early 1800s, one island, Unalaska, produced 1000 of the animals annually.

In the 1936 Alaska Fisheries and Fur Seal Industries Report, Bower (1937) noted that five Coast Guard cutters were assigned to patrol the North Pacific Ocean and Bering Sea for the protection of fur seals and sea otters. Lieutenant Commander S. P. Swicegood, U. S. Coast Guard, commanding officer of the *Chelan*, reported a count of 814 sea otters on Amchitka (Swicegood, 1936).

1937. Comments on sea otters this year by Bower (1938) were:

> A substation on one of the western Aleutian Islands was established for the expansion of sea otter investigations and patrol . . . . Two trips [by the *Penguin*] were made to the western Aleutians—one in July and one in September—in connection with the sea otter patrol.

In this year Loy and Friden (1937) counted 1321 otters on Amchitka, almost all of them on the Pacific coast.

1938. Substantially more information appeared for this year in the report by Bower (1940, p. 161). A two-paragraph description with the heading "Substation for sea-otter patrol" reads:

> The Bureau's work for the furtherance of sea-otter investigations and patrol was continued. At the substation established on Amchitka Island in 1937, 4 additional overnight cabins, 8 X 10 feet, were built on the south side of the Island at 8-mile intervals. At the camp site in Constantine Harbor, a 10 X 16-foot powerhouse was constructed and a 5-horsepower engine was installed for use as a power plant. Two radio masts were erected on concrete bases, and radio antennae were strung leading to a receiving set and a transmitter. Buildings that had been erected in the previous year were given a coat of paint.
>
> The number of sea otters counted in the vicinity of Amchitka Island in 1938 was considerably less than the estimate for the previous year. Whether the difference was due to an error in the count or to a change in the habits and distribution of the animals was not known. It is anticipated that further light will be thrown upon this problem by investigations in succeeding years.

A partial count of sea otters around Amchitka numbered 1321 animals; this was extrapolated to arrive at an estimate of 1761 animals for the entire island.

1939. Reference to the Amchitka sea otter investigation was given coverage again in the 1939 Alaska Fisheries and Fur Seal Industries Report (Bower, 1941, p. 159) with the following statement: "The substation which was established on Amchitka Island in 1937 for sea-otter investigations and patrol, and which had been in operation each summer since that time was maintained on a year-round basis during 1939-40." The sea otter count this year was 1355 animals; the total-population estimate, including pups, was 1870 (Loy, 1940). Lensink (1962) also reports an earlier count that year of 1030.

1940. J. B. Mangan and Grant Ritter, sea otter wardens on Amchitka for the Bureau of Fisheries, estimated the Amchitka sea otter population to be 1650, 69 being pups, from a census made in July and August (U. S. Fish and Wildlife Service, 1940, unpublished report).

1943. The first known account of an aerial survey for sea otters is recorded in a letter dated September 28 from Frank L. Beals, Refuge Manager, Aleutian Islands National Wildlife Refuge, Kodiak, to Frank Dufresne, Regional Director, Fish and Wildlife Service, Juneau (U. S. Fish and Wildlife Service, 1943, unpublished report). Accompanying the letter is an outline chart of Amchitka and Rat Islands; numbers of otters seen are noted on the chart at the point of observation. The sea otter count on June 24 for Amchitka was 3417.

Mr. Beals was very active in the Aleutians before 1942 and made conspicuous efforts to continue this activity during the period of military operations. His letter is reproduced in its entirety:

> The following report is made of an attempt to estimate the sea otter population of Amchitka and Rat Islands, Alaska, through the use of aeroplanes.
>
> While engaged in regular patrol of the Aleutian Islands National Wildlife Refuge it became my good fortune to make the acquaintance of a Squadron of U. S. Navy Observation-Scout Pilots, then stationed on Amchitka Island. At their suggestion and with the permission and sanction of the Commander of the U. S. Army Force and the Captain of U. S. Navy Facilities for Amchitka Island I was taken on flights around Amchitka, Rat, Segula, and Little Sitkin Islands for the purpose of observing sea otter and estimating their number and general distribution.
>
> U. S. Navy Pilot G. T. Joynt, a former biology student already actively interested in sea otter, had on previous occasions observed their general location in this area. To Mr. Joynt belongs most of the credit for what success we had in checking their numbers in the

Amchitka–Rat Island area. The other pilots were willing and helpful with their time and personal observations but it was the old biology student who smelled them out and maneuvered his plane in position for effective observation.

The type of plane used was ideally suited for this work as it throttled down to fly safely and with stability at close to one hundred and thirty miles per hour. Good visibility from an open cockpit can be had if desired by simply cranking back the protective cowling and banking slightly when over the object to be observed.

Our method of procedure was to fly around the island a number of times to become familiar with landmarks and principal concentrations. Then over the plane's interphones to communicate our opinions and reach an agreement on each pod of sea otter observed and plot it on an outline chart of the island. An average size pod was selected and its actual number of animals counted as closely and accurately as possible. This was then used as a yardstick in estimating the number of otter in each of the other groups encountered.

The results of our survey are not offered as anything more than an approximation. I believe it was always our tendency to see and estimate more animals than actually were in the groups. Because of the sea otters peculiar and characteristic position in the water, that is of floating on its back with the two extremities of its body prominently displayed, head and forefeet at one end, hind flippers and tail at the other end and its midsection mostly submerged and hidden from view, one is inclined to see two animals where there is really only one and come out on the plus side in the count. Offsetting this somewhat is the fact that we did not count or include singles and pairs in the survey and they represent an appreciable number of otter when the entire island is considered.

The majority of groups observed were in the offshore margin of the kelp fringe that rings the islands. Singles and pairs, etc., were noted to keep closer inshore and often right in the middle of thick masses of kelp. Only rarely were sea otter observed in open water more than two miles from shore or half a mile from protective kelp patches. Mr. Joynt and his friends report that it is rare indeed that they have seen an otter as far as five miles offshore but that they have observed an occasional single animal idling along on its back as far as 10 miles from the nearest land.

I personally experienced difficulty in picking out young sea otter riding on their mothers midsection but Pilot Joynt, whose eyes are more alert and better trained, claims to have seen many of the little fellows. He thought as many as one juvenile to each ten or twelve adults. I would not want to offer an estimate of young sea otter around Amchitka and Rat Islands but judging from personal observations made from shore through high power field glasses, they do not appear to be less than I remember having observed on past visits to Amchitka.

It is interesting to note that the sea otters reaction to aeroplanes is entirely negative. They seem to accept the plane as something natural and quite ordinary. On several occasions we came down on them with engine roaring and approached as close as fifty feet above them. They only twitched their whiskers and went right on with their loafing. One or two of them might submerge but not with any display of great fright or concern. It seems to me that the plane is an ideal tool for making an accurate check on the distribution and approximate number of sea otter in the Aleutians.

Personal observations from the air were made in the vicinity of Amchitka, Rat, Segula, Little Sitkin, Attu (Massacre and southeastern part only), and Semidi [Semichi] island groups. The only successful flights were at Amchitka and Rat Islands. Poor visibility due to fog plus limited time for choosing good flying weather resulted in nothing of value being learned regarding sea otter about the other islands. Two trips were made from Amchitka to Davidoff and Khvostoff islands but each time fog whipped in and forced a hasty about face and hurried trip home. The planes were equipped with wheels and it was not considered prudent to tempt fate too far.

These same pilots have made many scouting flights around Semisopochnoi Island and report that they have never seen sea otter in that vicinity. Scattered individuals and small groups have been observed in the kelp beds around Davidoff and Khvostoff islands which lie between Segula and Little Sitkin. None of the Observation-Scout pilots at Attu island were familiar with sea otter or know where or how to look for them and say they have not observed the animals as I described them. A civilian boat captain claimed to know what he was talking about and maintains that they are often seen in the kelp off Massacre Bay and around the Semidi [Semichi] Island groups. In an attempt to check up on sea otter in the Semidi [Semichi] groups I encountered difficulty with General Copeland who was in command of the base there and was 'evacuated;' the general does not like civilians, particularly 'D—— Game Wardens.' One of the pilots from Amchitka reports having seen 'a thousand or more' in groups of islands around Ogliula and Skagul. A civilian boat captain and several different Army officers told of having seen them in the vicinity of Kagalaska strait and Adak island but I talked with Walt Kamsack, a civilian guide for the Alaska Defense command who has trapped on Adak for the past several years and has patroled Adak island and adjoining waters for the Army and Navy since its occupation by our armed forces, and in his opinion there are no more otter there than in past years before military activity in the western Aleutians.

1945. A partial count of 365 animals was made from a limited number of checkpoints on Amchitka (U. S. Fish and Wildlife Service, 1953, unpublished report).

1949. Aerial surveys of inshore waters of Amchitka and Rat Islands showed 1321 sea otters around the two islands (Jones, 1951). Lensink (1962) and Kenyon (1969) report that 1087 of these were around Amchitka and the remaining 234 around Rat Island.

1953. The Quarterly Narrative Report for the period September–December 1953, Aleutian Islands National Wildlife Refuge, is quoted (U. S. Fish and Wildlife Service, 1953, unpublished report):

> In 1873 (39 [38?] years before the sea otter season was closed in 1911) the Atka Natives took 129 sea otter on their hunting grounds (Buldir Island on the

west to Islands of Four Mts. on the east). The average annual take from 1873 to 1896 was 96 animals. Today, (1953), 82 [80?] years later we salvaged 50 pelts of sea otter from the island of Amchitka alone.

1954. A sea otter survey was conducted by Lensink on April 26 with the following results: "Observations were made from a Navy UF (Albatross) between 1130 and 1500 hours on April 26. Seas were flat, sky partly overcast to clear but visibility was excellent. Transects covered the Delarof Islands, the Andreanof Islands, and Gareloi Island." He reported 320 animals in the Delarof Islands, none at Gareloi, and 684 in the Andreanof Islands for a total of about 1000. "General impressions were that Tanaga and Kanaga have otter populations fully as dense as that of Amchitka. Otter were found on all of the Delarofs, indicating a good population although only one large pod was seen, that being on Amatignak. Characteristics of otter distribution on Amchitka if applied to animals on the Delarofs indicate far more otter are present than were actually counted" (U. S. Fish and Wildlife Service, 1954, unpublished report).

1956. Between May 10 and August 25, Lensink (1962) completed surveys on about half the Amchitka shoreline with binoculars and a telescope. In the first survey 1604 sea otters were counted, and in the second 2568, including 384 pups. Spot-checks on unsurveyed parts of the island indicated that the survey figures could be extrapolated to the entire island, indicating (from the second count) a total population of 5637 animals.

1959. Kenyon and Spencer (1960) made aerial counts of sea otters in the western Aleutian Islands in May and counted 9507 animals. The Amchitka sea otter count on May 19 was 1560.

1962. On March 29 and April 5–10, Kenyon (1969) and others (U. S. Fish and Wildlife Service, 1962, unpublished report) made an aerial survey of sea otters from Kiska Island to Amak Island in the Aleutian Islands, in the Sanak Islands, Sandman Reefs, and Shumagin Islands, and in areas along the south coast of the Alaska peninsula. A total of 10,364 sea otters was observed. Observation conditions were poor in the Rat and Andreanof Islands, but observation conditions east of the Andreanof Islands were generally excellent.

1965. An aerial survey of sea otters from Cold Bay to Attu Island was made during April and May. A total of 12,687 sea otters was counted. The count at Amchitka on May 2 was 1144 (Kenyon, 1969).

1968. From 1968 through 1974, helicopters were used for sea otter surveys on Amchitka Island, and the counts became so numerous that I have summarized them in Table 1.

On Nov. 7, 1967, a small conference was held in Columbus, Ohio, attended by representatives of the Bureau of Sport Fisheries and Wildlife, the Alaska Department of Fish and Game, the Battelle Columbus Laboratories, and the Atomic Energy Commission, to establish acceptable methods of assessing any immediate and long-range effects of underground nuclear tests on the Amchitka sea otter population. One of the conference's four recommendations was to conduct annual aerial surveys of sea otters around the island (Spencer, 1969). Later Spencer determined the following criteria to be "minimally acceptable for helicopter surveys:"

1. Wind velocity less than 15 to 17 knots, preferably westerly.
2. No heavy surf (frequently a residual condition from past storms, even when the present wind velocity is low).
3. Visibility of more than 5 miles.
4. Overcast skies to eliminate sun glare and reflection.
5. Minimum ceiling of 500 ft.
6. No rain.

With the use of these criteria, seven counts were made in August and September. The totals listed in Table 1 are the actual counts of otters seen without any correction for percentage seen. Two surveys were also made at Rat Island, one on September 24 yielded 431 sea otters and one on October 6 yielded 456 sea otters.

1969. A combination of aerial photography and visual observation from a helicopter was used to derive sea otter counts this year. Stephan (1971) reports a maximum count of 2354 otters on September 2. Later studies of the photographic record corrected these results, and the date of the highest survey yielded the three counts listed in Table 1.

1970. Surveys conducted after 1969 returned to visual observations made from a helicopter, following the basic criteria established in 1968. Five full counts and one partial count were made in September, as listed in Table 1 (U. S. Fish and Wildlife Service, 1970, unpublished report).

1971. In this year counts were made of the particular segment of coastline near the proposed Cannikin test; the results of this endeavor are reported by Estes (Chap. 21, this volume). Bad counting conditions allowed only one whole island count to be made, although several attempts were

Table 1—Summary of Amchitka Sea Otter Counts

Date		Method	Count	Observer	Comments
1935		Surface	1500	Hutchinson	Lensink says 1000
1936		Surface	814	Swicegood	Lensink says 804
1937		Surface	1321	Loy and Friden	
1938		Surface	1321	Loy and Friden	Extrapolated to 1761
1939		Surface	1030	Loy and Hewitt	
		Surface	1355	Loy	
1940		Surface	1650	Mangan and Ritter	Estimate
1943	6/24	Airplane	3417	Beals	Lensink says 3420
1945		Surface	365	Gray	Partial count
1949		Airplane	1087	Jones	
1956		Binoculars	1604	Lensink	Extrapolated to 3525
		Binoculars	2568	Lensink	Extrapolated to 5637
1959	5/19	Airplane	1560	Kenyon and Spencer	Extrapolated to 2080
1965	5/2	Airplane	1144	Kenyon and Spencer	Extrapolated to 1520
1968	8/27	Helicopter	2068	Sowl	
	9/16	Helicopter	2238	Spencer and Cater	
	9/17	Helicopter	1896	Spencer and Cater	
	9/18	Helicopter	1863	Spencer and Cater	
	9/20	Helicopter	2302	Spencer and Cater	
	9/21	Helicopter	1728	Cater	
	9/22	Helicopter	1624	Cater	
1969	9/9	Photo+helicopter	2066	Stephan and Mercier	
	9/16	Photo+helicopter	2113	Stephan and Mercier	
	9/23	Photo+helicopter	2395	Stephan and Mercier	
1970	9/3	Helicopter	1522	Cater	Partial count
	9/4	Helicopter	3402	Cater	
	9/5	Helicopter	3220	Cater	
	9/7	Helicopter	2119	Cater	
	9/8	Helicopter	3927	Cater	
	9/16	Helicopter	1648	Cater	Extrapolated to 3133
1971	10/2	Helicopter	3241	Cater	
1972	6/5	Helicopter	2564	Abegglen, Estes, and Schneider	
	8/23	Helicopter	3931	Abegglen and Estes	
	8/25	Helicopter	3524	Abegglen and Estes	
	9/11	Helicopter	4042	Abegglen and Estes	
	9/19	Helicopter	2230	Abegglen and Estes	
1974	5/26	Helicopter	1545	Abegglen and Schneider	
	5/29	Helicopter	3226	Abegglen and Schneider	

made. A survey on October 2 gave a count of 3241 sea otters (U. S. Fish and Wildlife Service, 1971, unpublished report).

1972. Surveys in 1972 were cooperative efforts. Representatives of the Bureau of Sport Fisheries and Wildlife, the University of Arizona Cooperative Wildlife Research Unit, and the Alaska Department of Fish and Game made surveys in May and June, and the former two in August and September. Five counts were made, as listed in Table 1. The September count of 4042 is the largest ever made at Amchitka Island.

1973. No counts were made this year because a helicopter was not available.

1974. During a return task force trip to Amchitka in May of this year, four helicopter surveys were made, two of which yielded whole island counts of sea otters (Kirkwood, 1975).

Population Status. Lensink (1962) and Kenyon (1969) have analyzed the population history of these islands and in particular of Amchitka where most of the population counts were made. Kenyon reports a population increase of about 10% per year up until 1945 and then a population crash to a third of its former peak. Kenyon relied principally on counts from boats and airplanes and concluded that there are now between 1500 and 2500 sea otters on Amchitka, exclusive of dependent young. Estes (Chap. 21, this volume), using more efficient methods of censusing, concludes that there are about 6400 sea otters on the island, but this is not to be construed as a real increase in numbers since Kenyon's work. Kenyon also concluded, as have others before and since, that the population is at the limit the habitat will support; that they migrate from island to island only under conditions of severe crowding; and

that, presumably because of depleted food resources, the Amchitka population consists of smaller animals than in less crowded areas.

Harvests. The best available analysis of the early sea otter productivity is by Lensink (1962), who said:

> It is impossible to reconstruct the complete history of maritime trade of the northwest coast and Aleutian Islands, but the records and approximation summarized below indicate that at least 600,000 sea otter skins were marketed during the period of Russian occupation and that the total number of sea otters that were pelted may have exceeded 800,000 animals.

Russian, 1742–1867 (Berkh, 1823; Petroff, 1884)	264,800
Foreign traders, 1785–1798 (Khlebnikov, 1835)	140,000
Americans, 1799–1803 (Sturgis, n.d.)	47,800
Landed in Canton, 1804–1818 (Roquefeuil, 1823)	129,900
Hudson's Bay Company, 1825–1857 (Douglas, n.d.)	5,400
Total	587,900

Bureau of Fisheries reports by Cobb (1906, 1907) and Marsh and Cobb (1908, 1909, 1910, 1911) provide a summary of the number of sea otters harvested in Alaskan waters between 1867 and 1911:

Years	Sea otters harvested
1868–1870	12,208
1871–1880	40,283
1881–1890	47,842
1891–1900	6,467
1901–1910	572
Total	107,372

The Fur Seal Treaty of 1911 caused this harvest to stop, except for poaching, from then until it was abrogated by Japan in 1941. When Alaska became a state in 1959, the statehood act provided that jurisdiction over game and furbearing animals, including the sea otter, should pass to the state. Soon state officials decided to harvest sea otter pelts. This phase of management of this resource began in 1962 and lasted until 1970, when it ended for a variety of political and economic reasons. The pelts taken in this harvest were sold at public auction, the first such taking place in Seattle on Jan. 30, 1968. According to Table 2, almost 2600 pelts were taken in these harvests. Additional notes on them follow.

1962. Between January 22 and February 13, 156 sea otters were harvested at Amchitka Island. This was the first sea otter harvest in 51 years and was conducted by the Alaska Department of Fish and Game with assistance from the U. S. Fish and Wildlife Service. An additional 24 pelts were collected on Amchitka between October 23 and November 3 (K. B. Schneider, Alaska Department of Fish and Game, personal communication).

1963. A harvest of 291 sea otters was made on Amchitka during the period from March 5 to April 12. An additional 20 were killed between July 31 and August 3 (K. B. Schneider, Alaska Department of Fish and Game, personal communication).

1967. The Alaska Department of Fish and Game harvested 300 sea otters at Adak and 205 at Amchitka.

1968. The Alaska Department of Fish and Game harvested 512 sea otters at Adak and Kanaga.

1970. This year the department harvested 955 sea otters in May: 205 from Amchitka, 144 from the Delarof Islands, and 606 from Tanaga.

1971. The Alaska Department of Fish and Game killed 93 sea otters on Amchitka for scientific studies. In Table 2 the "+" for 1971 refers to an unknown number killed by Cannikin.

Transplants. Following World War II, sea otter research continued efforts initiated in the mid-1930s. The natural reestablishment of sea otters in some areas was sufficiently great that concern was expressed by researchers over the carrying capacity of the habitat, particularly around Amchitka. This same concern was later expressed for the Prince William Sound area.

A method considered for reestablishing sea otter populations in areas where they had formerly lived was to physically transport the animals to these sites. One objective of the research program started in 1950 was to determine a suitable method of keeping sea otters in captivity and subsequently a feasible method for their transfer. Jones (1951) and Kenyon (1969) showed that sea otters could be maintained in captivity and could be transported without excessive mortality. Subsequent improvements in these techniques by the Alaska Department of Fish and Game have facilitated transplant activities, and now there is little mortality during actual transplants.

From 1955 until 1972, when the Marine Mammal Act of 1972 stopped the transplants, some 738 animals were moved from their native areas back into areas where they had historically been known to exist and 22 animals were sent to zoos in the United States and Canada (Table 2; the discrepancy between animals shown to be removed

Table 2—Summary of Sea Otter Removals*

	Removals from			Transplants to							
Year	Amchitka	Other Aleutians	Prince William Sound	Attu	Pribilofs	Southeastern Alaska	British Columbia	Washington	Oregon	Zoos	Harvests
1951	35										
1954	22									3	
1955	37				19					2	
1956	26			5						2	
1957	21									2	
1959	39				7						
1960		14									
1962	180										180
1963	311										311
1965	2		41			23				1	
1966			39			30					
1967	210	300								5	505
1968	494	512	2		55	301					512
1969	251					58	29	29		4	
1970	291	750	46				14	30	29		955
1971	188+								63		
1972			58				46			3	

*Sources: Kenyon, 1969; Vanya, 1970; K. B. Schneider, personal communication.

artificially from the population and transplanted or harvested is other loss, in capture or for use in scientific experiments or whatever.) A chronological résumé of some of the details of these transplants to natural-habitat areas and to zoos follows.

1951. An attempt to transplant sea otters this year failed because of lack of basic knowledge about the requirements of the animals. Thirty-five animals that had been captured on Amchitka Island died in captivity before the transplant could take place.

1954. A press release from Headquarters, Seventeenth Naval District, Kodiak, dated May 4 gave the following caption to an accompanying photograph:

> The first sea otter to be successfully transported from its native habitat of Amchitka Island in the Aleutians is taken ashore at the U. S. Naval Station, Adak, Alaska on April 20, 1954 from the seagoing tug USS TILLAMOOK. Lt. Francis Bean, USN, of Seattle, Washington, Commanding Officer of the TILLAMOOK, supervises unloading operations as Mr. Robert D. Jones, Jr., Manager, Aleutian Islands National Wildlife Refuge and Expedition Leader, and crew member take the first cage ashore.

This sea otter was one of four captured in March and April on Amchitka and transported to Adak to be held there until the end of May. One of the animals died on May 5. The remaining three sea otters were transported by naval vessel to Seattle to be placed in the Woodland Park Zoo on June 1. They remained there until July, when they were air shipped to the National Zoological Park, Washington, D. C. All three otters died within a week of arrival.

1955. Sea otters were transplanted from Amchitka to the Pribilof Islands by a chartered fishing vessel, the *Paragon,* between March 28 and April 4. The 19 survivors of the 31 sea otters aboard the ship were released at Otter Island, but Kenyon (1969) is reasonably certain that none survived. Three died within minutes after being placed in seawater.

Two sea otters were transported from Amchitka to Seattle by air and were released in the Woodland Park Zoo on October 10. One died within a few days. The second, a female named Suzy, lived until Oct. 27, 1961.

1956. On April 10 five sea otters captured on Amchitka Island were transported by ship and released on Bird Island in Attu's Massacre Bay by R. D. Jones (U. S. Fish and Wildlife Service, 1956, unpublished report). Jones notes in his report that he knows one of the five otters died after the release.

Two sea otters from Amchitka Island were placed in the Woodland Park Zoo in Seattle July 30 (Kenyon, 1969). One of the otters died 16 days later, after appearing to be in excellent condition on arrival.

1957. An attempt to transplant eight sea otters from Amchitka Island to St. Paul Island was made on December 11; bad weather caused an en route delay, and six otters died that night. A storm

canceled the flight to St. Paul Island, and the two remaining otters were taken to Seattle and placed in the Woodland Park Zoo on December 14. One of the two otters died December 16; the other lived until September 22, 1958 (Kenyon, 1969; Kenyon and Spencer, 1960).

1959. Seven sea otters were transplanted from Amchitka Island to St. Paul Island on May 20. These animals arrived at St. Paul Island in excellent condition after about a 3.5-hr flight from Amchitka (Kenyon and Spencer, 1960).

1965. Kenyon (1969) transplanted one sea otter from Amchitka to the Tacoma, Washington, aquarium in Defiance Park.

An experimental transplant of 23 otters from Prince William Sound to Khaz Bay, Chichagof Island, southeast Alaska, was conducted by the Alaska Department of Fish and Game.

1966. The Alaska Department of Fish and Game transplanted 30 sea otters in September from Prince William Sound to southeast Alaska, 20 to Khaz Bay and 10 to Yakutat Bay.

1968. The Alaska Department of Fish and Game, with cooperation from the Atomic Energy Commission and the Bureau of Sport Fisheries and Wildlife, transplanted 55 otters from Amchitka to St. George Island in the Pribilofs; 301 otters were transplanted from Amchitka to six locations in southeast Alaska.

1969. The Alaska Department of Fish and Game, with cooperation from the Atomic Energy Commission, transplanted 120 otters: 58 to Khaz Bay in southeast Alaska; 29 to Pt. Grenville, Washington; 29 to Vancouver Island, British Columbia; and 4 to the Tacoma aquarium to form a study colony.

1970. The Alaska Department of Fish and Game transplanted 14 sea otters from Prince William Sound to Checleset Bay, Vancouver Island, British Columbia, in July. One of the four taken to Tacoma in 1969 was transferred to the Vancouver, British Columbia, public aquarium. The Alaska Department of Fish and Game and the Atomic Energy Commission cooperated in the transplant of 62 sea otters from Amchitka on July 18—19, 1970: 31 went to the State of Washington (1 died and 30 were released near Lapush) and 31 went to Oregon (2 died shortly after arrival and 29 were released near Port Orford).

1971. The Alaska Department of Fish and Game, the Atomic Energy Commission, and the Oregon Game Commission cooperated in the transplant of 64 sea otters from Amchitka to the Oregon coast. Releases of 40 otters near Simpson Reef and Cape Arago and 24 otters at Port Orford were made on June 24.

1972. The Alaska Department of Fish and Game, with cooperation from the Fisheries Research Board of Canada and the British Columbia Fish and Wildlife Department, transplanted 46 sea otters from Prince William Sound to Checleset Bay, Vancouver Island, on July 19. In addition, 3 were given to the Vancouver, British Columbia, public aquarium.

Because of its history of near extermination, the sea otter has received more attention from wildlife scientists than any of the sea mammals in the Aleutians. Nevertheless, it has always been noted that large numbers of other sea mammals are also present in the same area. They apparently coexist because they do not compete for the same food supplies. Their numbers and biology are not nearly as well known as those of the sea otter, but the general consensus is that the populations of these other sea mammals are in good condition throughout the western Aleutians.

Northern Fur Seal (*Callorhinus ursinus*)

The Pribilof Islands were discovered in 1786 and 1787 by Gerassim Pribilof, Russian navigator and fur trader. This was the result of more than 18 years of search for the fur seal breeding colonies. Sims (1906) estimated the herd size at the time of discovery to be 2,500,000 animals. Beginning at that time and continuing for the next 150 years, there were periods of extreme exploitation and periods of no exploitation. In 1911, when the United States assumed control of the sealing industry, the herd size was estimated to be 215,000 seals.

The large number of fur seals moving north and south through the passes in the Aleutian Islands and east and west along the chain during migration periods made appearance of the fur seal not unusual.

The importance of the fur seal in the Aleutians is its numbers as a migrant and not as a resident species.

Steller Sea Lion (*Eumetopias jubata*)

This species, named after Georg Wilhelm Steller, was prominent among the sea mammals encountered by the earliest explorers in the Aleutians. The sea lion was also a victim of the ruthless killing of sea mammals by Russians and Americans, and, by the end of the 1800s, relatively few remained. Sea lions were common in the Aleutians, and today they have returned to what has been

estimated as close to their original numbers (Kenyon, 1971).

Scammon (1874) describes the use of sea lions by the Aleuts:

> The dead animals are then skinned, and their hides packed in tiers until fermented sufficiently to start the hair, when they are stretched on frames to dry, and eventually to become the covering or planking for the Aleutian baidarkas and baidaras. The fat is taken off and used for fuel, or the oil is rendered to burn in their lamps. The flesh is cut in thin pieces from the carcass, laid in the open air to dry, then tanned, and worked into water-proof clothing. The stomach is emptied of its contents, turned inside out, then inflated and dried for oil bottles, or it is used as a receptacle for the preserved meat; and what remains of the once formidable and curious animal is only a mutilated skeleton.

A systematic use of aerial photography for the evaluation of sea lion populations in Alaska gave Mathisen (1959) data for his count of 149,264 animals. An incomplete count for the Aleutian Islands derived from his data was 73,090 animals. Mathisen pointed out that the counts were of necessity minimum figures because only animals that were on land were counted; animals feeding or away from the rookeries and hauling grounds were not counted. Later analysis by Mathisen and Lopp (1963) increased the Aleutian Islands sea lion population to about 83,000 animals.

Kenyon and Rice (1961) estimated the sea lion population of all Aleutian Islands and areas near the end of the Alaska peninsula to be about 100,000 animals. This figure was derived from the first complete aerial survey of the Aleutian Islands. The estimated number of sea lions for Amchitka was 1250 with the following distribution:

Bird Rock	50
Chitka Point Islet	50
Ivakin Point	300
East Cape	200
St. Makarius Islet	50
Southwest islets and rocks	600

The Aleutian Islands appear to be the center of abundance for sea lions and the point from which seasonal movements occur.

Kenyon's aerial census of sea lions from the Islands of Four Mountains to Sandman Reefs, Mar. 3–4, 1960, was 55,325 animals (U. S. Fish and Wildlife Service, 1960, unpublished report).

1962. A sea lion census was made on March 29 and April 5–10 in connection with the sea otter census. A total of 54,704 animals was counted (U. S. Fish and Wildlife Service, 1962, unpublished report). Robert D. Jones made a census of Steller sea lions at Amchitka by dory. He counted a total of 3584 animals at the hauling grounds and rookeries on and adjacent to the island (U. S. Fish and Wildlife Service, 1962, unpublished report).

1965. The April 18–May 9 aerial census covering the Aleutian Islands and part of the Alaskan peninsula from Cold Bay to Attu showed a count of 63,933 sea lions. Of this number, 710 were counted at Amchitka (U. S. Fish and Wildlife Service, 1965, unpublished report).

Thorsteinson, Nelson, and Lall (1961) reported on an experimental harvest of sea lions in 1959 to determine the feasibility of a commercial venture. Five sea lion rookeries supplied 616 sea lions; 464 were processed into 200 tons of ground meat and 9 tons of whole liver. There were many technological problems, but the authors determined that sea lions could be taken in sufficient numbers to be profitable.

Private commerical hunters, regulated and monitored by the Alaska Department of Fish and Game, conducted an annual harvest of Steller sea lion pup skins from 1963 through 1972. The total harvest was 45,178 skins, with rookeries in the eastern Aleutians supplying 12,405 of these. None were taken from the western Aleutians.

Harbor Seal (*Phoca vitulina*)

The harbor, or hair, seal occurs throughout the Aleutian Islands, living in protected bays and river mouths and hauling out on small offshore islands and exposed reefs (Kenyon and Scheffer, (1955). Murie (1959) did not find it abundant in the Aleutians during his 1936 expedition, but historical and archaeological evidence indicates that this species was common. It is common today.

Very little research has been carried out on harbor seals exclusively in the Aleutians. Aerial surveys for sea otters have at various times included harbor seals and sea lions as additional species observed, but generally harbor seals have been neglected. The Alaska Department of Fish and Game has had active research and harvest programs in locations other than the Aleutians, and the bulk of seal skins bountied by Alaskan hunters came from more accessible areas.

A harbor seal population is difficult to count because the seals are scattered, breeding in small colonies rather than large rookeries as do fur seals and sea lions. A population estimate for Amchitka Island in 1971 was 900 to 1000 seals (C. Hardy, U. S. Fish and Wildlife Service, personal communication). The results of three harbor seal counts are listed below.

1960. An aerial count of harbor seals from the Islands of Four Mountains to Sandman Reefs,

March 3–4, gave a count of 3591 animals (U. S. Fish and Wildlife Service, 1960, unpublished report).

1962. An aerial count of harbor seals in conjunction with a sea otter census of March 29 and April 5–10 gave a count of 6000 plus animals (U. S. Fish and Wildlife Service, 1962, unpublished report).

1965. An aerial count of harbor seals conducted in conjunction with the April 18–May 9 sea otter survey gave a count of 4868 animals from Cold Bay to Attu Island (U. S. Fish and Wildlife Service, unpublished report, 1965).

Cetaceans

Statistics on how many of different species of cetaceans have been taken annually in recent years in and near the Aleutian Islands are given by Merrell (Chap. 15, this volume). The following species* have been observed or harvested in the area.

Blue Whale (*Balaenoptera musculus*). Blue whales are generally found in three summer locations: (1) the eastern Gulf of Alaska, (2) the area south of the eastern Aleutians, and (3) the area from the western Aleutians to Kamchatka. Doi, Nemoto, and Ohsumi (1967) calculated the summer population of blue whales to be about 1420, a drop of just over 1000 animals from a postwar population of 2430. Rice (1971) interprets these data as an indication that blue whales were never abundant in the eastern North Pacific and that there has been little decrease in their population size. Blue whales have been completely protected beginning with the 1966 season (International Commission on Whaling, 1967).

Finback Whale (*Balaenoptera physalus*). The summer range of finback whales includes the immediate offshore waters of lands around the North Pacific Ocean. The increased pressure of pelagic whaling on this species has reduced this stock to well below the maximum sustainable yield (Ohsumi, Shimadzu, and Doi, 1971).

Sei Whale (*Balaenoptera borealis*). The sei whale distribution in the summertime is similar to that for the finback whale except that sei whales rarely go north of the Aleutian Islands.

Sperm Whale (*Physeter catodon*). The sperm whale is widely distributed and is found north and south of the Aleutians. It is one of the larger cetaceans and is important to the whaling industry.

Little Piked Whale (*Balaenoptera acutorostrata*). The little piked whale is also known as the minke whale and is distributed widely in the North Pacific.

Baird's Beaked Whale (*Berardius bairdi*). The Baird's beaked whale is distributed throughout the Bering Sea in the North Pacific Ocean. It has been harvested by the Japanese whaling fleet.

Cuvier's Beaked Whale (*Ziphius cavirostris*). The range of the Cuvier's beaked whale includes the waters of the North Pacific Ocean and the Bering Sea. It does not go into the Arctic Ocean.

Stejneger's Beaked Whale (*Mesoplodon stejnegeri*). The Stejneger's beaked whale is found throughout the Aleutians and in the Bering Sea. Its distribution has been correlated with the distribution and migration patterns of Pacific salmon.

Beluga Whale (*Delphinapterus leucas*). Belugas range on both sides of the Bering Strait and down into Bristol Bay on the American side. This species is not known to migrate south of the Aleutian Islands and is only a rare visitor to the Aleutians.

Gray Whale (*Eschrichtius robustus*). The gray whale passes through the Aleutians en route to its summer feeding grounds in the Bering Sea and the Arctic Ocean and again en route to its breeding grounds in the bays and lagoons of Baja California, Mexico. The gray whale is completely protected from commercial whaling efforts.

Humpback Whale (*Megaptera novaeangliae*). Humpback whales are known to occur fairly close to shore in the eastern Aleutians.

Pacific Right Whale (*Balaena glacialis*). Rice (1971) says that the "Kodiak ground," which encompassed the entire Gulf of Alaska from Vancouver Island to the eastern Aleutians, was renowned in the nineteenth century as one of the best areas for hunting right whales during the summer. A few could be found in the southern Bering Sea and all across the North Pacific at that season. This species is protected by the International Whaling Commission.

Bowhead Whale (*Balaena mysticetus*). The bowhead whale is extremely rare in the Aleutians. Bowheads spend the winter in the loose southern edge of pack ice, which usually extends across the central Bering Sea from Kuskokwim Bay to the northern shores of Kamchatka peninsula. This species is protected by the International Whaling Commission.

*The authority for marine mammal nomenclature is Rice and Scheffer (1968). A monograph on the gray whale by Rice and Wolman (1971) revised the nomenclature for this species; the revised version is used here.

Pacific Whitesided Dolphin (*Lagenorhynchus obliquidens*). The Pacific whitesided whale is widely distributed and very common in the North Pacific Ocean.

Killer Whale (*Orcinus orca*). The killer whale is the most widely distributed marine mammal in the world and is commonly seen in the Aleutians.

Pilot Whale (*Globicephala scammoni*). Distribution of the pilot whale is considered to be the northern waters of the Pacific Ocean, including the Aleutian Islands and south to latitude 36° (Nishiwaki, 1967).

Harbor Porpoise (*Phocoena phocoena*). Murie (1959) saw two harbor porpoises on May 23, 1937, in the Shumagin Islands, and, on Aug. 13, 1937, he saw three in the harbor at Atka Island.

Dall Porpoise (*Phocoenoides dalli*). The Dall porpoise is widely distributed in the North Pacific Ocean.

Pacific Walrus (*Odobenus rosmarus*)

The Pacific walrus is associated with the Aleutian Islands because of the proximity of its wintering habitat, the Bristol Bay area. There are records of walruses being killed south of the Alaska peninsula, and Turner (1886, as cited by Murie, 1959) recorded the kill of a 2-year-old male walrus at Attu Island in September 1880. More recently, in 1960 Jones (U. S. Fish and Wildlife Service, 1960, unpublished report) found the intact carcass of a young walrus near South Bight on Amchitka Island. These animals must be regarded as strays; the Aleutian Islands are not a usual part of the walrus range. The rare occurrence of walruses in the Aleutians is reflected in the absence of identifiable walrus midden remains from Aleutian archaeological investigations.

Steller Sea Cow (*Hydrodamalis gigas*)

Murie (1959) says:

> Our knowledge of the sea cow depends mainly on the account of Steller, who, in the disastrous winter when Bering's expedition was wrecked on Bering Island after discovery of Alaska in 1741, had ample opportunity to study this animal at first hand. The sea cow furnished food for Bering's party, as well as for other expeditions that used the Commander Islands as a starting point for Alaska. It was exterminated by 1768.*

*Sea cows were very numerous about the coast of Kamtshatka, and the Aleutan islands, at the time when they were first discovered; but the last of this species was killed in 1768 on Bering's island, and none have been ever seen since (Sauer, 1802, p. 181).

> There has always been a question whether this animal had ever occupied the Aleutian Islands. Stejneger (1883, p. 84) said Wosnessenski had obtained a rib of a sea cow from Attu Island, and, in conversation, Stejneger expressed the belief that sea cow remains might be found on Agattu Island.
>
> Goode et al. (1884, p. 136) wrote as follows concerning this find: 'Wosnessenski found a rib of the animal on Attu, the last island of the archipelago, but as Brandt suggests, it may have been derived from a *Rhytina* washed thither by the waves. Mr. Lucien Turner kindly informed me that an aged woman stated that *Rhytina* had been seen at Attu by her father, but such testimony is, perhaps, not altogether satisfactory.'
>
> Thus, we may have some evidence that the sea cow may have occurred on the westernmost Aleutian Islands, and it would be extremely interesting to have identification of bones from old Aleut village sites. To date, studies of such midden material have not revealed the presence of sea cow remains, and, on the whole, it is likely that this animal never inhabited these islands except as an accidental straggler.

Recent studies on the archaeology of Amchitka (Desautels et al., 1970; Cook et al., 1972) bear out Murie's statement that midden material has not yet verified the presence of sea cows at those particular locations.

However, a Pleistocene *Hydrodamalis* was discovered on Amchitka in 1969 from interglacial beach sand and gravel (Gard, Lewis, and Whitmore, 1972). The Pleistocene find was identified as *Hydrodamalis* Retzius, 1794. Fragments of the bones and associated pecten shells were submitted for uranium series dating, and this indicated their age to be about 135,000 years.

Berzin, Tikhomirov, and Troinin (1963, cited by Nishiwaki, 1967) reported that six large sea animals were seen by men on the whale catcher *Buran* near Cape [Point] Navarin on the Siberian coast in July 1962. It was presumed that these animals were Steller's sea cows.

Doctors Colin and Kate Bertram (1964), having read the account by Berzin et al., speculated (in English) on the survival of sea cows, citing the survival of fur seals and sea otters as evidence of this possibility, as well as the remoteness and rarely visited nature of the Point Navarin area. However, the very identification of these animals as sea cows has been questioned by Hepter (1965).

CONSERVATION MEASURES

The earliest exploitation of Alaskan fur bearers by the Russians and by poaching Americans and Englishmen can only be described as ruthless and ignorant. Even today the early opinion occasionally crops up that the animals were disappearing, not because they were being overhunted, but because they were moving away to avoid hunting

pressures (Fedorova, 1973, p. 105). Yet, when the Russian government finally interested itself in these faraway territories, it was partly on the basis of regulating and even conserving the fur resources. Thus the Russian–American Company was formed in 1799 by a forced merger of existing companies and given a monopoly to eliminate competition and consequent wastefulness as well as to increase the imperial revenues and to make contact with the natives more humane. In 1805, Rezanov, a nobleman from the court, made a personal inspection trip to Russian America and, among other things, put a stop to the indiscriminate killing of fur seals (Bancroft, 1886, p. 446). In 1833, Governor Muraviev established seasons and quotas and areas where hunting was forbidden (Bergsland, 1959, p. 75; Fedorova, 1973, p. 189).

The purchase of Alaska by the United States in 1867 was in some respects a setback. Congress did concern itself with the fur seal population by acts of 1868 and 1870, under which a monopoly on taking fur seals at the Pribilof Islands was leased to the Alaska Commercial Company. There was no control over the taking of any other fur-bearing animal. Even the number of fur seals continued to decline. It was the actions of 1911 that turned the tide: total protection for the sea otter, a ban on pelagic sealing, and a closely regulated harvest of the fur seals by the government itself. To this has been added recently the State of Alaska's action in transplanting sea otters back into portions of their former range where they had disappeared. These measures have been outstandingly successful. Both populations, fur seals and sea otters, are healthy and viable by any standard.

This section lists the succession of pertinent federal laws and orders relating to the conservation, protection, and management of sea mammals in the Aleutian area. Also included are treaties and international agreements to which the United States is a party. These statutes and agreements are the basis for the status of marine mammals in the Aleutian Islands today.

Acts of 1868 and 1879 applying to the harvest of fur seals in the Pribilof Islands.

A treaty between the United States and Great Britain (acting for Canada) was concluded on Feb. 29, 1892, at Washington, D. C., for the purpose of submitting to arbitration certain questions concerning the preservation of fur seals.

On Feb. 21, 1892, the 52nd Congress acted to extend to the North Pacific Ocean the provisions of earlier statutes protecting fur seals and other fur-bearing animals.

The Tribunal of Arbitration at Paris made certain awards, and the 53rd Congress acted on Apr. 6, 1894, to give effect to these awards. Congress, on Dec. 29, 1897, acted to prohibit the killing of fur seals in the waters of the North Pacific Ocean.

The Act of Apr. 21, 1910, prohibited the killing of sea otters or fur seals within the limits of Alaska or in the waters of Alaska.

On July 7, 1911, the governments of the United States, Great Britain (on behalf of Canada), Japan, and Russia signed a Convention for the Preservation and Protection of Fur Seals (and sea otter) (37 Stat. 1542, Treaty Series 564). This convention, commonly known as the Fur Seal Treaty of 1911, prohibited pelagic sealing and sea otter killing in high seas waters north of the 30th parallel of north latitude. It also prohibited the importation of sea otter skins into the four treaty member countries unless the skins had been authenticated as to legality of origin. The treaty was terminated when Japan abrogated it on Oct. 23, 1940, effective Oct. 23, 1941.

The existence of the Aleutian Islands National Wildlife Refuge stems from Executive Order 1733, dated Mar. 3, 1913. Its full text is given in Appendix A of Chap. 6 of this volume.

A Convention for the Regulation of Whaling was concluded at Geneva on Sept. 24, 1931, and came into force on June 17, 1932. The convention and the international agreements following it are the basis for the present International Convention for the Regulation of Whaling. In making this agreement, the various world governments signing it proclaimed that they recognized the interests of nations of the world in safeguarding for future generations the great natural resources represented by the whale stocks. They recognized that the history of whaling had been one of fishing one area after another and of one species after another to such a degree that it had become necessary to protect all species of whales from further overfishing.

They further recognized that the whale stocks were capable of natural increases if whaling was properly regulated. Increases in the size of whale stocks would permit increases in the number of whales that could be captured without endangering these natural resources. Realizing that it was in the common interest to achieve the optimum level of whale stocks as rapidly as possible by con-

fining whaling operations to those species which were best able to sustain exploitation, a system of international regulations for whale fisheries was established to ensure effective conservation and development. The International Convention with Schedule of Whaling Regulations, signed at Washington on Dec. 2, 1946, entered into force for the United States on Nov. 10, 1948. A 1956 protocol extended the application of the convention to helicopters and other aircraft and included provisions for inspection. The protocol entered into force on May 4, 1959.

The International Whaling Convention is not generally believed to be as successful as its high principles would indicate, but this is too sensitive a matter of current history to go into here.

The lengthy history of the International Whaling Convention is being repeated by the 1954 International Convention for the Prevention of Pollution of the Sea by Oil. This convention entered into force for the United States on Dec. 8, 1961, and sets forth measures to prevent pollution of the sea by oil discharged from ships. A resolution on marine pollution adopted on Oct. 21, 1969, by the United Nations General Assembly acknowledged a significant contribution by oil to pollution of the sea. It noted also effects that might arise from the exploration and exploitation of resources of the sea bed and ocean floor. For that and other reasons, the Assembly convened in 1973 an international conference on marine pollution for the purpose of preparing a suitable international agreement for placing restraints on the contamination of the sea, land, and air by ships, vessels, and other equipment operating in the marine environment.

The Fish and Wildlife Act of 1956 (16 USC 742a-754) established a comprehensive national fish and wildlife policy. It established the present U. S. Fish and Wildlife Service and directed the Secretary of the Interior to provide continuing research, extension, and information services and to take any necessary steps to develop, manage, and conserve fishery and wildlife resources.

In 1957, Canada, Japan, Russia, and the United States executed an interim convention on conservation of North Pacific fur seals. This convention was amended by protocol on Oct. 8, 1963.

The Alaska Statehood Act of July 7, 1958 (48 USC Chap. 2—Alaska, Sec. 6; P.L. 85-508) authorized the transfer of administration and management of the fisheries and wildlife of Alaska to the State of Alaska. It also authorized the transfer to the state of real and personal property of the United States which is in Alaska and specifically used for the conservation and protection of the fisheries and wildlife of Alaska.

Executive Order 10857 terminated federal functions in Alaska and transferred property held by the United States to the State of Alaska.

The Fur Seal Act of 1966 (16 USC 1151-1187; P.L. 89-702) repeals the Fur Seal Act of 1944. It continues the responsibility of the Secretary of the Interior for conservation and harvesting of North Pacific fur seals and for administration of the Pribilof Islands reservation for various purposes, including conservation of fur seals and other wildlife. It contains provisions specifically protecting sea otters. It authorizes contracts for research on fur seals and sea otters with persons and agencies and provides for payment to the State of Alaska pursuant to the Alaska Statehood Act of 70% of the net proceeds from the sales of fur seal skins taken in harvest programs. It also provides for payments to Alaska of 70% of the net proceeds from sea otters taken by the Secretary on the high seas or within the Aleutian Islands National Wildlife Refuge.

The Endangered Species Conservation Act of 1969 (P.L. 91-135) provided broad authority and policy guidance for a comprehensive program for the conservation, restoration, and propagation of native fish and wildlife threatened with extinction. The Endangered Species Act of 1973 has replaced it.

In establishing the Marine Mammal Protection Act of 1972 (16 USC 1371-1384, 1401-1407; P.L. 92-522), Congress found that certain species and population stocks of marine mammals are or may be in danger of extinction or depletion as a result of man's activities. These should not be permitted to diminish beyond the point at which they cease to be a significant functioning element in the ecosystems of which they are a part and should not be permitted to diminish below their optimum sustainable population. Further measures should be taken to replenish any species or population stock that has already diminished below that population. In particular, efforts should be made to protect the rookeries, mating grounds, and areas of similar significance of each species of

marine mammal from the adverse effects of man's actions.

Beginning on Dec. 21, 1972, there was an indefinite complete ban on the taking of marine mammals and on the importation into the United States of marine mammals and marine mammal products. The Act allows the Secretary of the Interior to issue permits for scientific research and public displays. It also allows the taking of marine mammals by Alaskan Indians, Aleuts, and Eskimos for subsistence purposes or for creating and selling authentic native articles and clothing when not accomplished in a wasteful manner. The Act has jurisdiction over walruses, sea otters, polar bears, manatees, seals, whales, sea lions, and porpoises.

The Endangered Species Act of 1973 (16 USC 1531-1543; P.L. 93-205) extends the principle of protection of endangered species to plants as well as to fish and wildlife. A new category of threatened species has been established. The definition of fish and wildlife is broadened to include any mammal, fish, bird, amphibian, reptile, mollusk, crustacean, arthropod, or other invertebrate. The Secretary of the Interior has been directed to establish a list of endangered and threatened species and to establish regulations for the protection of these species. This legislation also provides for cooperation with and assistance to the individual states and foreign governments. Except for certain limited purposes and under regulations, the importation or exportation of endangered or threatened fish and wildlife is prohibited.

REFERENCES

Bancroft, H. H., 1886, *History of Alaska, 1730–1885*, A. L. Bancroft & Co., San Francisco, Calif.

Bergsland, K., 1959, Aleut Dialects of Atka and Attu, *Trans. Amer. Phil. Soc.*, 49(3): 1-128.

Berkh, V. N., 1823, *A Chronological History of the Discovery of the Aleutian Islands.* Translated by R. A. Pierce, Limestone Press, Kingston, Ontario, 1974. (Materials for the Study of Alaska History, No. 5.)

Bertram, Colin, and Kate Bertram, 1964, Does the "Extinct" Sea Cow Survive? *New Scientist*, 24(415): 313.

Berzin, A., E. A. Tikhomirov, and V. I. Troinin, 1963, Was Steller's Sea Cow Exterminated? *Priroda*, 52: 73-75 (in Russian) (not seen by Abegglen).

Bower, W. T., 1941, Alaska Fishery and Fur Seal Industry in 1939. Administrative Report No. 40. Appendix II to the Report of the Commissioner of Fisheries for Fiscal Year 1939, pp. 97-184, Department of Commerce, Washington.

——, 1940, Alaska Fishery and Fur Seal Industries in 1938. Administrative Report No. 36. Appendix II to the Report of the Commissioner of Fisheries for Fiscal Year 1939, pp. 83-168, Department of Commerce, Washington.

——, 1938, Alaska Fishery and Fur Seal Industries in 1937. Appendix to the Report of the Commissioner of Fisheries, pp. 125-150, Department of Commerce, Washington.

——, 1937, Alaska Fishery and Fur Seal Industries in 1936. Appendix to the Report of the Commissioner of Fisheries, pp. 326-347, Department of Commerce, Washington.

Clark, D., 1968, Koniag Prehistory, Ph. D. Dissertation, University of Wisconsin, Madison (not seen by Abegglen).

Cobb, J. N., 1907, The Fisheries of Alaska in 1906, Department of Commerce and Labor, Bureau of Fisheries Document No. 618.

——, 1906, The Commercial Fisheries of Alaska in 1905, Department of Commerce and Labor, Bureau of Fisheries Document No. 603.

Cook, J. P., E. J. Dixon, and C. E. Holmes, 1972, Archaeological Report, Site 49-Rat-62, Amchitka Island, Alaska, USAEC Report HN-20-1045, University of Alaska.

Desautels, R. J., A. J. McCurdy, J. D. Flynn, and R. R. Ellis, 1970, Archaeological Report, Amchitka Island, Alaska, 1969–1970, USAEC Report TID-25481.

Doi, T., T. Nemoto, and S. Ohsumi, 1967, Memorandum on Results of Japanese Stock Assessment of Whales in the North Pacific, International Commission on Whaling, Report of the Commission, pp. 111-115, London.

Douglas, J., n.d., Fur Trade Returns, Columbia District and New Caldonia 1825–1857, Archives of British Columbia, Victoria. Ms. 408 (not seen by Abegglen).

Elliott, H. W., 1887, The Sea-Otter Fishery, in *The Fisheries Industries of the United States*, U. S. Commission of Fish and Fisheries, Section V. History and Methods Text, Vol II, pp. 483-491, G. Brown Goode and Associates.

Fedorova, S. G., 1973, *The Russian Population in Alaska and California, Late 18th Century—1867* (translated and edited from the 1971 Russian Original by R. A. Pierce and A. S. Donnelly), Limestone Press, Kingston, Ontario (Materials for the Study of Alaska History, No. 4).

Gard, L. M., G. E. Lewis, and F. C. Whitmore, 1972, Steller's Sea Cow in Pleistocene Interglacial Beach Deposits on Amchitka, Aleutian Islands, *Geol. Soc. Amer., Bull.*, 83: 867-870.

Golder, F. A., 1914, *Russian Expansion on the Pacific: 1641–1850* (reprinted 1960 by Peter Smith, Gloucester, Mass.).

Goode, G. B., et al., 1884, The Fisheries and Fishery Industries of the United States, Sec. 1, Part 1, 47th Congress, 1st Session, Senate, Misc. Doc. 124, Washington.

Heptner, V. G., 1965, More About Steller's Sea Cow, *Priroda*, 54(7): 91-94 (in Russian).

Hrdlička, A., 1945, *The Aleutian and Commander Islands and Their Inhabitants*, The Wistar Institute of Anatomy and Biology, Philadelphia.

International Commission on Whaling, 1967, Seventeenth Report of the Commission, London.

Jones, R. D., 1951, Present Status of the Sea Otter in Alaska, Wildlife Management Institute, in *Transactions of the 16th North American Wildlife and Natural Resources Conference*, pp. 376-383, Wildlife Management Institute, Washington, D. C.

Kenyon, K. W., 1971, Status of Marine Mammals in the Eastern North Pacific Ocean, U. S. Department of the Interior 102 Statement.

—, 1969, *The Sea Otter in the Eastern Pacific Ocean*, U. S. Department of the Interior, Bureau of Sport Fisheries and Wildlife, North American Fauna, No. 68.

—, and D. W. Rice, 1961, Abundance and Distribution of the Steller Sea Lion, *J. Mammalogy*, 42(2): 223-234.

—, and V. B. Scheffer, 1955, The Seals, Sea Lions, and Sea Otter of the Pacific Coast, Circular No. 32, U. S. Fish and Wildlife Service.

—, and D. L. Spencer, 1960, Sea Otter Population and Transplant Studies in Alaska, 1959, Special Scientific Report, Wildlife No. 48, U. S. Fish and Wildlife Service.

Khlebnikov, K., 1835, *Biography of Alexander Andreivitch Baranoff: Governor-General of the Russian Colonies in America*, Navy Printing Office, St. Petersburg (in Russian). (Excerpts translated by George Guilsher. Otherwise not seen by Abegglen.) (Also translated by M. B. Ricks in *The Earliest History of Alaska*, Cook Inlet Historical Society, Anchorage, 1963. Also translated by R. A. Pierce, Limestone Press, Kingston, Ontario, 1973.)

Kirkwood, J. B. (Comp.), 1975, Bioenvironmental and Hydrologic Studies, Amchitka Island, Alaska. Fall 1974 Task Force Report, ERDA Report BMI-171-158, Battelle Memorial Institute.

Lensink, C. J., 1962, The History and Status of Sea Otters in Alaska, Ph. D. Thesis, Purdue University, Xerox University Microfilms, Ann Arbor, Mich.

Loy, C. L., 1940, Sea Otter Report of Amchitka Island, Alaska, July 10, 1939 to January 15, 1940. Unpublished Report in FWS files.

—, and O. A. Friden, 1937, Sea Otter Survey of Amchitka Island, Alaska, July 11 to September 1, 1937. Unpublished Report in FWS files.

Marsh, M. C., and J. N. Cobb, 1911, The Fisheries of Alaska in 1910, Department of Commerce and Labor, Bureau of Fisheries Document No. 746.

—, and J. N. Cobb, 1910, The Fisheries of Alaska in 1909, Bureau of Fisheries Document 730.

—, and J. N. Cobb, 1909, The Fisheries of Alaska in 1908, Bureau of Fisheries Document 645.

—, and J. N. Cobb, 1908, The Fisheries of Alaska in 1907, Bureau of Fisheries Document 632.

Mathisen, O. A., 1959, Studies on Steller Sea Lion *(E. jubata)* in Alaska, in *Transactions of the 24th American Wildlife and Natural Resources Conference*, pp. 345-356, Wildlife Management Institute, Washington, D. C.

—, and R. J. Lopp, 1963, Photographic Census of the Steller Sea Lion Herds in Alaska, 1956–1958. Special Scientific Report—Fisheries No. 42, U. S. Fish and Wildlife Service.

Murie, O. J., 1959, *Fauna of the Aleutian Islands and Alaska Peninsula*, U. S. Fish and Wildlife Service, North American Fauna, No. 61.

Nishiwaki, M., 1967, Distribution and Migration of Marine Mammals in the North Pacific Area, Bulletin No. 1, Ocean Research Institute, University of Tokyo.

Ohsumi, S., Y. Shimadzu, and T. Doi, 1971, The Seventh Memorandum on the Results of Japanese Stock Assessment of Whales in the North Pacific, International Commission on Whaling, 21st Report of the Commission, London.

Petroff, I., 1884, Alaska: Its Population, Industries, and Resources, in *Tenth Census of the United States*, Vol. VIII, U. S. Department of the Interior.

Rice, D. W., 1971, Whales and Whale Research in the Eastern North Pacific, in Proceedings of the Conference on Biology of Whales, Luray, Virginia, June 1971, U. S. International Biological Program.

—, and V. B. Scheffer, 1968, A List of the Marine Mammals for the World, Special Scientific Report—Fisheries No. 579, U. S. Fish and Wildlife Service.

—, and A. A. Wolman, 1971, *The Life History and Ecology of the Gray Whale (Eschrichtius robustus)*, The American Society of Mammalogists, Special Publication No. 3.

Ricks, M. B., 1963, *The Earliest History of Alaska*, Cook Inlet Historical Society, Anchorage.

Rocquefeuil, C., 1823, Journal d'un Voyage Autour du Monde, Pendant les Annees 1816, 1817, 1818 et 1819, par M. Camille de Roquefeuil, Ponthieu, Paris (not seen by Abegglen).

Sauer, M., 1802, *An Account of a Geographical and Astronomical Expedition to the Northern Parts of Russia* (reprinted 1972 by Richmond Publishing Co., Ltd., Richmond, Surrey, England).

Scammon, C. M., 1874, *The Marine Mammals of the Northwestern Coast of North America* (new introduction by V. B. Scheffer. Republication of original work published in 1874), Dover Publications, Inc., New York, 1968.

Sims, E. W., 1906, *Report on the Alaskan Fur Seal Fisheries*, House Document 251, 59th Congress, 2nd Session, U. S. Government Printing Office, Washington, D. C.

Spaulding, A. C., 1962, *Archaeological Investigations on Agattu, Aleutian Islands*, Anthropology Papers No. 18, Museum of Anthropology, University of Michigan (not seen by Abegglen).

Spencer, D. L., 1969, Amchitka Bioenvironmental Program Interim Report, Sea Otter Surveys, Amchitka Island, Alaska, August 27–October 6, 1968, USAEC Report BMI-171-120, Battelle Memorial Institute.

Stejneger, L., 1883, Contributions to the History of the Commander Islands. No. 1—Notes on the Natural History, Including Descriptions of New Cetaceans, *Proc. U. S. Natl. Mus.*, 6(4): 58-89 (not seen by Abegglen).

Stephan, J. G., 1971, Bioenvironmental Surveillance Employing Photogrammetric Techniques, *BioScience*, 21(12): 667-682.

Sturgis, W., n.d. (circum 1799), Fur Traders in the North Pacific, Archives of British Columbia, Victoria, Pac. Ms. K. 33 (not seen by Abegglen).

Swicegood, Lt. Comdr. S. P., 1936, Amchitka Sea Otter Survey Expedition. Unpublished memo from Commanding Officer, U. S. Coast Guard Cutter *Phelan*, 31 August 1936, (in U. S. Fish and Wildlife Service files).

Thorsteinson, F. V., R. W. Nelson, and D. F. Lall, 1961, Experimental Harvest of the Steller Sea Lion in Alaskan Waters, Special Scientific Report—Fisheries No. 371, U. S. Fish and Wildlife Service.

Turner, L. M., 1886, *Contributions to the Natural History of Alaska*. Arctic Series Publication No. 2. Signal Service, U. S. Army, Washington (not seen by Abegglen).

Vanya, John, 1970, Memo to James A. Harper, Director, Division of Game, Juneau. Subject: Sea Otter Transplant. Alaska Department of Fish and Game, June 9, 1970.

Veniaminov, I., 1840, *Notes on the Islands of the Unalaska District* (translation from the original Russian, Human Relations Area File, New Haven).

Population Estimates and Feeding Behavior of Sea Otters

*James A. Estes**
Arizona Cooperative Wildlife Research Unit,
University of Arizona, Tucson, Arizona

Feeding behavior and the abundance of sea otters were studied at Amchitka Island, Alaska, between November 1970 and September 1972. Observations of feeding sea otters suggest no differences between sexes with regard to the amount of time spent diving or on the surface. Apparently, diving and surface times both increase in deeper water, but the percentages of time spent on the surface and submerged remain approximately constant throughout the day. No differences in either the pattern or the percentage of time spent feeding, resting, or grooming were observed between summer and winter.

Shore-based counts of sea otters are consistently higher than aerial counts from helicopters. This probably is attributable primarily to the increased amount of time that can be spent viewing an area from shore-based stations and thus the detection of animals that otherwise would have been submerged and consequently not counted as the aircraft passed overhead. In 1972 the Amchitka Island sea otter population was estimated at about 6400 animals, approximately 40% of which were in the Bering Sea and 60% of which were in the Pacific Ocean. This distribution corresponds with the distribution of sea otter feeding habitat. Assuming that sea otters live within the 30-fathom (55-m) depth contour, I estimate an island-wide sea otter density of 59 animals per square nautical mile of habitat (17 per square kilometer). This estimate may be separated into 68 animals per square mile (20 per square kilometer) in the Bering Sea and 54 animals per square mile (16 per square kilometer) in the Pacific Ocean. I believe that several earlier estimates of the number of sea otters at Amchitka Island were biased low.

The sea otter (*Enhydra lutris*) evolved as an integral part of the near-shore ecosystem in the North Pacific Ocean. During the 150 years from the mid-1700s to the beginning of the twentieth century, this species was driven to the verge of extinction by white fur traders. Exploitation of sea otter populations continued until 1911, at which time the animals were protected by an international convention between the United States, Russia, Japan, and Great Britain. Happily, a few remnant populations survived in the remote Aleutian Islands and along the rugged coast of central California. Presently, populations are increasing, and the sea otter has become reestablished over about one-third to one-half its original range (Kenyon, 1969).

The first extensive account of the sea otter, by Barabash-Nikiforov, was published in 1947. In 1969 a monograph on the sea otter by Kenyon was published which set forth the results of his own research, which spanned more than a decade, and brought up to date virtually everything known about the species. Subsequently it has been the most germane reference for several investigations, including studies sponsored by the U. S. Atomic Energy Commission on the sea otter population at Amchitka Island.

Kenyon (1969) considered the population status and dispersal trends of sea otters throughout their range as habitat was reoccupied. Subsequently the abundance of sea otters has been estimated several times at Amchitka Island. These efforts have produced a confusing array of results and probably some invalid suggestions of current population trends.

Distribution, female reproduction, and metabolic physiology of the sea otter are becoming more thoroughly understood. Conversely, little is known about reproduction in the male sea otter. Age and sex specific mortality, age class distribution, and a myriad of other aspects of sea otter population biology are either poorly understood or completely unknown.

*Present address: National Fish and Wildlife Laboratory, U. S. Fish and Wildlife Service, Marine Mammal Substation, 4454 Business Park Boulevard, Anchorage, Alaska.

This chapter considers population numbers and feeding behavior of sea otters at Amchitka Island. I assume that the population is fluctuating through time about some point of stable equilibrium. This assumption is supported primarily by conclusions made by Kenyon (1969) and is confirmed by my own observations on natural mortality (Estes and Smith, 1973). I also assume that competition for food is limiting further population growth. The amount of time budgeted by the population for foraging activity should reflect this limitation.

MATERIALS AND METHODS

Feeding Behavior of Sea Otters

I observed feeding and diving behavior of sea otters from November 1970 until September 1972. Most of this work was done during January and February 1971 and during July and August 1972. During early phases of the study, I randomly selected observation areas in some of the more remote coastal regions of Amchitka Island. Inclement weather and logistic difficulties soon proved this method of selection impractical and forced the use of only those areas which were easily accessible by road. For this reason Kirilof Point and Constantine Point were most frequently used during later phases of the study. Large numbers of sea otters were always present and observable at these areas. Most of my observations were made along the Bering Sea coast of Amchitka Island because viewing conditions were generally superior there as compared to coastal areas of the Pacific Ocean.

The primary objectives of behavioral studies were to determine (1) the amount of time feeding sea otters spend submerged, (2) the diurnal pattern of feeding and other activity, and (3) seasonal variation in population feeding behavior.

I recorded diving and surface times of feeding sea otters. When possible, the following information also was noted during each observation:

1. The sex and age of the animal (i.e., male, female, and female with pup). Sex was determined by the presence of a penis or teats.* All animals were classified as either adults or pups.
2. The approximate water depth in which the animal was feeding. Water depth was estimated from the approximate position of the animal as plotted on a depth contour map.
3. Food items captured.
4. Weather conditions.

The minimum sample size for estimating diving and surface times per individual was determined by incorporating the sample variance among diving times (s^2), obtained from a pilot study, and the desired confidence interval of mean diving times (2b) into the formula: $n = s^2 t^2 / b^2$, where $t = t_{\alpha/2,\nu}$ (α is 0.05 and ν is degrees of freedom determined by the sample size of the pilot study).

From this formula (Steel and Torrie, 1960) I determined the number of observations (n) required for a particular confidence interval (2b) at the 0.05 level of statistical significance. Preliminary estimates of mean diving and surface times were gathered from two feeding sea otters. The means and variances of diving and surface times recorded for these two animals are shown below:

	Diving		Surface	
	$\bar{X}$, sec	s^2	$\bar{X}$, sec	s^2
Sea otter No. 1 (female with large pup)	36	106	40	44
Sea otter No. 2 (lone female)	22	91	19	10

Because of the nonhomogeneous sample variance between the diving times of the two animals, the larger sample variance (i.e., 106) was used to calculate n. I arbitrarily defined the desired confidence interval at ±10 sec, and thus n = 4.8. A minimum of five observations of diving and surface times were taken from each animal; more observations were taken when possible. Between observations food items were identified with binoculars or a spotting scope. Food items were simply classified as fish or invertebrate unless they could be more specifically identified.

Diurnal patterns in the feeding behavior of sea otters also were estimated from the same study areas at Amchitka Island. I originally attempted to observe continuously a single individual animal through long periods of time. This technique was impractical and was soon abandoned. I subsequently noted the activity of all sea otters within the viewing range of 10x binoculars at one-half hour intervals and during daylight hours. Sea otter activity was divided into the following categories: (1) feeding, (2) grooming, and (3) resting. Following some experience sea otter activity could be categorized after only several seconds of observa-

*Sex determination of sea otters in the field was more difficult than I had originally suspected. After examining several subadult males that were held in captivity, I concluded that definite sex determination of anything but adults at close range is not possible. Even at short ranges sexually identifying characteristics of subadult animals are often not apparent (i.e., the male's penis or the female's teats). Adult females with pups are obvious at long ranges.

tion of a single animal. Animals whose behavior could not be classified or whose behavior did not fall into one of the above categories were not tabulated. Most of the sea otters I observed could be classified easily into one of the three behavioral categories.

The following criteria were used to categorize feeding sea otters:

1. Possession of a food item.
2. The exhibition of a characteristic chewing movement in which the head moves sharply up and down.
3. Rolling in the water to wash accumulated food scraps from the fur.
4. The close accompaniment of gulls in search of discarded food scraps.
5. Repeated diving.

Sea otters vigorously cleaning their fur were categorized as grooming. Often this involved repeated rolling or violent splashing in an apparent attempt to force air into the pelage. At long distances grooming behavior occasionally may be mistaken for feeding.

Resting sea otters lie motionless on their backs in the water or "haul out" on land.* Frequently resting animals congregate into large closely associated groups, although solitary resting individuals are not uncommon.

I observed sea otter activity during the summer (July and August) and winter (January and February) seasons. The number of observations and the total number of animals observed during each time period, in summer and winter, are shown in Fig. 1.

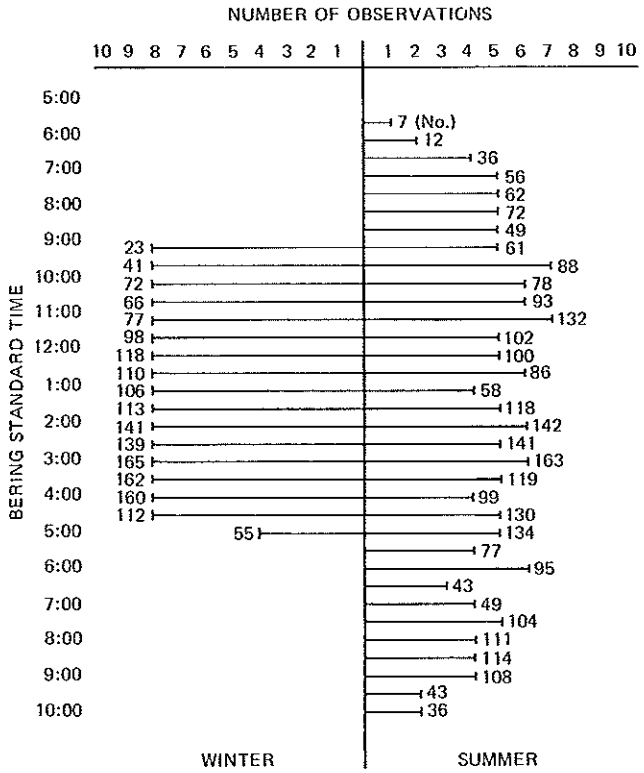

Fig. 1—Numbers of behavioral observations and total numbers of animals observed. Bar length indicates the number of days for which observations were made at a particular time and season. Numbers at end of bars indicate the total number of animals observed.

Techniques for Estimating the Abundance of Sea Otters

Sea otters were counted from shore-based stations with 10× binoculars and a 15 to 60× variable-powered spotting scope and from air by observers who were seated in an Alouette II helicopter. The boundaries of shore-based counting areas are given in Fig. 2. Two study areas each were selected on the Pacific Ocean and Bering Sea sides of Amchitka Island (labeled A through D in Fig. 2). Area A is located adjacent to the Cannikin site along the Bering Sea coast.† Area B was selected with prior knowledge of the sea otter population structure (Kenyon, 1969; personal observation) and the belief that it contained relatively large numbers of sea otters as compared to other areas around Amchitka, Areas C and D were selected without prior knowledge of either the population structures or the relative abundances of animals that occupied the areas. Within each study area a number of shore-based viewing stations were selected from which animals could be counted with binoculars and spotting scopes. The helicopter transported observers to these viewing stations. Immediately preceding or following a shore-based count in a given area, sea otters were counted from the air. Aerial counts originally were made by a single observer who was seated beside the pilot. However, later efforts showed that two observers counting animals on either side of a line bisecting the longitudinal axis of the aircraft provided higher numbers, and this technique was subsequently used. Aerial counts with two observers were also made for the entire island.

Animals were counted from shore at each viewing station within a given study area. When people and equipment were available, counters began at either end of the study area and worked toward the center. After several visits to each study area, observers became familiar with confines of viewing stations and were able to avoid overlapping

*"Hauled out" is commonly used to describe marine mammals resting out of the water.

†Cannikin is the code name of an underground nuclear detonation by the U. S. Atomic Energy Commission in 1971.

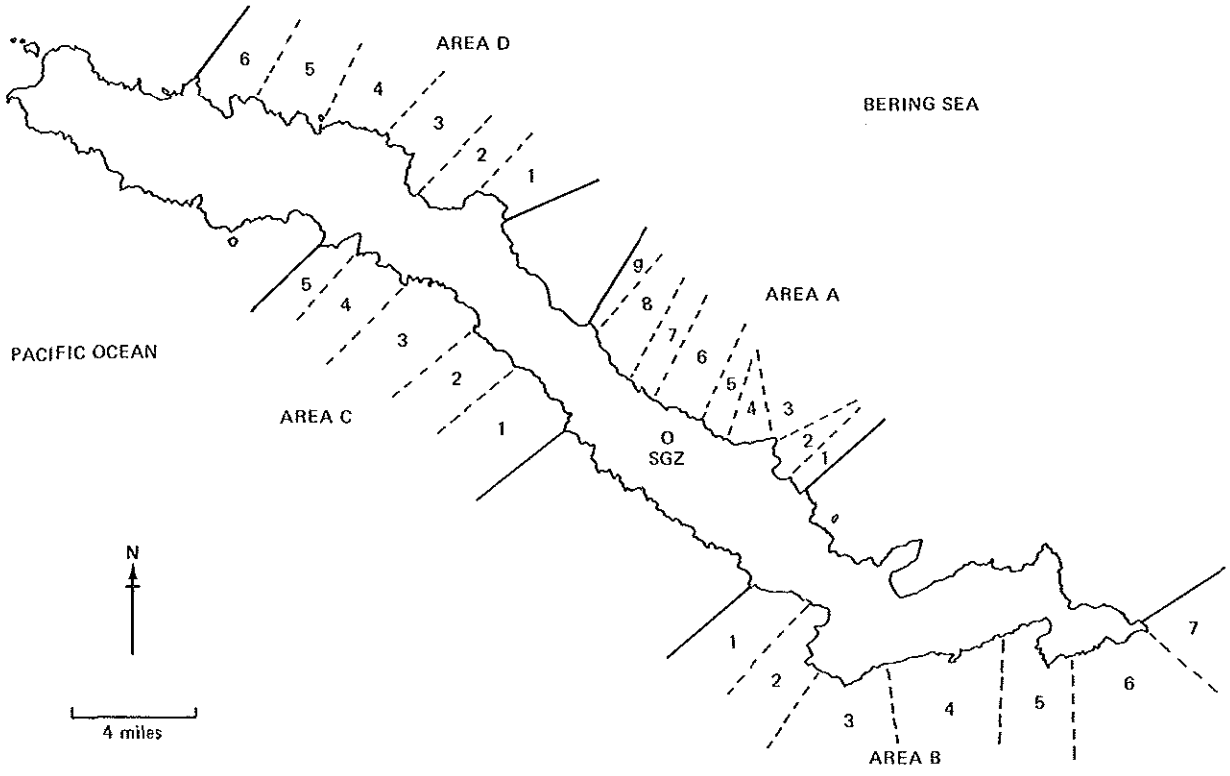

Fig. 2—Map of Amchitka Island showing the location of shore-based counting areas.

counts of contiguous stations. All observable sea otters were counted by scanning the viewing stations from border to border. Some diving animals as well as others in obscure locations on the surface inevitably were missed. However, virtually no animals were counted twice during a scan of the viewing station. At viewing station boundaries, errors were introduced either by counting one animal twice or by not including it in either station. I believe that the mean of these errors tends toward zero because of the large number of observations and the effort that was made to count only those animals within the predescribed boundaries. Kelp beds or offshore rocks were used as markers or reference points between viewing stations.

We made aerial counts around the entire coast of Amchitka Island or along large coastal segments of the island between June 1971 and September 1972. A number of people assisted with these operations, depending on availability. An additional person recorded the number of sea otters observed in 45 segments into which the Amchitka coastline was divided during all island-wide counts (Fig. 3).

The helicopter was flown counterclockwise around Amchitka at an altitude of approximately 150 ft (45 m) and sufficiently close to shore that the near-shore observer could easily see animals onshore. The helicopter pilot was located at the right front of the aircraft. Observers were located at the left-front and right-rear seats, and the recorder sat in the left-rear seat. A zigzag pattern was flown through kelp beds or shallow areas extending far offshore. The same pilot was used throughout the aerial counting operation, and flight patterns remained relatively constant after the first several counts. We frequently flew several miles offshore at the east and west ends of Amchitka and at several other places on the Pacific Ocean coast because these areas are shallower than those along the Bering Sea coast.

A subjective classification of sea state and weather conditions was assigned at the beginning of each counting operation. These conditions frequently changed slightly during the census or between areas around the island.

Viewing classification	Description of conditions
1	Ocean surface glassy. Air clear. Sea otters can be seen at maximum range of 10× binoculars. Viewing conditions excellent.
2	Wind velocity 5 to 10 knots (2.6 to 5.1 m/sec). Light riffle on ocean surface. Sea calm. Sea otters far offshore may not be seen.
3	Water choppy. White caps present.
4	Heavy seas.

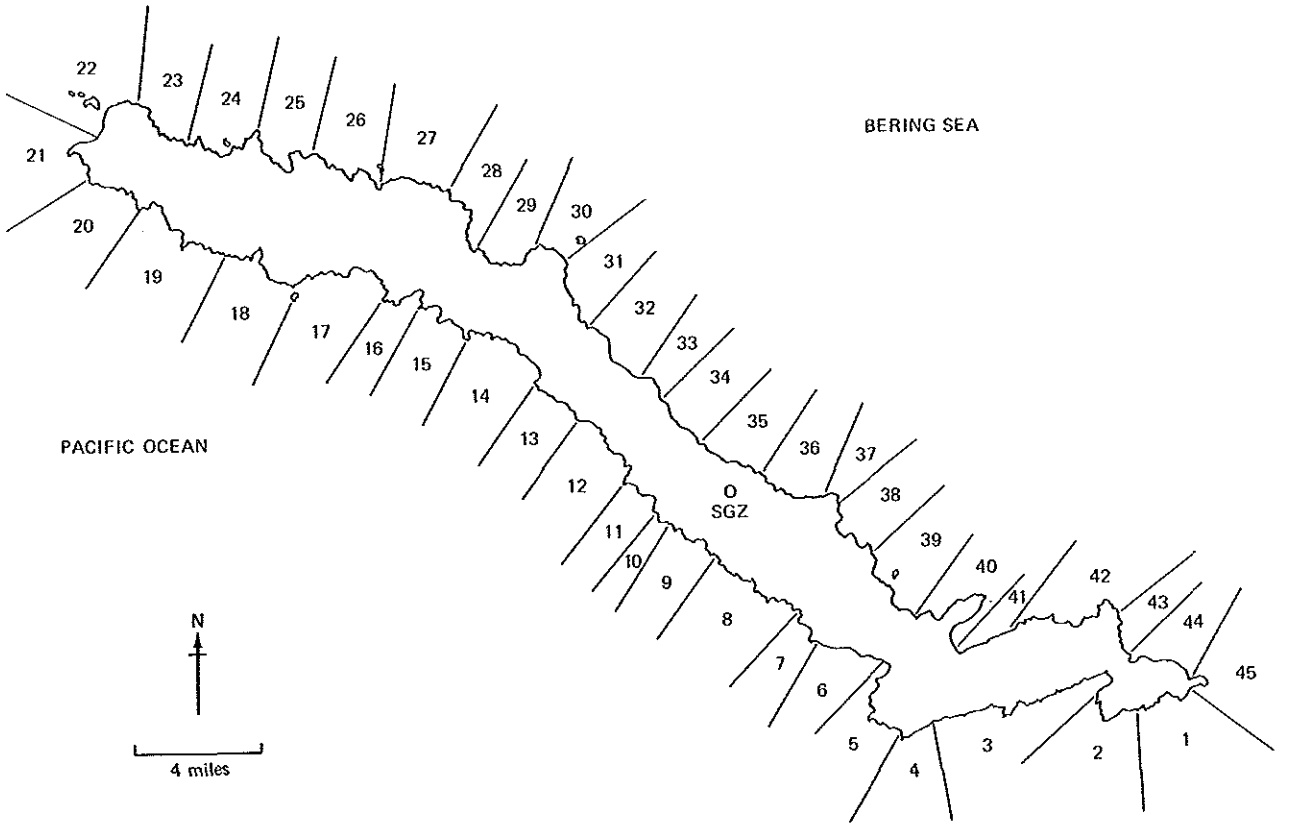

Fig. 3—Amchitka Island showing the shoreline segments used in island-wide aerial surveys.

Aerial counts were made only when the viewing classification was 1 or 2. Reliable shore-based counts could only be made when viewing conditions were nearly perfect (i.e., classification 1). Viewing classifications 3 and 4 are equally inadequate for both shore-based and aerial counting.

RESULTS

Feeding Behavior

The diving and surface times of feeding sea otters at Amchitka Island are summarized in Table 1. The sex of the animals, the approximate depth of water in which they were feeding, and the food items they were eating are also included.

No differences between sexes in either diving or surface times of feeding sea otters are apparent from these data. Female sea otters averaged 50 sec per dive and 43 sec per surface period. Males averaged 50 sec per dive and 41 sec per surface period.

Feeding in deeper water apparently causes an increase of both diving and surface time intervals, although this conclusion must remain tentative because of the small amount of data from animals feeding in deep water. The mean diving and surface times of sea otters feeding in water estimated to be 0 to 5 fathoms (0 to 9 m) in depth were 47 and 41 sec, respectively. The mean diving and surface times of sea otters feeding in water estimated to be between 5 and 15 fathoms (9 to 27 m) in depth were 83 and 84 sec, respectively. Feeding sea otters spend 52% of the time submerged and 48% of the time on the surface.

I attempted to obtain diving and surface times from sea otters feeding in water deeper than 15 fathoms (27 m). Unfortunately the animals took alarm before I could get close enough to obtain any data. Therefore most of my observations on feeding sea otters are from areas less than 5 fathoms (9 m) in depth and where they could be watched from shore.

The available data are insufficient to indicate differences in diving behavior between sea otters feeding on fish or invertebrates. Fish is an important sea otter food item in some areas (Lensink, 1962; Kenyon, 1969; Burgner and Nakatani, 1972). My observations of feeding sea otters indicate that fish are taken opportunistically and that individuals cannot be classified exclusively as either fish or invertebrate feeders.

Diurnal patterns in the activity of sea otters are summarized in Fig. 4. No differences in feeding,

Table 1—Mean Diving and Surface Times, Estimated Water Depth, and Forage Items of 25 Sea Otters Observed Feeding at Amchitka Island

Status of animal	Mean diving time, sec	Mean surface time, sec	Water depth, fathoms	Forage items
Female	42	19	0 to 5	Unknown
Female	44	19	0 to 5	Unknown
Female	43	17	0 to 5	Unknown
Female	37	18	0 to 5	Unknown
Female	47	36	0 to 5	Unknown
Female	38	34	0 to 5	Unknown
Female	48		0 to 5	Unknown
Female	43	31	0 to 5	Invertebrates
Female	55		0 to 5	Fish and invertebrates
Female	79		0 to 5	Fish
Female	44	94	0 to 5	Invertebrates
Female	50	56	0 to 5	Invertebrates
Male	50	25	0 to 5	Invertebrates
Male	38	37	0 to 5	Invertebrates
Male	38	43	0 to 5	Invertebrates
Male	74	60	5 to 15	Invertebrates
Female with pup	36	22	0 to 5	Unknown
Female with pup	90	85	5 to 15	Invertebrates
Female with pup	57	82	0 to 5	Invertebrates
Female with pup	47	39	0 to 5	Invertebrates
Unknown	84		0 to 5	Unknown
Unknown	31	27	0 to 5	Invertebrates
Unknown	47	43	0 to 5	Invertebrates
Unknown	52	71	0 to 5	Invertebrates
Unknown	40	39	0 to 5	Invertebrates
Unknown	86	108	5 to 15	Unknown
$\bar{x}_{Female}$	50 ± 4* n = 16	43 ± 8 n = 13		
$\bar{x}_{Male}$	50 ± 9 n = 4	41 ± 18 n = 4		
$\bar{x}_{0 \text{ to } 5 \text{ fathoms}}$	47 ± 3 n = 23	41 ± 5 n = 19		
$\bar{x}_{5 \text{ to } 15 \text{ fathoms}}$	83 ± 5 n = 3	84 ± 14 n = 3		
$\bar{x}_{Total}$	52 ± 3 n = 26	48 ± 6 n = 22		

*$\bar{x} \pm s_{\bar{x}}$.

resting, or grooming behavior are evident between summer and winter. These seasons represent extremes in daylight and weather. Therefore diurnal patterns in sea otter activity probably are relatively constant throughout the year, at least regarding the amounts of time budgeted for feeding, grooming, and resting.

Two peaks in feeding activity, with concurrent declines in resting activity, are evident during summer days. A peak in feeding occurs about 8:00 a.m. and another peak occurs about 5:30 p.m. Bering Standard Time (subtract 1 hr for local sun time). During winter it is dark at these times. However, a decline in feeding activity from the morning peak is apparent. Diurnal patterns of resting activity of sea otters are inversely related to patterns of feeding activity. The highest percentages of resting animals were during early morning and late evening. An extended peak in resting activity also occurs between about 9:30 a.m. and 3:30 p.m. Grooming activity remains relatively constant throughout the day during both winter and summer.

My observations on feeding sea otters indicate that about 52% of their time is spent submerged. This information, in conjunction with the diurnal feeding pattern, can be used to calculate the expected percentage of the population that is submerged during daylight hours. Let a_i equal the percentage of the population feeding at time t_i. Grooming and resting sea otters spend 100% of the time on the surface and therefore need not be considered. Thus $0.52a_i$ gives an estimate of the percentage of the sea otter population (excluding small pups) that is submerged at time t_i.

The expected percentage of the population that is submerged as a function of time of day is shown in Fig. 5. The increased percentage of the population that is submerged during morning and evening compared with the middle of the day

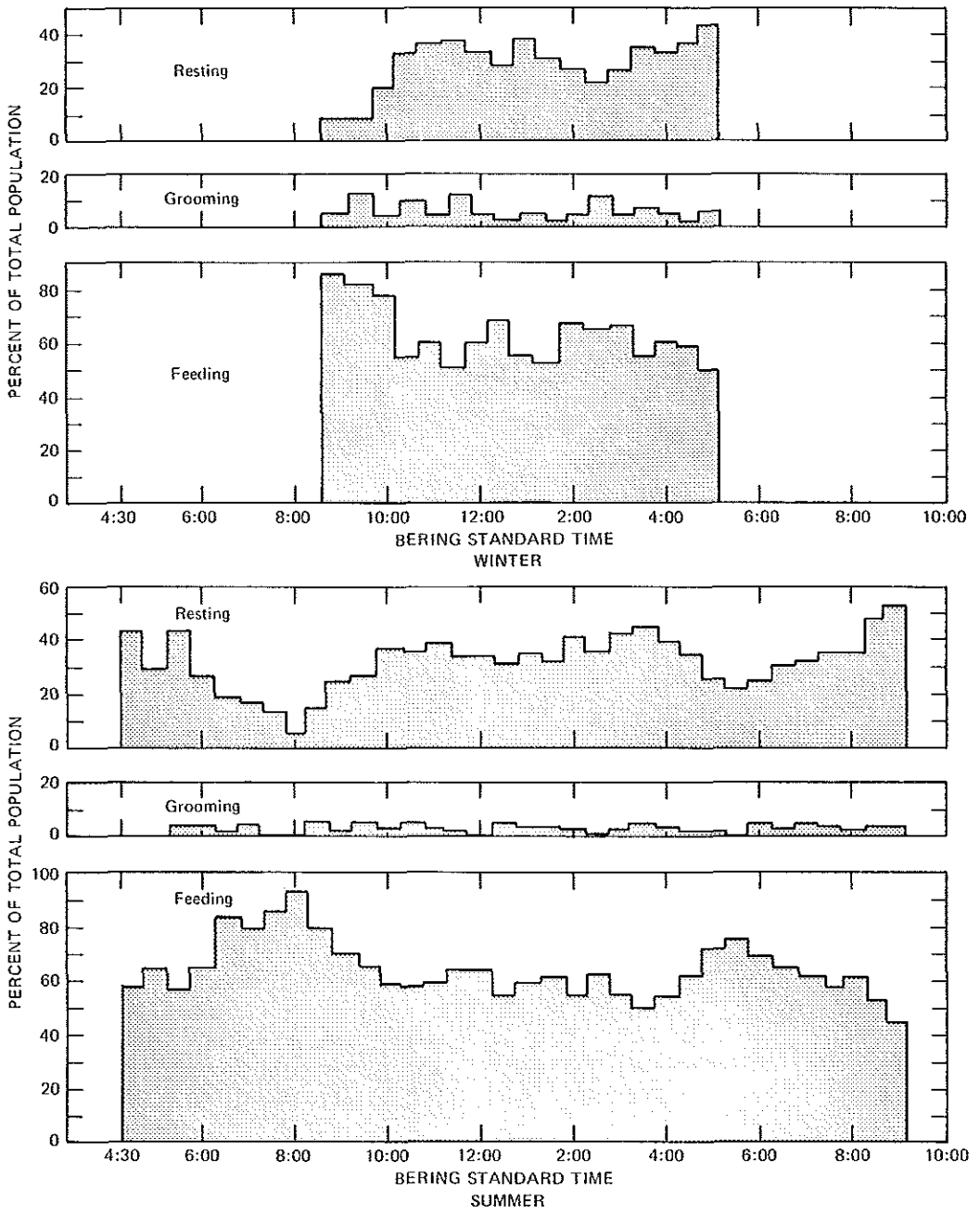

Fig. 4—Diurnal and seasonal patterns in feeding, grooming, and resting activity of sea otters at Amchitka Island.

corresponds with increased feeding activity. Diurnal patterns during summer and winter are generally consistent, and the percentages of the population that are submerged are nearly equal during both seasons.

Kenyon (1969) presented data collected at Amchitka Island which indicate that during the month of August sea otters spend 55% of the time feeding. My data are in general agreement, although they show a somewhat higher percentage of time spent feeding. Of 1758 sea otters that I observed during the winter of 1971, 1095 (or about 62%) were feeding. Sixty-five percent (1910) of 2918 sea otters observed during the summer of 1972 were feeding.

The sea otter population at Attu Island was observed during a 1-day visit to Chichagof Harbor on June 22, 1972. This population probably contained fewer than 100 animals (Kenyon, 1969; personal observation). Several sea otters observed at Attu were feeding on mussels (*Modiolus* sp.), false jingle shells (*Pododesmus* sp.), and sea urchins

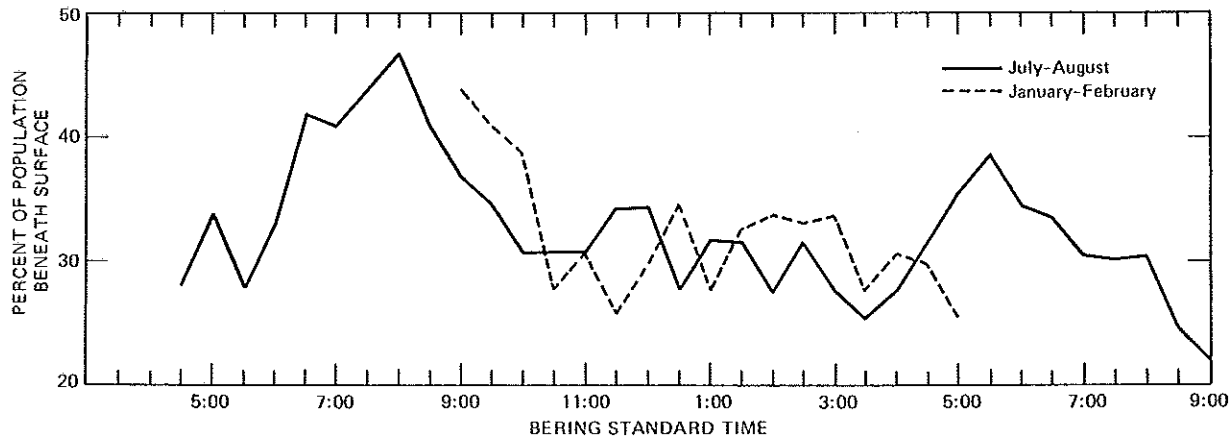

Fig. 5—Diurnal and seasonal patterns of the estimated percentage of sea otters that are submerged at Amchitka Island.

(*Strongylocentrotus polyacanthus*). One sea otter was observed pounding two mussels together on its chest. This behavior also is common to sea otters off the coast of California and is used to break open food items with exoskeletons that are too thick for the animals to open with their teeth. Sea otters at Amchitka rarely pound food, apparently because few large invertebrates are available owing to intense food use there.

I observed no sexual segregation in the sea otter population at Attu. This contrasts with the situation at Amchitka where sexual segregation is well defined.

Estimates of Sea Otter Abundance

The results of island-wide aerial sea otter counts are shown in Table 2. The results of simultaneous shore-based and aerial sea otter counts which were obtained from the study areas shown in Fig. 2 are given in Table 3.

I estimated the number of sea otters at Amchitka by considering simultaneously obtained shore-based and aerial counts and island-wide aerial counts. I assume that shore-based counts accurately represent the abundance of sea otters within localized study areas.

A least-squares technique was used to estimate the sea otter population number (Y_0) at Amchitka Island because, if certain assumptions are satisfied, it provides an unbiased estimate of the parameter (vector). Two linear models for regressing shore-based counts from aerial counts were investigated. Strictly speaking, shore-based counts (Y_i) and aerial counts (X_i), respectively, are random variables representing the *i*th simultaneous observation. A technique for analyzing linear models when X and Y both are random (Acton, 1959) is based on the estimation of any two of the following parameters [Var (X); Var (Y); Cov (X,Y)], which in turn is possible only when repetitive observations of X_i and Y_i are available at some assumed fixed value of the independent variable ξ_i. However, if a linear model, such as $Y_{ij} = \mu + X_i\beta + \epsilon_{ij}$, is fit to the data of this study, there appears to be no means of separately estimating μ, β, and the variances of X and Y. For this reason classical regression procedures in which the X_i are considered fixed will be used.

Model I assumes that the regression of shore-based to aerial sea otter counts passes through the origin. Intuitively, this is a logical assumption because one would expect shore-based and aerial counts in a given area to be related by a simple ratio. However, at Amchitka Island there are large numbers of sea otters in all sufficiently large coastal segments, and therefore the regression function near the X and Y axes is only conceptual. Realistically, shore-based counts and aerial counts within relatively large study areas [i.e., about 10 miles (16 km) of coastline] are both much greater than zero, and a best-fit line through these points may well depart significantly from the origin.

By model I,

$$Y_i = X_i\beta_1 + \epsilon_1 \qquad (1)$$

where Y_i = *i*th shore-based sea otter count (estimated population number within study area)
X_i = *i*th aerial sea otter count within the study area
β_1 = slope of the regression equation
ϵ_1 = error

For an estimate of the total number of sea otters at Amchitka (Y_0), it is sufficient to substitute X_0 into Eq. 1 to give $\hat{Y}_0 = X_0\beta_1$, where X_0 is

Table 2—Numbers of Sea Otters Counted Within Areas Indicated in Fig. 3 During Island-Wide Aerial Surveys

	6/5/72		8/23/72		8/25/72		9/11/72	
Subunit Pacific	No.	Proportion of subtotal	No.	Proportion of subtotal	No.	Proportion of subtotal	No.	Proportion of subtotal
1	31	0.0274	16	0.0068	40	0.0223	55	0.0244
2	79	0.0697	67	0.0284	43	0.0240	64	0.0284
3	165	0.1456	103	0.0436	177	0.0989	96	0.0426
4	25	0.0221	27	0.0114	110	0.0615	82	0.0364
5	99	0.0874	300	0.1270	30	0.0168	223	0.0990
6	39	0.0344	70	0.0296	10	0.0056	84	0.0373
7	78	0.0688	177	0.0749	34	0.0190	120	0.0533
8	66	0.0583	147	0.0622	35	0.0196	113	0.0502
9	44	0.0388	83	0.0351	25	0.0140	156	0.0693
10	46	0.0406	66	0.0279	50	0.0279	77	0.0342
11	59	0.0521	139	0.0588	113	0.0631	66	0.0293
12	28	0.0247	110	0.0466	229	0.1279	84	0.0373
13	55	0.0485	103	0.0436	104	0.0581	26	0.0115
14	30	0.0265	132	0.0559	48	0.0268	158	0.0702
15	22	0.0194	76	0.0322	52	0.0290	42	0.0187
16	23	0.0203	36	0.0152	54	0.0302	85	0.0377
17	44	0.0388	70	0.0296	87	0.0486	55	0.0244
18	45	0.0397	97	0.0410	128	0.0715	111	0.0493
19	35	0.0309	176	0.0745	99	0.0553	97	0.0431
20	48	0.0424	76	0.0322	52	0.0290	137	0.0608
21	72	0.0635	292	0.1236	270	0.1508	321	0.1425
Subtotal	1133		2363		790		2252	
Percent of total	44		60		51		56	

	6/5/72		6/7/72		8/23/72		8/25/72		9/1/72	9/11/72	
Subunit Bering	No.	Proportion of subtotal	No.	Proportion of subtotal	No.	Proportion of subtotal	No.	Proportion of subtotal	No.	No.	Proportion of subtotal
22	84	0.0587	135	0.0881	171	0.1059	120	0.0692	101	168	0.0939
23	50	0.0349	53	0.0346	65	0.0415	37	0.0213	27	33	0.0184
24	69	0.0482	63	0.0411	54	0.0344	84	0.0484	46	49	0.0274
25	68	0.0475	66	0.0431	81	0.0517	91	0.0525	50	64	0.0358
26	71	0.0496	60	0.0392	95	0.0606	50	0.0288	51	42	0.0235
27	45	0.0314	48	0.0313	20	0.0128	20	0.0115	41	52	0.0291
28	41	0.0287	81	0.0529	24	0.0153	32	0.0185	23	58	0.0324
29	45	0.0314	15	0.0098	37	0.0236	50	0.0288	35	43	0.0240
30	98	0.0685	195	0.1273	149	0.0950	129	0.0744	88	132	0.0737
31	31	0.0217	34	0.0222	62	0.0395	101	0.0582	90	93	0.0520
32	51	0.0356	70	0.0457	30	0.0191	87	0.0502	53	45	0.0251
33	59	0.0412	54	0.0352	82	0.0523	78	0.0450	46	123	0.0687
34	38	0.0266	59	0.0385	18	0.0115	41	0.0236	22	63	0.0352
35	43	0.0300	28	0.0183	13	0.0083	41	0.0236	26	50	0.0280
36	40	0.0280	33	0.0215	16	0.0102	104	0.0600	39	77	0.0430
37	67	0.0468	47	0.0307	123	0.0784	60	0.0346	39	87	0.0486
38	42	0.0294	58	0.0379	104	0.0663	35	0.0202	53	100	0.0559
39	69	0.0482	125	0.0816	8	0.0051	149	0.0860	98	119	0.0665
40	37	0.0259	45	0.0294	11	0.0070	25	0.0144	7	20	0.0112
41	7	0.0049	4	0.0026	10	0.0064	28	0.0161	↑	18	0.0101
42	184	0.1286	135	0.0881	106	0.0676	137	0.0790	not	140	0.0782
43	20	0.0140	14	0.0091	43	0.0274	22	0.0127	complete	27	0.0151
44	37	0.0259	73	0.0479	76	0.0485	57	0.0329	↑	79	0.0441
45	135	0.0943	37	0.0242	170	0.1084	156	0.0900		108	0.0603
Subtotal	1431		1532		1568		1734		935	1790	
Percent of total	56				40		49			44	
Total	2564				3931		3524			4042	

Table 3—Comparison of Shore-Based and Aerial Sea Otter Counts from Selected Study Areas Around Amchitka Island*

Date	Viewing conditions	Shore based	Aerial	Study area†	Shore-based to aerial count ratio
5/20/72‡	II (rain)	192	50	A‡	3.84§
5/21/72	II (clear)	641	191	D	3.36§
5/25/72	II	346	172	A	2.01
5/25/72	II–III	420	215	D	1.95
5/26/72	II	343	185	C	1.85
5/27/72	II	382	221	A	1.73
5/29/72	I	602	186	D	3.24
5/29/72	I–II	452	202	A	2.24
6/07/72	I	450	288	A	1.56
8/24/72	I	521	297	A	1.75
8/24/72	I	797	436	D	1.83
8/31/72	II	501	348	A	1.44
			Mean		1.96 ± 0.17 n = 10

*No data were obtained from area B.
†See Fig. 2 for location of these study areas.
‡Only segments 1 to 4 counted.
§Not used in later analysis.

the island-wide aerial count (4042 sea otters). The 4042 sea otter count was the highest island-wide aerial count. I believe this count is most nearly representative of aerial counts made within study areas under near ideal viewing conditions. With the standard least-squares technique of parameter estimation (i.e., by evaluating the normal equations), $\hat{\beta}_1 = 1.82$. An analysis of variance of model I is given in Table 4.

Model II assumes that the regression line is linear but not constrained to pass through the origin. By model II,

$$Y_i = \mu + X_i\beta_2 + \epsilon_2 \qquad (2)$$

where μ is the Y intercept, β_2 is the slope of the regression equation in model II, and ϵ_2 is the *residual error in model II.*

Equation 2 is an estimator of shore-based sea otter counts (or the estimated number of sea otters) within the *i*th study area. If μ proves significant, the $\hat{Y}_i$ must be summed around the entire island rather than simply substituting X_0 for X_i (as in model I) because μ must be accounted for on an island-wide basis. Thus

$$\hat{Y}_0 = \sum_{k=1}^{n} (\hat{\mu}_k + X_k\hat{\beta}_2) = n\hat{\mu} + \sum_{k=1}^{n} X_k\hat{\beta}_2$$

where $\mu_1 = \mu_2 = \ldots = \mu_n$ and n is the number of segments of coastline (which are of similar length to the study areas) contained within the island perimeter. With this method the line is not being extrapolated beyond the data but rather is the sum of interpolated values. The analysis of variance of model II is given in Table 4. Elements of the parameter vector (i.e., μ and β_2) are estimated by the normal equations. To test the significance of μ, I set up two hypotheses: $H_0, \mu = 0$, and $H_a, \mu \neq 0$. By H_0 [total sum of squares − (sum of squares $\hat{\beta}_2$ + sum of squares ϵ_2)]/(mean square ϵ_2) is distributed as $F_{1,8}$. The level of significance was arbitrarily chosen at 0.05; thus $P(F_{1,8} \geqslant 5.32) = 0.05$. Because 253 (the observed value of F) $\geqslant$ 5.32, H_0 was rejected, and model II was used to estimate the island-wide population number. From model II, $\hat{Y}_0 = 1581 + (1.20)(4042) = 6432$ sea otters (an arithmetic error has been pointed out to me in my earlier estimate of 6918 sea otters). Under stated assumptions of the model, this statistic is an unbiased estimate of the number of sea otters at Amchitka. A 95% confidence interval around this estimate is 5226 to 7638 animals.

Figure 6 shows 30- and 50-fathom (55- and 91-m) depth contours around Amchitka. Within the 30-fathom depth contour, there are 38 square miles (or 35% of the total area) on the Bering Sea side of Amchitka and 72 square miles (or 65% of the total area) on the Pacific Ocean side (Kenyon, 1969, p. 150). Data from island-wide population surveys suggest that a greater proportion of the sea otter population lives on the Pacific Ocean side than on the Bering Sea side of the island. On Aug. 23, 1972, when viewing conditions were comparable on both sides of Amchitka for counting sea otters, 40% of the animals were observed on the Bering Sea side and 60% were observed on the Pacific Ocean side. On Sept. 11, 1972, the day of the highest aerial count of the entire island, 44% of the animals were seen on the Bering Sea side and 56% were seen on the Pacific Ocean side. Thus the distribution of the population between the two

Table 4—Analysis of Variance of Model I and Model II Regressions of Shore-Based vs. Aerial Sea Otter Counts

Source	Degrees of freedom	Sum of squares	Mean square
	Model I		
Due to $\hat{\beta}_1$	1	2384250	
Due to ϵ_1	9	102298	11366
Total	10	2486548	
	Model II		
Due to $(\hat{\mu},\hat{\beta}_2)$	2	2412847	
Due to ϵ_2	8	73701	9213
Total	10	2486548	

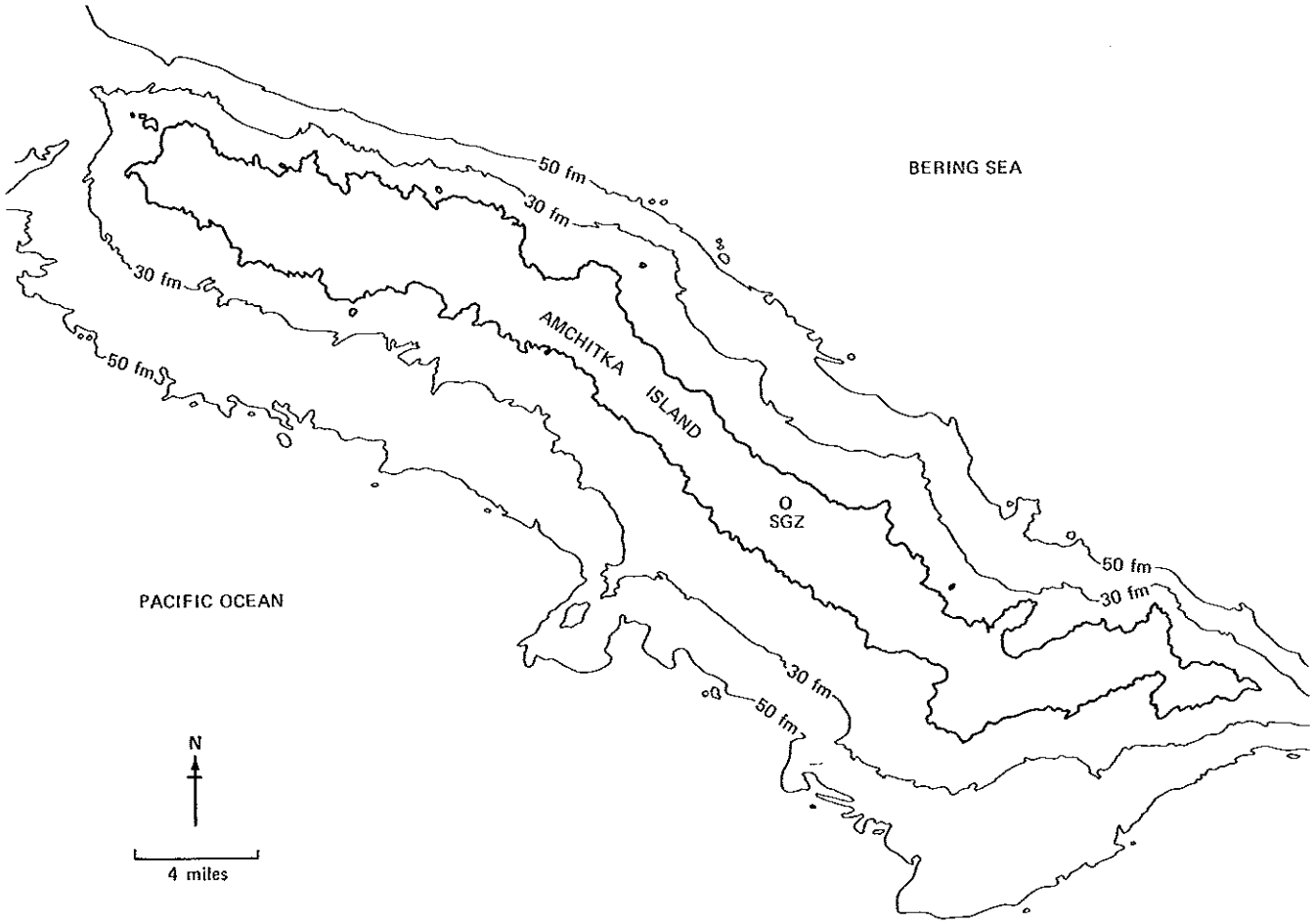

Fig. 6—The 30- and 50-fathom depth contours at Amchitka Island.

sides of Amchitka is similar to the distribution of available habitat.

On the basis of Kenyon's (1969) discussion and my own observations, to estimate roughly the sea otter density at Amchitka, I assumed that most of the sea otters are unable to dive deeper than 30 fathoms (55 m). I also assumed that the entire area within a particular depth contour is usable sea otter habitat and of equal value to the population. Two factors which also may be important but which I have chosen not to consider in the interest of simplicity (and lack of information) are variation in productivity as a function of depth and heterogeneity of substrate type and configuration.

I estimate that 6432 sea otters live at Amchitka, 60% of which are on the Pacific Ocean side and 40% of which are on the Bering Sea side of the island. By assuming that these animals occur within the 30-fathom (55-m) depth contour, I calculated an island-wide sea otter density of 59 animals per square nautical mile (17 per square kilometer) of habitat. This estimate may be divided into 68 animals per square mile (20 per square kilometer) of habitat in the Bering Sea and 54 animals per square mile (16 per square kilometer) of habitat in the Pacific Ocean.

Variable weather conditions and variations in the distribution of sea otters are probably the two most important factors influencing the numbers of animals counted during aerial surveys. I previously mentioned that flat glassy calm seas and high cloud cover provide the most ideal counting conditions. That the distribution of animals is also important is evident from the results of two island-wide counts. On Aug. 25, 1972, we counted 3524 sea otters (island wide) with near ideal viewing conditions. On Sept. 11, 1972, we observed 4042 animals with viewing conditions of light surface chop and occasional rain. On August 25 sea otters were scattered throughout the kelp beds and offshore areas whereas on September 11 large numbers of otters were bunched at the outer edges of kelp beds. Even though superior viewing conditions existed on August 25, a greater island-wide sea otter count was obtained on September 11 because the animals occurred in groups and thus were easier to count than on August 25 when they were more dispersed.

DISCUSSION

Population Time Budget

Prolonged rough seas certainly cause many sea otters to seek shelter near shore (Lensink, 1962; Kenyon, 1969). However, I have observed individuals feeding in extremely rough water, and I also have noted that the number of animals hauled out or concentrated in sheltered areas during severe storms never approaches the number of animals known to inhabit those same areas. I therefore conclude that a substantial portion of the sea otter population at Amchitka is able to maintain itself in the open sea despite inclement weather. This conclusion is supported by the observation that certain sea otter populations in other geographical areas (i.e., north of Unimak Island in southern Bristol Bay) rarely, if ever, come ashore (K. Schneider, personal communication). However, the severe storms common to the Aleutian Islands make observational work difficult, and undetected changes in population behavior may accompany changes in the weather. On calm days at least, I have seen sea otters at distances of about 2 miles from shore.

The similar diurnal time patterns and percentages of feeding activity during summer and winter (Fig. 4) suggest either that sea otters feed during hours of darkness in winter or that less food is consumed by the population during winter than during summer. Because of their high and continual nutritional requirements (Kenyon, 1969; Morrison, Rosenmann, and Estes, 1974; Morrison, Rosenmann, and Estes, Chap. 23, this volume), I believe that decreased food consumption over long periods of time is unlikely. Kenyon (1969) presented evidence that sea otters have well-developed tactile and olfactory senses, and thus it is not inconceivable that they can feed in the absence of light. However, no data are available which prove that sea otters are nocturnal feeders. Therefore the significance of Fig. 4 remains unresolved.

The apparent increase in grooming during winter over summer (Fig. 4) probably is not real but probably is an artifact of limited offshore visibility during winter months. At long distances grooming animals are difficult to distinguish from those which are feeding. Therefore a smaller percentage of the population was identified as grooming during summer months.

A limitation of the observational technique which I have used is that a superficial knowledge of the structure and behavior of the local sea otter population is required before an assumption can be made that the area is representative of the entire population. For example, resting sea otters tend to congregate into groups at traditionally used areas. If these areas are not included in the observation areas, a bias will exist toward feeding activity. Conversely, when poor viewing conditions exist, a bias toward resting activity would be observed in an area where sea otters are resting. For this reason the technique is valid only on days when visibility is such that a sufficiently large (representative) expanse of ocean can be observed. My opinion is that this generally should include at least several miles of coastline. Furthermore, home range, territoriality, individual movements, and factors that relate to spatial strategies of sea otters are not well understood. In view of these unknowns, any supposition that a representative segment of the population is being observed should, at the very least, be considered with skepticism.

In the results section I mentioned a small discrepancy between my data and data collected by Kenyon (1969) on the percentage of time sea otters budget for feeding. Differences between my data and Kenyon's may be the result of different study techniques or real changes in feeding activity since 1955 when his data were collected. As I suggested earlier, the differences that my data indicate between summer and winter feeding activity probably do not represent changes in population foraging strategies.

In contrast to Amchitka, the sea otter population at Attu is far below equilibrium density. This probably results in an abundant food supply for those animals living at Attu. Sea otters observed feeding at Attu were all near shore [I estimated 200 yards (183 m) or less], and they moved only small distances while feeding. Feeding sea otters at Amchitka frequently are scattered to over a mile from shore, and often they move considerable distances during a feeding period. These behavioral differences are probably related to an abundant near-shore food supply at Attu. Conversely, the sea otter food supply at Amchitka probably is being maximally exploited. Sea otters must therefore search more and dive to their maximum capabilities to obtain sufficient food under these circumstances. This probably results in greater amounts of time spent in foraging activity by sea otters at Amchitka compared with those at Attu. Although I have no quantitative data from Attu to compare with the diurnal feeding pattern at Amchitka, most of the animals I saw at Attu were resting.

Sea Otter Population Estimates

For a parameter estimate $\hat{\theta}$ to be of practical utility, it should be unbiased and relatively precise. By definition, a parameter estimate is unbiased if the expected value of that estimate $E(\hat{\theta})$ is equal to

the parameter θ for all θ. In this study θ is the total number of sea otters at Amchitka Island. Bias is the difference between the expected value of the parameter estimate and the true value of the parameter [i.e., $E(\hat{\theta} - \theta)$; Hoel, 1971]. Direct population counts are almost always biased low as estimates of population numbers because some individuals are invariably missed.

An estimate should also be relatively precise. From a set of estimators of θ, the estimate that has minimum variance is referred to as the best estimate. Frequently the estimate with minimum variance is not unbiased and thus perhaps not best in terms of study objectives. Therefore, when one selects an estimation technique, the tolerability of bias and lack of precision should be carefully considered. Obviously estimates with large and unknown bias are only valuable as population indexes and are relatively worthless as estimates of population numbers. Conversely, highly variable estimates, even though they may be unbiased, are of little value unless a large number of repetitions are available. Furthermore the variance of an estimate can be determined through repetition of the sample whereas bias may remain obscure unless specific techniques are developed to evaluate its magnitude and direction. For this reason many investigators in wildlife biology are intuitively more aware of variance than bias. Thus the concepts of bias and precision are critical, and they must be considered carefully when evaluating population estimates. I will consider the sea otter population at Amchitka with these concepts in mind.

The first large-scale studies of sea otters in Alaska were done by the U. S. Fish and Wildlife Service. Usually they censused sea otters from a DC-3 aircraft flying at about 120 knots (222 km/hr) between altitudes of 200 and 400 ft (61 and 122 m). Two observers in the cockpit counted sea otters. From these aerial counts the number of sea otters at Amchitka was estimated to be from about 1500 to 2500 animals between the years 1949 and 1965 (Kenyon, 1969).

On the basis of aerial counts and counts made from headlands with binoculars and a spotting scope, Lensink (1962) estimated that between 4000 and 7000 sea otters lived at Amchitka in 1956. These estimates were dismissed by Kenyon (1969) and apparently were not considered seriously in subsequent work.

Helicopters were first used as vehicles from which to count sea otters by the U. S. Fish and Wildlife Service in 1968. The technique and preliminary results were discussed by Spencer (1969). A single observer seated beside the pilot counted sea otters as the aircraft was flown at about 150 ft (46 m) altitude and at a maximum speed of about 70 knots (130 km/hr). In 1970, 3927 sea otters were counted during island-wide censuses. From this count the population at Amchitka was estimated at slightly over 4000 animals (U. S. Fish and Wildlife Service, unpublished data).

Stephan (1971) used oblique infrared color photography to estimate the number of sea otters at Amchitka. He photographed population concentrations with a helicopter-mounted camera and visually counted additional scattered animals. This technique led him to estimate that Amchitka Island contained . . . "as many but not more than 2800 sea otters" during 1969.

The primary advantage of fixed-winged aircraft (airplanes) as census vehicles is that large areas can be covered in relatively short periods of time. Considering the hundreds of miles of shoreline inhabited by sea otters, from the western Aleutian Islands to Prince William Sound, this technique was most practical for early U. S. Fish and Wildlife Service studies. The primary contribution of these studies was the establishment of trends in sea otter distribution and density over the entire Alaskan range of the species. Many animals undoubtedly were missed because of limitations imposed by the large rapidly flying aircraft.

Kenyon (1969) concluded from his studies that the majority of sea otters live within the 20-fathom (37-m) depth contour, and rarely they are found in waters as deep as 30 fathoms (55 m). Although there are occasional reports of sea otters diving in deeper areas (K. Schneider, personal communication), Kenyon's conclusion defines the area within which counting efforts should be concentrated. This conclusion also implies that coastal areas where the subtidal platform descends gradually will be more difficult to census than areas where the sea otter habitat is narrower.

I believe that the number of sea otters estimated from this study was biased low. In view of techniques and the scope of these investigations, no data were collected with which to estimate the magnitude of bias. Additionally, the relative precision of these estimates is unknown because the censuses were not replicated over sufficiently short time periods.

Data obtained from U. S. Fish and Wildlife Service helicopter censuses which began in 1968 are summarized in Table 5. Only maximum counts are included for each survey period.

Watson, Jolly, and Graham (1969) showed that helicopters are significantly better vehicles than airplanes from which to census terrestrial mammal populations. The primary advantages of helicopters over airplanes as vehicles for counting sea otters are greater maneuverability and slower flying speed.

Table 5—Summary of Aerial and Photogrammetric Sea Otter Counts of Amchitka Island Made Between 1968 and 1972

	Maximum count				
	1968	1969	1970	1971	1972
Bureau of Sport Fisheries and Wildlife*	2302(7)†		3927(5½)†	3241(1)†	
Battelle Memorial Institute‡		2354	2773		
University of Arizona*					4042(4)†

*Visual counts.
†Number in parentheses is the number of counts.
‡Visual and photographic counts.

Thus kelp beds, offshore islands, and otherwise inaccessible areas can be thoroughly searched. Consequently estimates of sea otter numbers at Amchitka Island during these studies are almost twice as large as earlier estimates obtained with airplanes.

Because of the time interval between Kenyon's study and more recent efforts by the U. S. Fish and Wildlife Service, differences in population estimates might be construed as an increase in population size. There is no other evidence to support this argument. In fact, Kenyon (1969) presented data which suggest that the sea otter population at Amchitka Island was limited by food availability during the time of his early studies. I believe that the reported differences in sea otter population numbers are primarily the result of reduced bias. However, there were no attempts during either of these studies (other than by intuition) to statistically estimate bias, and even these later estimates probably greatly underestimated the size of the sea otter population at Amchitka.

All direct visual counts of sea otter populations are distinctly unprecise (i.e., the counts, when repeated, are highly variable). This high variability apparently is correlated primarily with variable viewing conditions and an unpredictable spatial distribution of sea otters. Poor viewing conditions are caused by inclement weather, which prevails almost continuously in the Aleutian Islands. Strong winds may blow at any time of the year, and fog and rain are common during calmer months. Sea otters are most easily seen when seas are glassy calm and the air is clear with a high unbroken overcast. Such ideal viewing conditions are never common but prevail most frequently during late May through early June and late August through late September or early October.

Sea otters also tend to congregate into large groups at times and to scatter in a more random spatial distribution at other times. Clumped distributions of sea otters tend to increase the size of the total counts.

A summary of the sea otter counts that were obtained at Amchitka Island from infrared color photogrammetry is also given in Table 5. The advantage of this technique apparently is a more precise estimate of the population number. Presumably, infrared photography reduces the counting variability due to the effects of weather. This would be an obvious advantage in the Aleutian Islands. However, there are also several disadvantages. Population numbers estimated by this technique were considerably lower than direct visual counts from a helicopter during the same years. Thus, although possibly there is a gain in precision from the photogrammetric technique, it is accompanied by increased bias. Perhaps with further improvements, specifically the development of a method to estimate and correct for bias, photographic or other remote sensing techniques may prove valuable. There are, however, additional disadvantages. The cost is very high. A large amount of film would be required to cover all the sea otter habitat between shore and the 30-fathom (55-m) depth contour, even along relatively small expanses of coastline. Species are also difficult to identify from photographs (i.e., sea otters may be confused with harbor seals).

With a spotting scope from shore-based stations, Lensink (1962) counted about 1.75 times more sea otters in a given area than he was able to see through binoculars. This suggests that many animals at Amchitka Island are distributed far offshore. Lensink's estimate of the number of sea otters at Amchitka Island has been criticized on the basis of overlap between contiguous counting

areas and localized movement of animals. The U. S. Fish and Wildlife Service observers believed that they were seeing 50 to 75% of the sea otter population during counts from airplanes and that Lensink's estimates were biased high (Kenyon, 1969). I believe that Lensink's technique, although not statistically designed to provide an unbiased estimate, applies a logical estimate of correction for bias. The lack of replication precludes any comment on precision.

There are several disadvantages to the shore-based counting technique. During Lensink's study the lack of a helicopter necessitated travel by foot between counting areas. This was a time-consuming process which limited the amount of coastline that could be covered in a single day. Simultaneous shore-based and aerial counts of the same area also were not possible during the period of Lensink's work, thus precluding the development of an index by which shore-based and aerial counts could be compared.

Counting from shore offers the advantage that an adequate amount of time can be spent thoroughly searching for sea otters in a given area. This is important when one considers the large percentage of time spent feeding (and therefore diving) by sea otters at Amchitka. Even during periods of minimum feeding activity, approximately 30% of the population is beneath the surface at any given instant (see Fig. 5). An instantaneous observation of a given area during this time, such as a photograph, will therefore detect approximately 70% of the sea otters in that area. If we assume that individual dives are independent events and that the duration of dives is approximately constant among individuals, the cumulative percentage of surfaced animals will increase approximately as a linear function of time. Furthermore, this cumulative percentage will approach 100% after a time equivalent to the duration of a dive. Thus photographs (or other instantaneous observations), no matter what their quality or how inclusive their area, will never detect more than about 70% of the sea otter population at Amchitka Island. Visual aerial counts are also biased low by the effect of diving animals, but by $100\ t/(s + \mu)$ percent less than are instantaneous observations (McLaren, 1961), where t is the observation time of a given area, s is the surface time of sea otters, and μ is the diving time of sea otters. Also, the observation time required to correct for bias due to diving activity will be greater in deep water (where μ and s are relatively long) than in shallower water (where μ and s are shorter).

In summary, aerial counts are biased estimates of the number of sea otters at Amchitka Island because a large percentage of the population is submerged at any given time. Animals which are on the surface but which simply are not seen contribute further to low bias. Thus I believe even the highest aerial counts are biased low by 30% or more. Shore-based observations on days when surface visibility is very good provide a crude means by which to account for this bias.

ACKNOWLEDGMENTS

This work was supported by contract AT(21-6)-520 to the University of Arizona. I thank C. Abegglen, R. Anthony, S. Brown, G. V. Byrd, J. Faro, R. Glinski, C. Hardy, K. Kenyon, K. Schneider, V. Schultz, N. Smith, L. Sowls, and R. Stein for assistance and helpful comments.

The following people assisted me with shore-based sea otter counts: C. Abegglen and C. Hardy, U. S. Fish and Wildlife Service; J. Faro and K. Schneider, Alaska Department of Fish and Game; R. Anthony, S. Brown, and R. Glinski, University of Arizona.

The following people assisted me with island-wide aerial sea otter counts: C. Abegglen and G. V. Byrd, U. S. Fish and Wildlife Service; K. Schneider, Alaska Department of Fish and Game; R. Anthony and R. Glinski, University of Arizona.

To W. Matthews, a very capable helicopter pilot, I am especially grateful.

REFERENCES

Acton, F. S., 1959, *Analysis of Straight Line Data*, John Wiley & Sons, Inc., New York.

Barabash-Nikiforov, I. I., 1947, Kalan (The Sea Otter) Soviet Ministrov RSFSR. Glavnoe upravlenie po Zapovednikam. (In Russian.) Translated by Dr. A. Birron and Z. S. Cole. Published for the National Science Foundation by the Israel Program for Scientific Translations, Jerusalem, 1962.

Burgner, R. L., and R. E. Nakatani, 1972, Amchitka Bioenvironmental Program. Research Program on Marine Ecology, Amchitka Island, Alaska. Annual Progress Report, July 1, 1970—June 30, 1971, USAEC Report BMI-171-144, Battelle Memorial Institute.

Estes, J. A., and N. S. Smith, 1973, Amchitka Bioenvironmental Program. Research on the Sea Otter, Amchitka Island, Alaska, USAEC Report NVO-520-1, Nevada Operations Office.

Hoel, P. G., 1971, *Introduction to Mathematical Statistics*, John Wiley & Sons, Inc., New York.

Kenyon, K. W., 1969, *The Sea Otter in the Eastern Pacific Ocean*, U. S. Department of the Interior, Bureau of Sport Fisheries and Wildlife, North American Fauna, No. 68.

Lensink, C. J., 1962, The History and Status of Sea Otters in Alaska, Ph. D. Thesis, Purdue University, Xerox University Microfilms, Ann Arbor, Mich.

McLaren, I. A., 1961, Methods of Determining the Numbers and Availability of Ringed Seals in the Eastern Canadian Arctic, *Arctic*, 14: 162-175.

Morrison, P., M. Rosenmann, and J. A. Estes, 1974, Metabolism and Thermoregulation in the Sea Otter, *Physiol. Zool.*, 47: 218-229.

Spencer, D. L., 1969, Amchitka Bioenvironmental Program. Sea Otter Surveys, Amchitka Island, Alaska, August 27–October 6, 1968, USAEC Report BMI-171-120, Battelle Memorial Institute.

Steel, R. G. D., and H. J. Torrie, 1960, *Principles and Procedures of Statistics*, McGraw-Hill Book Company, New York.

Stephan, J. G., 1971, Bioenvironmental Surveillance Employing Photogrammetric Techniques, *BioScience*, 21: 677-682.

Watson, R. M., G. M. Jolly, and A. D. Graham, 1969, Two Experimental Censuses, *East Afr. Agric. For. J.*, Special Issue Vol. XXXIV: 60-62.

22

Ecological Interactions Involving the Sea Otter

*John F. Palmisano**
Fisheries Research Institute, University of Washington
James A. Estes†
Cooperative Wildlife Research Unit, University of Arizona

A comparison of western Aleutian Islands with and without sea otters shows this species to be important to the organization of the nearshore communities. Sea otters control herbivorous invertebrate populations and indirectly affect wave exposure and the composition of the rocky intertidal community. The removal of sea otters causes increased herbivory and ultimately results in destruction of macrophyte associations. Our observations suggest that a dense sea otter population indirectly supports fauna associated with macrophyte primary productivity.

One of the most striking features of the nearshore community at Amchitka Island is the dense population (approximately 6400 animals) of sea otters, *Enhydra lutris* (Estes and Smith, 1973; Estes, Chap. 21, this volume). The estimated density of 17 sea otters per square kilometer (59 animals per square nautical mile) of feeding habitat, waters 55 m (180 ft) or less in depth (Kenyon, 1969), is one of the highest concentrations of this predator ever recorded (Estes and Palmisano, 1974; Estes, Chap. 21, this volume; Lowry and Pearse, 1973; Kenyon, 1969; and Odemar and Wilson, 1969). The high density of sea otters and the importance of predation in structuring communities, as noted by Paine (1966; 1971), Harper (1969), and Addicott (1974), suggest a major role for the sea otter in the organization of the nearshore community at Amchitka Island.

NEARSHORE COMMUNITY

Definition. For purposes of this discussion, the nearshore community comprises that group of organisms (marine, avian, and terrestrial) inhabiting either side of the shoreline and dependent either exclusively on the marine environment or on both the marine and terrestrial environments for some resource. For convenience the marine portion of this community has been divided into two areas: (1) the intertidal area, or that part of the shore alternately flooded by water and exposed to air by the rhythmic movements of the tides; and (2) the subtidal area, or that area from lowest lower low water to the 55-m (180-ft) depth contour.

FACTORS CONTROLLING THE STRUCTURE OF MARINE COMMUNITIES

Island Biogeography. To properly understand the marine community of Amchitka, we must realize that the study of island communities presents a special problem in the explanation of community composition. Although environmental factors operate here as at the edge of continents, species richness, immigration rates, and extinction rates are different on islands (MacArthur and Wilson, 1963; 1967; Carlquist, 1965; 1973). The number and kind of species on islands are directly related to the dispersal abilities of organisms, to the distance from source areas, and to island size (MacArthur and Wilson, 1967). Large islands and islands nearer to source areas have more species than do small or distant islands. Thus organisms may be absent from islands simply because they failed to arrive or because, if the island is small, they have become extinct. As in all geographical areas, physical and biological factors also may prevent colonization.

Not all work on island biogeography has been theoretical. Results of field studies (Preston, 1962; Simberloff and Wilson, 1970; Diamond, 1969; 1973) are in agreement with most theoretical arguments. However, most work has been on

*Present address: National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, Alaska.
†Present address: U. S. Fish and Wildlife Service, National Fish and Wildlife Laboratory, Marine Mammal Substation, Anchorage, Alaska.

terrestrial groups of organisms and may not be applicable to marine communities.

Tidal amplitude affects intertidal community structure (Ricketts and Calvin, 1968). It also tends to be less extreme on islands than on continents, a situation that may produce differences in intertidal communities between islands and continents. In terrestrial communities increased island size increases species richness through the direct effect of area and through increased physical heterogeneity. In marine communities increased island size probably affects species diversity but not necessarily because of increased physical heterogeneity. There is little reason to expect the intertidal area of a large island to be physically more heterogeneous than a small island. The intertidal environment is not extensive, vertically or horizontally, and does not have the same possibilities for physical heterogeneity as does the more expansive terrestrial environment.

The reproductive strategies of many marine organisms strongly influence their ability to disperse and colonize (Vance, 1973; Strathmann, 1974). For example, organisms with pelagic larvae frequently may reach oceanic islands. However, they may fail to colonize because the same currents on which they arrived also may remove their larvae. These species might be successful colonists only in embayments or on coastlines devoid of currents or otherwise where new larvae arrive periodically. Organisms with nonpelagic larvae are poor dispersers, but, once they reach an island, they should colonize more successfully and thus should be more common on continental islands, in archipelagoes, or on older islands. More simply stated, species with pelagic larvae may be capable of rapid and extensive colonization but probably are subject to high extinction rates. Conversely, nonpelagic larvae may restrict or inhibit dispersal but probably facilitate low extinction rates.

Because Amchitka is an oceanic island (i.e., its biota is not a relict from a continental land mass), the composition of its marine community is determined primarily by dispersal capabilities of marine organisms and secondarily by physical and biological factors. Organisms may be absent from Amchitka because of local extinctions caused by stochastic events (i.e., severe weather and food shortage) and by coactive forces (competition and predation). Extensive predation by dense populations of sea otters may lead to local extinction of prey species and associated communities. Competition from dense populations of sea otters may cause other species to become locally extinct. Where sea otters themselves become locally extinct, e.g., the Near Islands, organisms and communities associated with dense populations of this predator may also disappear. These and other factors will be considered in the assessing of the role of sea otters in the community ecology of Amchitka.

Physical and Biological Factors. For years physical factors were considered to be largely responsible for the distribution and composition of plants and animals in marine communities. This concept was especially popular for intertidal communities where physical and chemical tolerances of plants and animals were thought to correspond to physical and chemical ranges of environmental factors, such as wave shock, substratum, temperature, and dissolved gases, that existed at different tidal levels. Thus the resulting assemblages of plants and animals into vertical zones were believed to result primarily from air exposure within different vertical levels in the intertidal area (Doty, 1946; Hewatt, 1937; Newell, 1970). Light was considered responsible for the distribution of subtidal algal associations (Neushul, 1965; 1967; Kain, 1966; Crossett, 1967; Blinks, 1955; Haxo and Blinks, 1950).

Recent works in the marine rocky intertidal area by Connell (1961a; 1961b; 1970; 1972), Paine (1966; 1969; 1971), Dayton (1971), and others have aptly demonstrated that biological factors (predation and competition) are extremely important in influencing composition and structure in rocky intertidal communities. Connell contends that the upper limits of plants and animals are probably determined by physical factors and that lower limits are set by biological factors. Vadas (1968) and Paine and Vadas (1969) have demonstrated that grazing affects the distribution of subtidal algal associations.

Another advance in marine ecology has been the recognition of key species responsible for determining structures and dynamic relationships within communities. Paine (1969) has referred to these as "keystone species." They are usually predators or herbivores whose feeding activities profoundly affect community structure.

Effects of Grazing on Marine Vegetation. Destruction of subtidal and intertidal kelp and seagrass beds as a result of overgrazing by dense populations of sea urchins has been observed over a wide geographical range. Himmelman and Steele (1971) believe that sea urchins are responsible for the scarcity of noncoralline algae in many coastal areas of Newfoundland. Kain and Jones (1965) stated that grazing by sea urchins determines the vertical distribution of algae on the Isle of Man. Kitching and Ebling (1961) and Jorde and Klavestad (1963) found that the distribution of dense sea

urchin populations and abundant algal growth were almost mutually exclusive in the sublittoral area of the northeastern Atlantic Ocean. Dayton, Rosenthal, and Mahan (1973) reported a reduced macrophyte association due to sea urchin grazing in the Chilean archipelago. The reduction of benthic macrophyte populations by sea urchin grazing along the coast of California has been described by North (1965) and in the Gulf of Mexico by Camp, Cobb, and Van Breedveld (1973). The removal of sea urchins by experimental manipulation (Paine and Vadas, 1969; Kitching and Ebling, 1961) and by accidental oil spills (Nelson-Smith, 1968) has resulted in the development of extensive beds of marine vegetation. Because community structure differs in the presence or absence of these beds (Limbaugh, 1955; Kitching and Ebling, 1961; McLean, 1962; North, 1965; Quast, 1968) and because prey density in the marine environment can be significantly influenced by predation (Paine, 1966; 1971; Porter, 1972), the structure of a marine community should be affected by the intensity of herbivore predation.

SEA OTTERS

Trophic Level, Food Habits, and Energy Requirements. The sea otter is a top carnivore in the nearshore trophic–dynamic ecosystem at Amchitka Island. It is also an opportunistic feeder, preying primarily on benthic invertebrates, especially sea urchins, and bottom fishes (Lensink, 1962; Kenyon, 1969; Burgner and Nakatani, 1972). Adult captive sea otters require 20 to 23% of their body weight in food daily, and in the natural environment energy requirements are perhaps even greater (Kenyon, 1969; Morrison, Rosenmann, and Estes, 1974; Morrison, Rosenmann, and Estes, Chap. 23, this volume). In view of the preceding discussion and of the abundance of sea otters at Amchitka and considering that the average sea otter weighs about 23 kg (50 lb) (Kenyon, 1969), we estimate that about 35,000 kg km^{-2} $year^{-1}$ (200,000 lb square $mile^{-1}$ $year^{-1}$) of animal biomass is removed by the sea otter in foraging activities (Estes and Palmisano, 1974).

HYPOTHESIS OF SEA OTTER PREDATION

We suggest that sea otters affect the structure of the nearshore community at Amchitka, and their presence or absence is the prime cause for differences observed between nearshore communities at Amchitka, Adak, Shemya, and Attu Islands (Table 1 and Fig. 1). Our hypothesis holds that a dense population of sea otters controls sea urchins, which, when uncontrolled, can consume and destroy large quantities of kelp. The resultant release from grazing pressure permits an increase in the size of nearshore and intertidal kelp beds and associated communities (Jones and Kain, 1967; Paine and Vadas, 1969). Thus we hypothesize that sea otters are responsible for the extensive subtidal and intertidal kelp beds and for the lack of dense populations of certain benthic invertebrates in the subtidal and intertidal communities at Amchitka.

A corollary to this hypothesis is that a small population or the absence of sea otters enables the sea urchin population to increase, which in turn causes a significant reduction in the size of kelp beds and associated communities. The absence of large offshore kelp beds increases exposure to the intertidal area because all wave energy now reaches shore. Increased herbivory and exposure provide open patches in intertidal kelp beds which permit settling and establishment of sessile invertebrate populations.

Thus we hypothesize that the primary influence of sea otter predation is on subtidal communities; however, the intertidal area also is directly affected by sea otter predation at high tide. Indirectly, sea otter predation affects intertidal communities by reducing grazing pressure on subtidal–intertidal transients, by reducing recruitment, and by decreasing the physical shock of wave impact by permitting the presence of large kelp beds.

STUDY AREA

Location and Description

Field observations were made at Amchitka periodically from October 1970 to August 1973, at Shemya for 1 week each in September 1971 and July 1972, at Attu for 4 days in July 1972, and at Adak for 9 days in September 1972. An estimate of sea otter population at each island studied is given in Table 2. All these islands except Adak have well-developed intertidal rock benches. Only Amchitka has extensive offshore kelp beds and large accumulations of drift kelp [up to 0.7 m (2.3 ft) deep and 7 m (23 ft) wide] along the shoreline. The climate, sea conditions, tidal ranges, and mean tidal levels are comparable at all four islands (U. S. Department of Commerce, Coast and Geodetic Survey, 1968; personal observation).

Amchitka. The most prominent physical features of the marine environment of Amchitka (Fig. 2) are the uniform maritime climate (Armstrong, Chap. 4, this volume) and the extensive intertidal rock platform (bench) that extends seaward from the base of cliffs surrounding much of the perimeter of the island (Gard, Chap. 2, this volume; Lebednik and Palmisano, Chap. 17, this volume).

Table 1—Major Biological Features of Nearshore Communities at Four Western Aleutian Islands, 1971–1973

Island	Sea otter population	Sea urchin		Benthic algal beds	Barnacle and mussel populations on intertidal bench
		Size	Population		
Amchitka	Dense	Small	Sparse	Extensive and little grazed	Sparse
Adak	Dense	Small	Sparse	Extensive and little grazed	Sparse
Attu	Sparse	Large	Dense	Sparse and heavily grazed	Dense
Shemya	None	Large	Dense	Sparse and heavily grazed	Dense

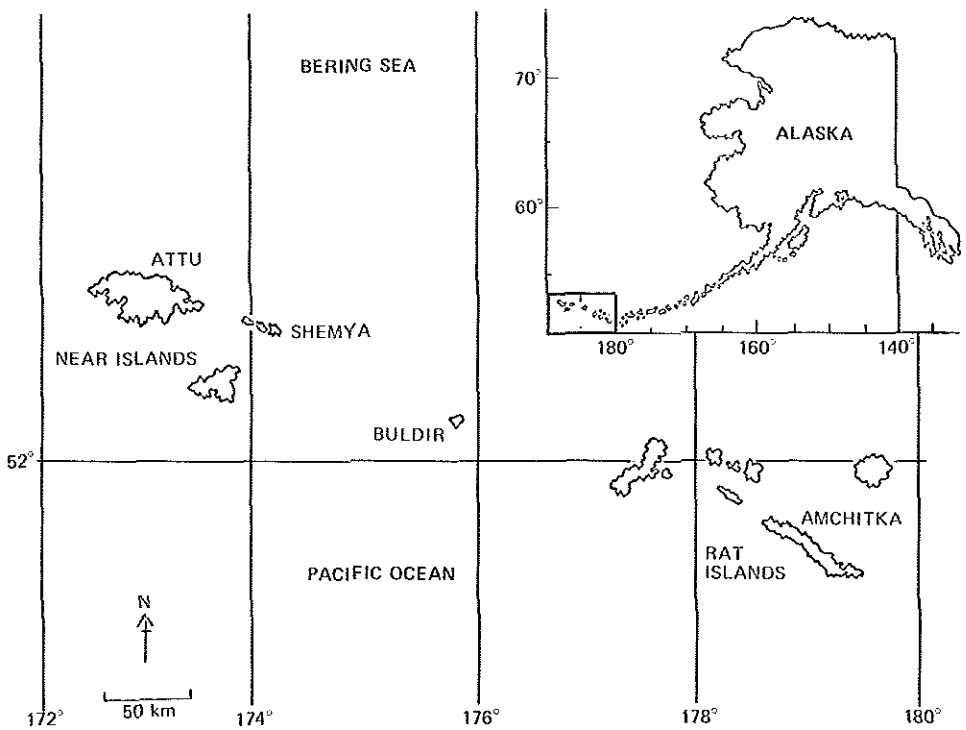

Fig. 1—Map of western Aleutian Islands showing the Near and Rat Island groups.

The landward edge of the bench is almost always adjacent to cobble or sand beaches, but at times it terminates against rock faces. The bench is not continuous around the island but is interrupted by cobble or sand beaches. The elevation of the bench is approximately mean sea level (Powers, Coats, and Nelson, 1960). The bench is best developed along the Pacific Ocean side of the island where it is 100 m (330 ft) wide in places (Fig. 3). The bench is flat, porous, and soft enough in most places (except at headlands) to fasten nails with a hammer and even to be pulled apart by hand. Channels, tide pools, boulders, and sea stacks (Lebednik and Palmisano, Chap. 17, this volume) are not abundant but do occur.

Headlands and areas with narrow or no intertidal benches are more exposed to wave action than are bays, harbors, and areas with a wide bench. Offshore kelp beds also protect the shoreline from wave action, as Moore (1958), Lewis (1964), and MacGinitie and MacGinitie (1968) have observed elsewhere. These more-protected areas have more silt deposition than do areas exposed to waves. In general, the intertidal bench on the Bering Sea is narrower (Fig. 4) and thus more exposed than the intertidal bench on the Pacific Ocean, even though the Pacific Ocean is more turbulent than the Bering Sea (Gard, Chap. 4, this volume).

Tidal range is approximately +2.3 to −0.7 m (+7.5 to −2.3 ft). Mean tide level is approximately +0.5 m (+1.6 ft). Spring tides are diurnal (one high and one low per day). Neap tides are mixed semidiurnal (two highs of unequal levels and two

Table 2—Sea Otter Counts, Estimates, and Densities at Four Western Aleutian Islands, 1932–1972

Year	Otters counted	Otters estimated	Otters estimated per square kilometer of habitat	Source
		Attu		
1932*	0	0	0	Kenyon, 1969
1959	0	0	0	Kenyon, 1969
1965	13	ND†	ND	Kenyon, 1969
1972	25	ND	ND	Estes and Smith, 1973
		Shemya		
1932*	0	0	0	Kenyon, 1969
1959	0	0	0	Kenyon, 1969
1965	10	ND	ND	Kenyon, 1969
1971	0	0	0	Personal observation
1972	0	0	0	Personal observation
		Amchitka (377 km^2 of habitat)‡		
1936	814	3100	8	Kenyon, 1969
1937	1321	3302	9	Kenyon, 1969
1939	1355	3387	9	Kenyon, 1969
1943	3417	4556	12	Kenyon, 1969
1949	1087	1449	4	Kenyon, 1969
1959	1560	2080	6	Kenyon, 1969
1965	1144	1520	4	Kenyon, 1969
1968	2302	3940	10	Estes and Smith, 1973
1969	2354	4029	11	Estes and Smith, 1973
1970	2773	4746	13	Estes and Smith, 1973
1971	3241	5547	15	Estes and Smith, 1973
1972	4042	6432	17	Estes and Smith, 1973
		Adak (257 km^2 of habitat)		
1947*	0	0	0	Kenyon, 1969
1951	0	0	0	Kenyon, 1969
1952	0	0	0	Kenyon, 1969
1954	48	80	<1	Kenyon, 1969
1957	399	997	4	Kenyon, 1969
1959	1718	2291	9	Kenyon, 1969
1962	2260	3013	12	Kenyon, 1969
1965	1336	1781	7	Kenyon, 1969
1972	ND§	ND§	ND§	Personal observation

*These islands had sea otter populations prior to the period of unregulated hunting (1741–1911), especially where Aleut populations were small or absent (see Kenyon, 1969).

†ND, no data.

‡The increase of population estimates of sea otters at Amchitka after 1965 probably reflects improved survey technology and should not be construed as a real increase in abundance. (See Estes, Chap. 21, this volume, for details.)

§Although no counts or estimates were made, sea otter densities appeared to be similar to those observed at Amchitka in 1972.

lows of unequal levels per day). Low tides occur during daylight in spring and summer and at night in autumn and winter. The intertidal area has been divided into three regions: (1) supralittoral fringe, (2) midlittoral region (*Fucus, Hedophyllum,* and *Alaria* zones), and (3) sublittoral fringe (*Laminaria* zone) [see Lebednik and Palmisano (Chap. 17, this volume) for complete details]. The annual range of ocean temperature is 3 to 9°C, and salinity varies from 27 to 35 parts per thousand. The sea is ice-free year round. It is shrouded in fog during summer and stormy during all seasons.

Most of our studies were conducted on the southeast portion of the island. Intensive studies were made at Makarius Bay,* Rifle Range Point, and Duck Cove on the Pacific Ocean side and at Square Bay, Cyril Cove, Bat Island, Kirilof Point, Kirilof Rocks, Constantine Point, and Constantine Harbor on the Bering Sea side (Fig. 5).

Shemya, Attu, and Adak. We were unable to observe annual variations in biotic and nonbiotic

*Also known as St. Makarius Bay.

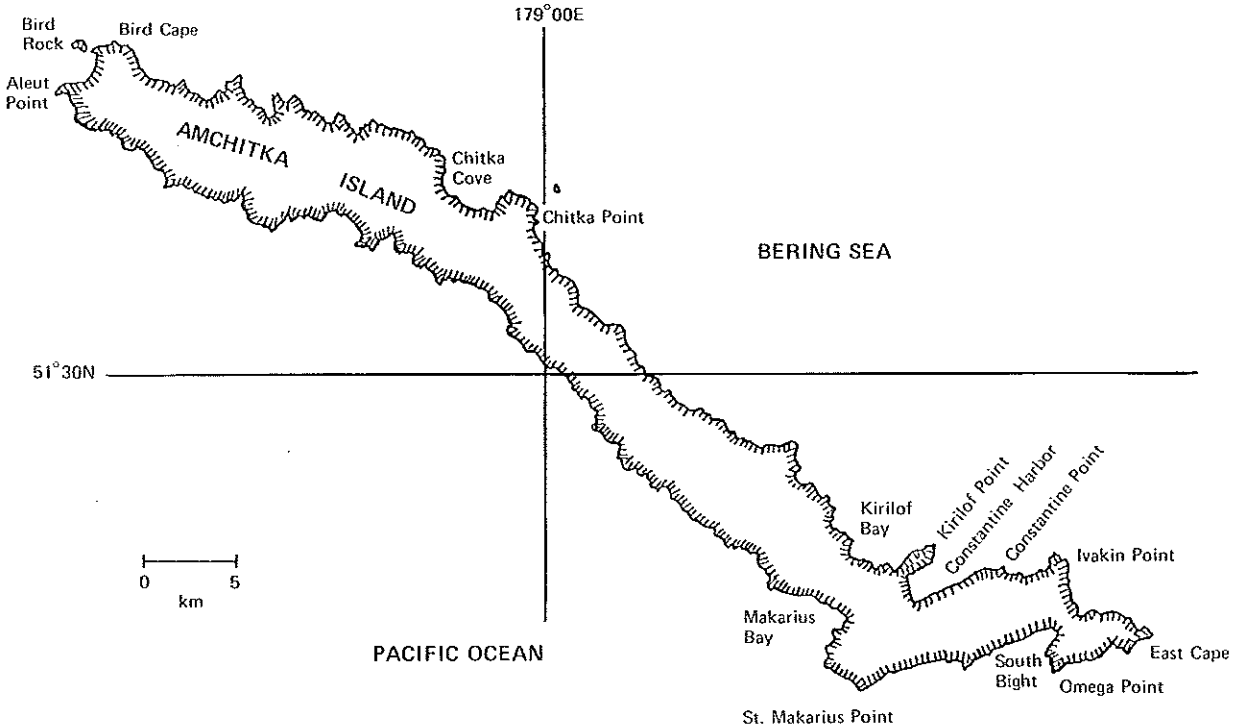

Fig. 2—Map of Amchitka Island, Alaska.

Fig. 3—Wide intertidal rock bench at low tide south of Rifle Range Point on the Pacific Ocean coast of Amchitka Island, Alaska (Aug. 7, 1971).

Fig. 4—Narrow intertidal rock bench at low tide south of Square Bay on the Bering Sea coast of Amchitka Island, Alaska (Aug. 22, 1971).

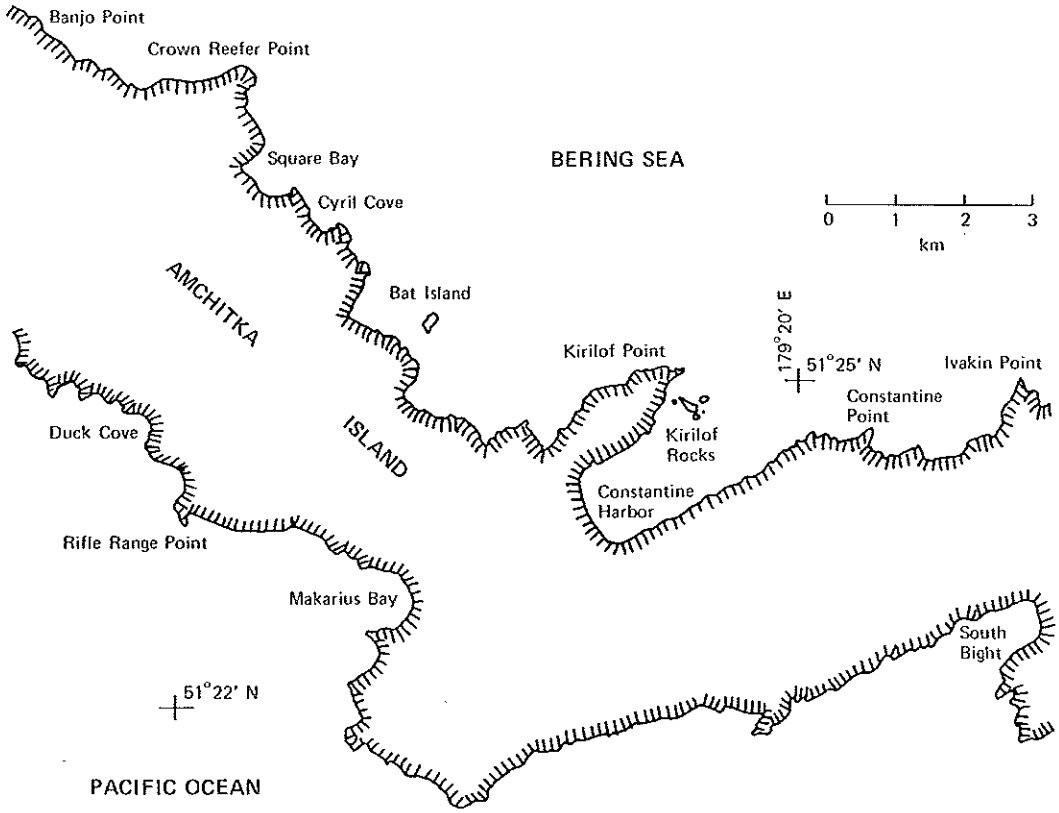

Fig. 5—Map of southeastern portion of Amchitka Island, Alaska, showing study areas referred to in this chapter.

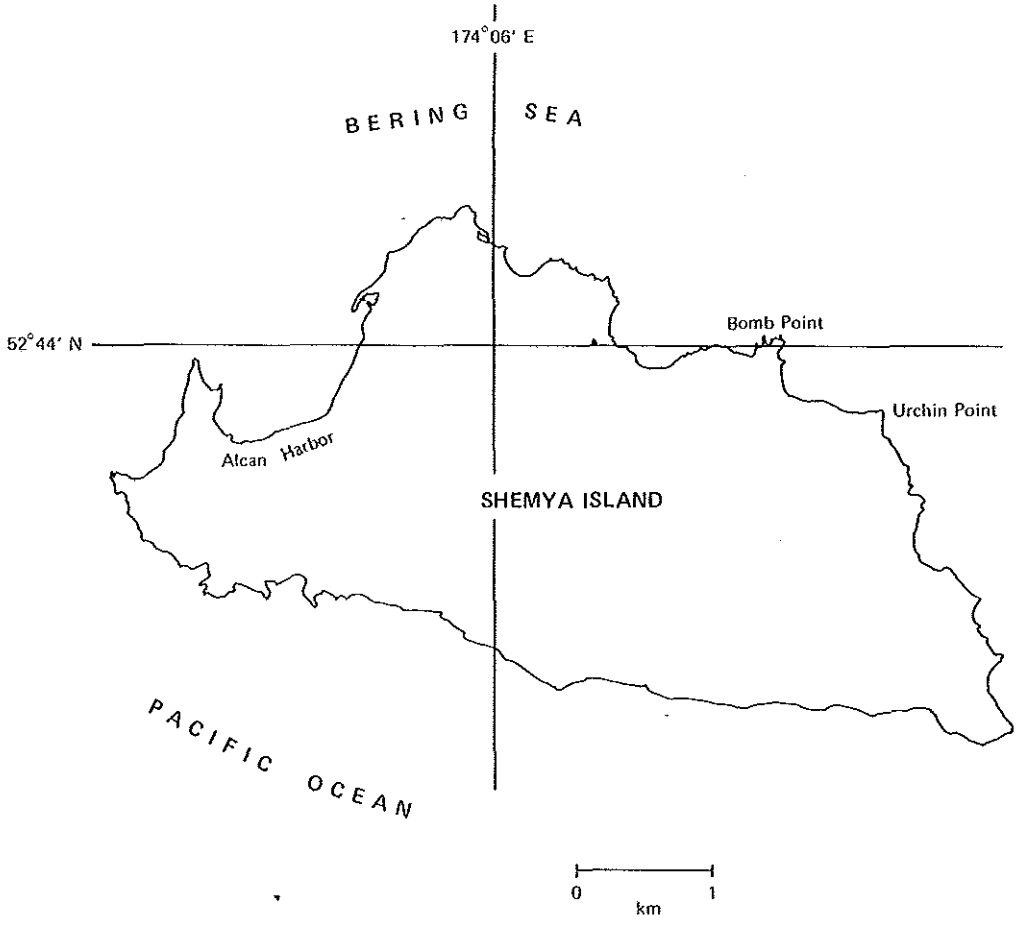

Fig. 6—Map of Shemya Island, Alaska, showing study areas referred to in this chapter.

factors at these islands because they were visited only once or twice for short periods of time. However, conditions observed at these islands (climate, water temperature, salinity, and seasonal development of invertebrate and algal communities) were comparable to those at Amchitka during similar times of the year.

Shemya is significantly smaller than the other three islands. A road adjacent to the shore circles the island and provides complete access to the shoreline. The Bering Sea side has a continuous sand beach. The Pacific Ocean side has a rocky shoreline composed mostly of boulders and cobble. There are well-developed benches on the northeast portion of the island at Bomb Point and Urchin Point (these names were assigned by the authors), which were the primary study areas (Fig. 6). The benches are similar to those at Amchitka except that they have more and larger tide pools.

Attu is larger than Amchitka. The intertidal area is generally inaccessible because of the lack of roads, and thus only a small portion of the eastern end of the island was visited (Fig. 7). Here the intertidal area contained rock benches and cobble beaches similar to those at Amchitka. The well-developed bench at Massacre Bay was the primary study area (some gravel areas occurred on this bench). Murder Point and Chichagof Harbor were also studied.

Adak is similar to Attu in size, and its coastline is also generally inaccessible because of the lack of roads. Its many bays and harbors are protected from the open sea. Only a small portion of the northeastern corner of the island was visited (Fig. 8). Here the intertidal area is predominantly steep cobble beaches. There are also sand beaches and areas of large boulders. Adak does not have well-developed intertidal benches, although some narrow benches [10 to 15 m (33 to 50 ft) wide] at Kuluk Bay and at Cape Adagdak were studied. A large number of boulders and small sea stacks made the bench surface irregular. Because of these features and the vertical walls adjacent to the bench, Adak has more vertical space in the intertidal area than the other islands studied. Zeto Point, Finger Bay, the breakwater at Sweeper Cove, and Clam Lagoon were also studied.

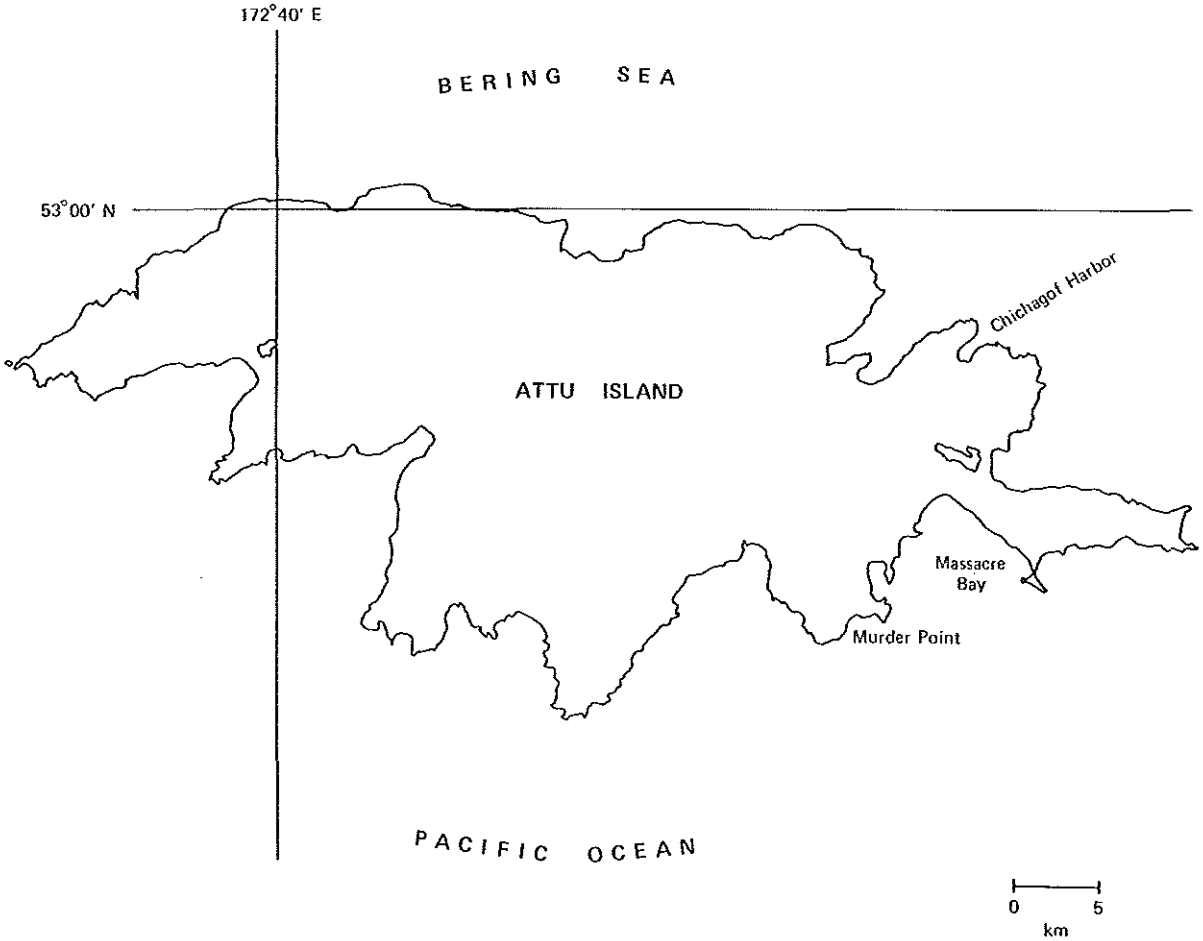

Fig. 7—Map of Attu Island, Alaska, showing study areas referred to in this chapter.

METHODS

Rationale

Islands often may serve as natural experiments for testing biological hypotheses (Carlquist, 1965; MacArthur and Wilson, 1967; MacArthur, 1972). The advantage of this method is that certain variations among islands may be considered experimental treatments, and thus results can be obtained immediately. The disadvantage is that geographically isolated islands are allopatric; thus uncontrolled extraneous variation may creep into interpretations of results more than in well-controlled experiments.

The direct manipulation of sea otter population densities in the western Aleutian Islands (by introducing or removing animals) would have revealed their role in structuring nearshore communities. Such a study was not possible owing to resource and time limitations. We attempted, however, to determine the role of the sea otter indirectly by (1) comparing nearshore communities of nearby islands similar in most respects except for sea otter densities; (2) comparing in time nearshore communities at islands where sea otter densities have recently undergone large changes (Amchitka and Adak); and (3) observing, manipulating, and experimenting with organisms (primarily invertebrates and kelp) that we suspected of being affected by sea otter predation.

Sea otters have been near equilibrium density in the Rat Island group of the Aleutian archipelago (Fig. 1) for about the last 20 to 30 years, following almost complete annihilation by Russian and American fur traders during the eighteenth and nineteenth centuries (Kenyon, 1969; Estes, Chap. 21, this volume). Conversely, the sea otter population has not reestablished itself in the Near Islands (Fig. 1). The once abundant sea otter population there also was extirpated by overexploitation, but immigrants from the densely populated Rat Islands were unable to reach the Near Islands, which are approximately 330 km (200 miles) to the west northwest of Amchitka and are separated from the Rat Islands by wide deep oceanic passes. Since 1959 there have been scattered reports of sea otters in the Near Islands (Kenyon, 1969), although no major population

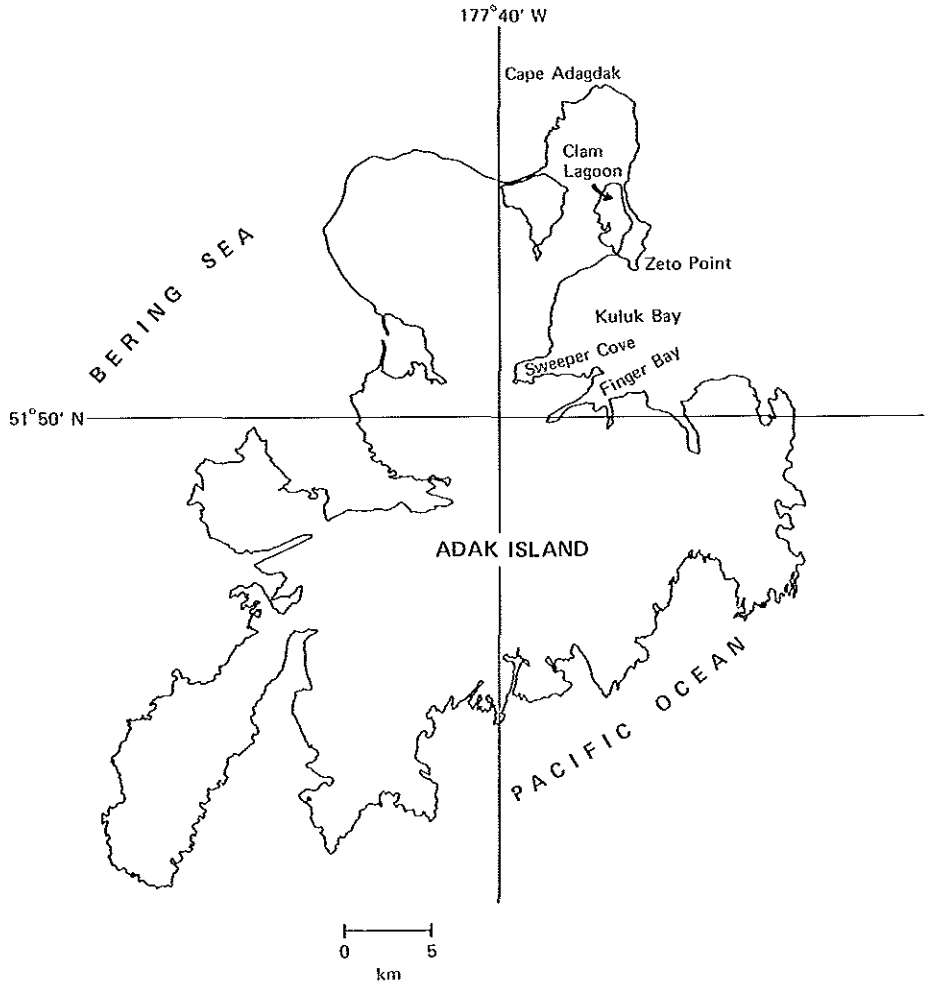

Fig. 8—Map of Adak Island, Alaska, showing study areas referred to in this chapter.

reestablishment has occurred. Thus the presence and absence of sea otters in the Rat and Near Islands, respectively, serve as our natural experiment. After careful consideration and consultation, we believe that other factors, such as climate and tides, which are capable of dynamically influencing nearshore marine community structure, are sufficiently similar between the two island groups that they need not be seriously considered, and thus we should be able to determine the actual effect of sea otter predation on the nearshore community simply by comparing the Rat and Near Islands.

Intertidal Community

Most of our observations were restricted to the midlittoral area [+0.8 to 0 m (+2.6 to 0 ft)] and sublittoral fringe [0 to −0.7 m (0 to −2.3 ft)] of rock benches because these areas provided the greatest biotic diversity (Weinmann, 1969; O'Clair, Chap. 18, this volume).

We determined the size and density of plants and animals either by removing all materials from inside $1/16$-, $1/4$-, or 1-m^2 sample frames and returning them to our laboratory for measurements or by measuring these parameters in situ. Sample plots were selected by tossing a frame arbitrarily into selected algal associations and by placing a frame at random intervals along either side of a random transect which was perpendicular to shore and which transversed the entire association of intertidal algae (O'Clair and Chew, 1971). Food habits of intertidal invertebrates were determined by observing feeding animals or by examining gut contents of collected animals. We collected additional information during "beach walks" along many kilometers of shoreland during daylight low tides.

Grazing Studies. To test the effect of sea urchin grazing on intertidal algae at Amchitka (i.e., to simulate low sea otter densities), we placed twenty 19-mm-diameter sea urchins (*Strongylocentrotus polyacanthus*) from the subtidal area at Constantine Harbor (Fig. 5) in each of four 0.5-m^2 plastic (Vexar) mesh cages (mesh,

3 by 4 mm) with aluminum mesh tops (mesh, 13 by 13 mm). Two cages were permanently secured (nailed) in areas with a canopy of either 100% *Laminaria longipes* or *Hedophyllum sessile* in Makarius Bay (Fig. 5) in September 1971. A control cage without sea urchins was also provided for each algal type, and the percentage of algal cover in all cages was recorded bimonthly from December 1971 to June 1972.

To determine the development of marine algae at Shemya in the absence of grazing by sea urchins (i.e., to simulate high sea otter densities), in September 1971 we removed all sea urchins from two tide pools (6 by 3.3 by 1.5 m and 3.5 by 1 by 0.8 m) that contained only coralline algae and *Thalassiophyllum clathrus*. Two adjacent tide pools with sea urchins were selected as controls. In July 1973 the species and percentage of cover of algae and the number of sea urchins were recorded for all four tide pools.

We studied the effect of limpets (*Collisella pelta*) grazing on intertidal algae by using fifteen 133-cm^2 bottomless plastic dog dishes (Dayton, 1970) with aluminum mesh tops as inclusion and exclusion cages. Three cages each were secured in 1-m^2 areas that had recently been denuded of *L. longipes, H. sessile,* and *Halosaccion glandiforme* at Makarius Bay and of *Corallina vancouveriensis* and *Alaria crispa* at Duck Cove (Fig. 5) in July 1971. Two cages in each area contained three 30-mm-long limpets, and the third cage served as a control. Two weeks before the experiment, the study areas were cleared of plants and animals with a shovel, putty knife, and wire brush and by burning twice with a 1 : 1 mixture of fuel oil and unleaded gas. Species composition and the percentage of cover of algae in all dishes were recorded bimonthly until August 1973.

We selected four areas (50 to 150 cm^2) of bare rock in the midlittoral region at Makarius Bay, each of which contained one or two limpets (20 to 40 mm long). Each area was marked with a nail and rope. Beginning in July 1971, limpets were removed and subsequently kept from two areas, and the other two areas served as controls. Algal cover was recorded bimonthly in all four areas until August 1973.

Because the dense standing crop of algae at Amchitka is not noticeably grazed by epibenthic herbivores, we wondered if this abundant resource is used by other herbivores after it is dislodged from the substrate. To determine if drift kelp would be eaten by small intertidal crustaceans (amphipods and isopods), we collected and cut into 1-cm^2 pieces *L. longipes, H. sessile, A. crispa,* and *A. fistulosa.* Six pieces of each alga were placed in 240-ml cups containing either filtered fresh seawater, seawater and four isopods (*Idotea wosnessenskii*), or seawater and four amphipods (*Parallorchestes ochotensis*). The 12 cups were kept outdoors and were observed several times a day. The water was changed after each observation, and the condition of the algae was recorded. This experiment proceeded for 2 days and was then repeated with another group of similar plants and animals.

Growth and Feeding Studies. The small diameter of sea urchins in the intertidal area at Amchitka could be due to extensive predation or to genetic limitation. To determine which factor is most important, in May 1971 we transported five sea urchins ($\bar{x}$, 15.2 mm in diameter) to the marine laboratories at Friday Harbor, Washington, and placed them in a permanently filled continuous-flow seawater table. Water temperature ranged from 4 to 15°C during the experimental period. The water table was periodically supplied with brown algae, mostly *Nereocystis luetkeana* and *Costaria costata*. The diameters of the sea urchins were measured bimonthly. This growth experiment was terminated in June 1972 after all five sea urchins had died, apparently because of low dissolved oxygen and low salinity.

Intertidal sea stars and snails prey on barnacles and mussels (Connell, 1972; Spight, 1972). The small size of these predators on the benches at Amchitka may be due to low densities of barnacles and mussels or to genetic limitations. To test this, in May 1971 we transported 20 sea stars [*Leptasterias alaskensis* ($\bar{x}$, 14.9-mm arm radius; $\bar{x}$, 1.5 g live weight)] to Friday Harbor. Their water table was periodically supplied with opened live clams (*Protothaca staminea*), mussels (*Mytilus edulis*) (4 to 8 cm long), and live barnacles (*Balanus glandula*). The weight and arm radius were determined bimonthly until all 20 sea stars died (June 1972). Twenty predacious snails (*Thais lima*; $\bar{x}$, 18 mm total length) were transported from the benches at Amchitka to the Department of Zoology, University of Washington, in July 1971 where they were placed in liter beakers containing seawater and several live barnacles (*B. glandula*) at a controlled temperature of 10°C. This experiment was terminated after 1 month (R. T. Paine, personal communication).

Mussel (*M. edulis*) densities may be low at Amchitka because of predation or inadequate food. To determine this, in April 1972 we transported about 50 subtidal mussels (*M. edulis*; $\bar{x}$, 17 mm long) from Puget Sound to Amchitka. Twelve mussels were placed on each of three 1-cm-diameter polyethylene ropes, and four mussels were placed in each of three 700-ml perforated

polyurethane bottles. The ropes and bottles were suspended from the dock in Constantine Harbor with the mussels just below the water surface at the −0.7-m (−2.3-ft) tidal level. The mussels were measured every four months until August 1973.

Selective grazing by sea urchins on a competitively dominant intertidal alga could affect community composition by reducing competition for space and thus permitting more algal species to coexist. To determine if sea urchins at Amchitka feed selectively, at Constantine Harbor we conducted food-preference tests in a 1.5-m(5-ft)-diameter by 30-cm(12-in.)-deep plastic wading pool supplied with constantly flowing fresh seawater. A weighted wooden "Y" maze divided the pool into three equal sections. Five 19-mm-diameter sea urchins from the intertidal area at Amchitka were placed in one branch of the maze; *T. clathrus* (a subtidal kelp) was placed in another; and either *L. longipes, A. crispa*, or *H. sessile* (all lower intertidal kelp) was placed in the third. *Thalassiophyllum clathrus* was used in all tests, and one of the other three kelps was used during two consecutive days. Fresh kelp was provided daily. At 0800 and 2000 each day, the location and activity of each sea urchin was recorded. The sea urchins were replaced to their original location (twice daily), and the position of the two kelp species was exchanged. Each test ran for six consecutive days and then was repeated with five different sea urchins. Two similar tests were carried out at Amchitka with two groups of 75-mm-diameter sea urchins from the intertidal region at Shemya.

Siltation Studies. Silt accumulates in protected areas and is capable of smothering barnacles and mussels. We conducted experiments at Amchitka to determine the intertidal areas of silt accumulation and the effects of siltation on mussel survival.

To determine areas of silt accumulation in the intertidal region, we nailed two plastic dishpans [10 cm (4 in.) high and 560 cm^2 in area] in each of the same five 1-m^2 denuded areas used in the limpet grazing experiments. These pans were placed over areas that contained 100% cover of young algae (either *Ulva lactuca, Fucus distichus, H. glandiforme, H. sessile,* or *A. crispa*) in July 1972. For water movement and light penetration, the pan tops were removed and four equally spaced 4- by 2-cm openings were placed 2 cm above the bottom. The areas covered by the pans were examined periodically until the pans were removed in August 1973.

On Dec. 15, 1972, we placed two groups of 15 mussels (*M. edulis,* 20 to 60 mm long) each from the subtidal region in Puget Sound in secured dog dishes in the *Laminaria* and *Halosaccion* zones at Makarius Bay to test the effects of siltation on mussel survival. The mussels appeared to be attached to the substratum when the dishes were removed on Dec. 19, 1972. The condition of the mussels was observed in April and August 1973.

Settling Studies. The absence of appreciable barnacle (*Balanus* spp.) and mussel (*M. edulis*) sets on the benches at Amchitka may be due to the absence of larvae or to the absence of available substrate. To determine if barnacle or mussel larvae would set if space were provided, in December 1971 we nailed one each of five 1-m-long stainless-steel wires, each holding five 15-cm(6-in.)-long oyster shell halves (*Crassostrea gigas*) from Puget Sound, in the same five 1-m^2 denuded areas used in the limpet grazing studies. The shells as well as the denuded rock areas were checked bimonthly until August 1973 for settling animals.

Determination of Wave Exposure. Because we believe that the degree of exposure affects community structure, we wanted an independent quantitative measure that would enable us to compare the relative exposure of our study locations. Weinmann (1968) observed that the width of *L. longipes* blades reflected relative exposure (blades were wide in protected areas and narrow in exposed areas). Therefore we used the blade width of this kelp as an indicator of exposure.

Subtidal Community

Subtidal communities were observed at Attu and Shemya Islands in the Near Island group, at Amchitka Island in the Rat Island group, and at Adak Island in the Andreanof Island group. Qualitative observations over wider areas in these islands indicate that our study areas are representative of respective island groups.

Time limitations and logistic problems allowed only a single dive* on June 21, 1972, at Murder Point, Attu Island (Fig. 7). We also made nine dives during August and September 1971 and June 1972 at three different locations along the coast at Shemya Island. All these study areas were chosen primarily because of accessibility in view of the limited time available for work in the Near Islands.

We studied four subtidal areas at Amchitka between March 1971 and September 1972. Forty-six dives were made during the observation period.* All study areas were selected from the Bering Sea side of Amchitka Island for the following reasons:

*Refers to number of dives made by a "dive team."

1. The Bering Sea was logistically more convenient because support facilities were located at Constantine Harbor (Fig. 5).

2. Weather conditions are generally more favorable on the Bering Sea than on the Pacific Ocean. Prevailing westerly winds cause the Pacific Ocean to be rough, whereas the Bering Sea is comparatively more calm.

3. The underwater slope is steeper along the Bering Sea coast than it is along the Pacific Ocean coast of Amchitka (see the Geological Survey map in the pocket at the back of this volume); thus a diver can observe a relatively greater depth range without excessive swimming or boat work.

4. Several dives made in the Pacific Ocean in the vicinity of Makarius Bay (Fig. 5) confirm that the community structure in the Pacific Ocean is qualitatively similar to that in the Bering Sea.

Bat Island and Kirilof Rocks (Fig. 5) are heavily exposed during storms off the Bering Sea. Constantine Point is protected from the direct force of storm surf and is apparently only moderately exposed. Kirilof Point is well protected from heavy seas by Kirilof Rocks and the confines of Constantine Harbor. Our observations of the rocky subtidal communities at Amchitka therefore are more extensive and from a wider range of exposure of subtidal communities than at the Near Islands.

We observed depths of subtidal epibenthic communities to 25 m (80 ft) in the Near Islands and to about 40 m (130 ft) at Amchitka.*

The percentage of cover and vertical distribution of the following epibenthic algal groups and species were documented.

1. *Laminaria longipes.*
2. The digitate *Laminaria* life form. This includes *L. groenlandica, L. dentigera,* and *L. yezoensis.*
3. *Agarum cribrosum.*
4. *Thalassiophyllum clathrus.*
5. *Desmarestia* sp.
6. Foliose Rhodophyta.
7. Total macrophytic vegetation—The predominantly subtidal (digitate) species of *Laminaria* were grouped because they are not individually recognizable except on close examination. Although *L. yezoensis* is identifiable on close in situ examination, *L. groenlandica* and *L. dentigera* require stipe section for species identification (Druehl, 1968). Otherwise each of the preceding species or groups of species is easily recognized. Together these species contribute most of the biomass to the epibenthic macrophyte association in the subtidal area of the western Aleutian Islands.

We estimated the coverage of each species or species group at 3-m (10-ft) depth intervals, beginning at a depth of 3 m (10 ft) and starting from a point arbitrarily selected along the shore. Vegetation coverage was estimated to a depth of about 27 m (90 ft) (when possible), at which point the divers swam parallel to the shore for a sufficient distance to avoid overlap with the area observed during descent. They then made similar coverage estimates during ascent.

When depths to coverage estimates were assigned, tidal fluctuations were not considered. Water depth was determined by a standard oil-filled depth gage, which is probably not accurate to more than a few meters. Tidal fluctuations at Amchitka are not great. The tidal range is 1.2 m (4 ft) at Sweeper Cove on Adak Island (Coast and Geodetic Survey, 1968), and the tidal range at Amchitka Island is close to this value.

Data on vegetation coverage were transformed to Arcsin square-root percent values to approximate a normal distribution (Ostle, 1963). The mean, standard deviation, and 95% confidence interval were calculated within the transformation for each species or species group at each depth for data collected at Kirilof Point. The calculations then were retransformed to percentages from Arcsin square-root percent values. Only the means were determined for data collected at the remaining three study areas because of small sample sizes at each depth.

Sea urchin (*S. polyacanthus*) densities and size class distributions were estimated according to the technique described by Barr (1971). Briefly this involves random placement of a 0.25-m^2 quadrat on the ocean floor and counting the number of sea urchins within a quadrat. The animals were taken to the laboratory where their test diameters were measured. The data used to estimate size class distributions and the maximum density of sea urchins at Amchitka are from Barr (1971). Additionally, we measured sea urchin densities at 3-m depth intervals between the depths of 3 and 20 m (10 and 66 ft) at each of the four Amchitka study areas and at depths of 3, 10, and 25 m (10, 33, and 82 ft) at Shemya Island.

Sea urchin wet weight (blotted dry) and test diameter were measured from 110 individuals throughout the naturally occurring size spectrum at Shemya and Attu. We fit the linear model $yi = \mu + \beta (x_{ij}) + e_{ij}$ to the data by the method of least squares, where y is the log sea urchin mass in grams, x is the log sea urchin diameter in millimeters, μ is -7.875, and β is 2.992. A correlation

*Although at Amchitka we dived to 40 m (130 ft) on one occasion, most work was conducted between the surface and 27 m (90 ft).

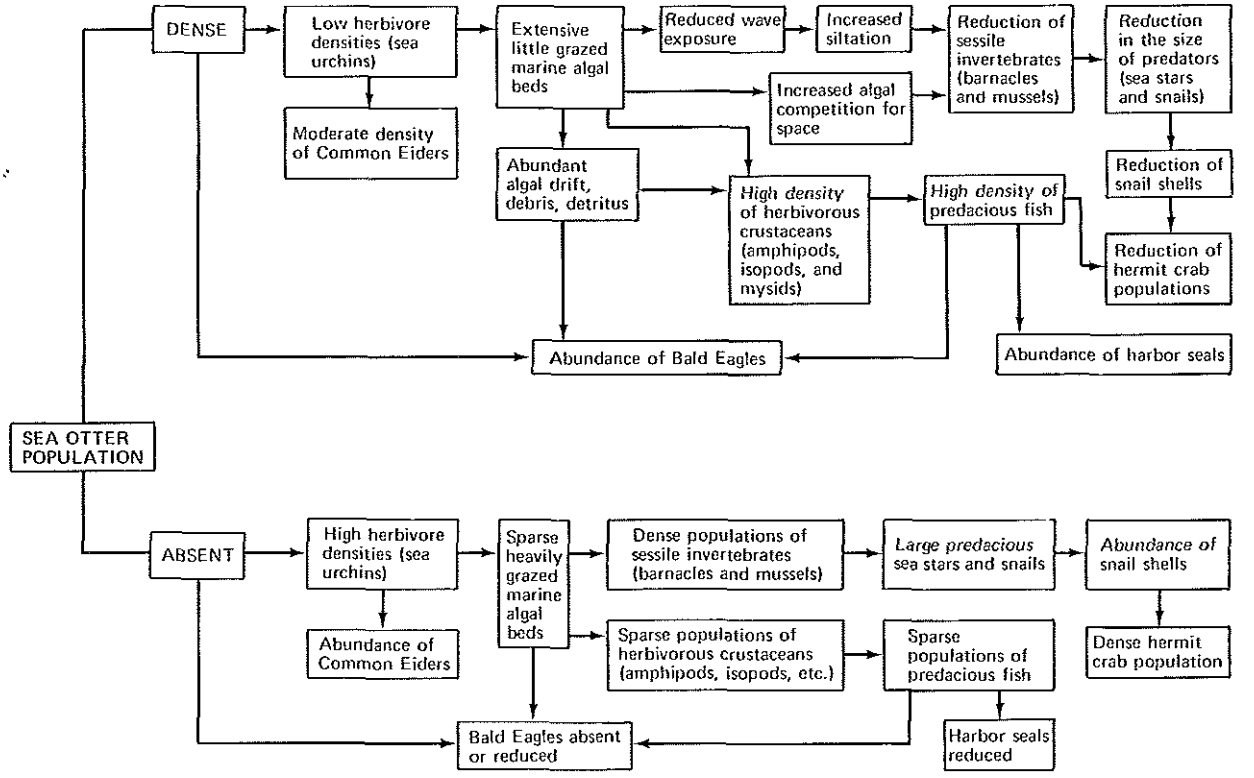

Fig. 9—Diagram of the interactions within nearshore communities with and without sea otter populations. See Discussion for complete details.

coefficient of 0.992 indicates a very good linear fit of the log–log transformation. Parametric interval estimates and tests of hypothesis are given in the appendix. The variance of (e) is quite small, and therefore simple least-squares estimators of μ and β are rather precise. With the use of this model as our estimator, biomass was superimposed on each size class distribution of sea urchins.

DESCRIPTION OF COMMUNITIES

Community Differences

The most prominent biological features of the marine community studied at Amchitka are the extensive little grazed subtidal and intertidal beds of marine algae and the sparse population of certain benthic invertebrates (Table 1). In contrast, the prominent biological features of the marine communities studied at Attu and Shemya are the sparse heavily grazed offshore and intertidal beds of marine algae and the dense population of large benthic invertebrates (Table 1). The marked decline in the population and size of sea urchins that occurred concurrently with an increase in the population of sea otters at Adak and Amchitka during the previous 15 years (Kenyon, 1969) suggests that sea otter predation has been the principal factor responsible for altering the composition of these marine communities (Fig. 9). Furthermore, the contents of Aleut kitchen middens at Amchitka indicate that sea urchins were larger centuries ago than today (Desautels et al., 1970) when, Kenyon (1969) speculates, there were fewer sea otters because of intensive native hunting pressure. That Desautels also found sea otter bones in these middens supports this speculation.

Intertidal Communities

Amchitka. A complete mat of virtually ungrazed algae occupies intertidal benches, channels, and tide pools at Amchitka (Fig. 10). *Laminaria longipes* completely covers the lowest portion of the intertidal region (sublittoral fringe). *Hedophyllum sessile* predominates in the lower midlittoral region in protected areas and on the landward side of wide benches. *Alaria crispa* occupies this portion of the lower midlittoral region in exposed areas and on narrow benches. *Halosaccion glandiforme, Iridaea cornucopiae,* and *Fucus distichus* cover the higher zones of the midlittoral region (see Lebednik and Palmisano, Chap. 17, this volume).

There is little evidence of grazing on larger plants in the kelp communities at Amchitka.

Fig. 10—Continuous mat of virtually ungrazed algae on intertidal rock benches at Amchitka Island, Alaska, at low tide (Aug. 7, 1971).

Grazed kelp is recognized by its serrated edges. This characteristic mark made by sea urchins and other benthic herbivores, such as chitons, was noticed in less than 1% of the attached kelp examined. Over 39% of young kelp [under 20 cm (8 in.) long] were grazed (Table 3); however, the size of the serrations and the abundance of small amphipods and isopods suggest that these small crustaceans may have grazed the smaller kelps.

Invertebrates are inconspicuous on the intertidal benches at Amchitka (Fig. 10). Barnacles (*Balanus glandula* and *B. cariosus*) and mussels (*Mytilus edulis*) (sessile filter-feeding invertebrates) and sea urchins (*S. polyacanthus*), chitons (*Katharina tunicata*), and limpets (*C. pelta*) (motile herbivorous invertebrates) are small and scarce (Tables 4 and 5). Some invertebrates (barnacles, limpets, and snails) are covered by silt or overgrown by algae in areas protected from wave action. Even the most abundant invertebrates [polychaetes, certain crustaceans (amphipods and isopods), sea anemones, sea cucumbers, and mollusks (clams and snails)] are inconspicuous because of their small size and occurrence under algal mats, in algal holdfasts, under rocks, and on the bottoms of pools and channels. Only small littorine snails in the mid and upper intertidal areas are conspicuous. Therefore in most areas intertidal algae appeared to be the sole inhabitants of the intertidal bench (a more complete description of intertidal invertebrates is given by O'Clair in Chap. 18, this volume). However, sessile filter-feeding invertebrates (barnacles and mussels) are more abundant in areas exposed to a higher degree of wave action, e.g., Banjo Point (Fig. 5), than in protected locations, e.g., Makarius Bay (Table 4).

No sea urchins were observed grazing intact vegetation on the bench, in channels (Fig. 11), or in tide pools. However, sea urchins did graze algal debris and detritus in these locations. Sea urchin guts contained macrophytic algae and diatoms.

Adak. Although the algal community of Adak covers the intertidal rock bench and is ungrazed, it is not as extensive as the one at Amchitka. The majority of the community is composed of *L. longipes* and *A. crispa. Hedophyllum sessile* is not abundant. *Thalassiophyllum clathrus* and *Cymathere triplicata*, normally subtidal kelp at Amchitka, are present in the intertidal area at Kuluk Bay.

At Adak, as well as at Amchitka, the invertebrates on the rock bench are small, scarce, and inconspicuous. There are, however, extensive mussel (*M. edulis*) beds and dense populations of barnacles (*B. glandula* and *B. cariosus*) on vertical walls, on sea stacks, and on the sides of large boulders. Dense populations of large predacious snails (*Thais lima*) were observed feeding in these areas (Table 6). The breakwater protecting

Table 3—Percentage of Intertidal Random Individual Kelp Plants Grazed and Random 0.25-m^2 Quadrats Containing Grazed Kelp, Amchitka and Shemya Islands, Alaska, 1971–1973

Item	Amchitka				Shemya			
	Sample size	Bench	Tide pools	Channels	Sample size	Bench	Tide pools	Channels
Random plants								
Laminaria longipes								
>200 mm long	16,000	<1	<1	<1	1600	ND*	100†	100†
Alaria crispa								
>200 mm long	3,000	<1	<1	<1	140	ND	100†	100†
<200 mm long	117	49.6	ND	ND	ND	ND	ND	ND
Hedophyllum sessile								
>200 mm long	4,200	<1	<1	<1	310	ND	100†	100†
<200 mm long	2,351	38.4	ND	ND	ND	ND	ND	ND
Random 0.25-m^2 quadrats								
Laminaria longipes	400	<1	<1	<1	40	80	100†	100†
Alaria crispa	400	<1	<1	<1	20	80	100†	100†
Hedophyllum sessile	400	<1	<1	<1	30	75	100†	100†

*ND, no data.

†All three species of kelp were absent from channels and tide pools, and all those overhanging these areas were grazed.

Table 4—Mean Numbers Per Square Meter of Selected Intertidal Invertebrates at Amchitka and Shemya Islands, Alaska, 1968–1973*

Invertebrate	Amchitka			Shemya‡		
	Makarius Bay	Banjo Point	All areas†	Bench	Tide-pool walls	Channel bottom
Sea urchin (*Strongylocentrotus polyacanthus*)	8	4	8	78	139	231
Limpet (*Collisella pelta*)	2	127	8	356	82	ND
Chiton (*Katharina tunicata*)	<1	<1	<1	38	ND	ND
Barnacles						
(*Balanus glandula*)	<1	114	6	2242	ND	ND
(*B. cariosus*)	<1	82	4	188	ND	ND
Mussel (*Mytilus edulis*)	<1	36	4	722	ND	ND
Snail (*Thais lima*)	2	3	3	32	ND	ND
Hermit crab (*Pagurus hirsutiusculus*)	<1	<1	<1	20	ND	ND

*Preliminary data from transect-line $\frac{1}{16}$-m^2 plots [Amchitka, N = 32; Shemya, N = 23 (O'Clair, in preparation)] and from randomly selected $\frac{1}{4}$-m^2 plots [Amchitka, N = 171; Shemya, N = 9 (see Estes and Palmisano, 1974)].

†Rifle Range Point, Duck Cove, Makarius Bay, and Banjo Point.

‡Urchin Point.

Sweeper Cove contained a dense population of sea urchins, (*S. polyacanthus*) among the large boulders (Table 5). This is the only area along the shore where live sea urchins were seen. Hermit crabs (*Pagurus* sp.) also occur at Adak. Mussels, clams (*Protothaca* sp.), and cockles (*Clinocardium nuttalli*) were observed in Clam Lagoon.

Shemya. Algae are heavily grazed in the lower intertidal area (Fig. 12), in channels (Fig. 13), and in tide pools (Fig. 14) at Shemya, and there is a definite browse line at the low water level (Fig. 12). Channels and tide pools beneath the low water level are devoid of most species of algae. *Laminaria longipes* does not form a complete mat

Table 5—Sizes of Selected Invertebrate Herbivores from the Western Aleutian Islands*

Area	$\bar{x}$	R	N	SD	CI
		Sea urchins			
Amchitka					
Intertidal bench	18.9	4 to 45†	224	5.7	±11.2
Subtidal area					
Constantine Dock‡	30.9	17 to 56	345	6.7	±13.1
10 to 20 m§	16.5	3 to 34	872	5.8	±11.4
45 to 80 m¶	41.1	26 to 80	207	10.4	±20.4
Shemya					
Intertidal bench	30.4	4 to 74	289	17.9	±35.1
Hedophyllum zone	22.8	4 to 70	153	16.0	±31.4
Laminaria zone	37.6	10 to 74	136	16.8	±32.9
Tide-pool walls	52.2	25 to 70	130	7.7	±15.1
Channel bottom	53.4	22 to 81	140	17.4	±34.1
Attu					
Intertidal bench	52.8	28 to 99	14	ND	ND
Channel bottom	87.5	78 to 108	13	ND	ND
Adak					
Breakwater**	28.4	10 to 50	121	8.6	±16.9
Growth experiment††					
May 1971	15.2	12 to 18	5	2.4	±6.7
May 1972	36.2	34 to 38	5	2.0	±5.6
Midden remains‡‡	69.7	21 to 106	1403	9.8	±19.2
		Limpets			
Amchitka					
Intertidal bench	27.8	18 to 51	60	1.8	±3.6
Adak					
Intertidal bench	25.1	10 to 42	75	1.5	±2.9
Shemya					
Tide-pool walls	ND	19 to 67	200	ND	ND
		Chitons			
Shemya					
Intertidal bench	67.2	23 to 88	77	18.1	±36.0

*$\bar{x}$, average individual size in millimeters (test diameter for sea urchins, total length of longest axis for others); R, range of individual sizes in millimeters; N, number of animals measured; SD, standard deviation; CI, 95% confidence interval; ND, no data.

†Only six sea urchins were larger than 29 mm in diameter.

‡Collected beneath dock with scuba [5 to 6 m (16 to 20 ft) deep].

§Barr, 1971.

¶Collected 45, 50, and 80 m (148, 164, and 262 ft) deep by bottom dredge.

**Collected at low tide between the rocks of the Sweeper Cove breakwater.

††Amchitka intertidal sea urchins fed at Friday Harbor Laboratories for 1 year.

‡‡Desautels et al., 1970.

in the sublittoral fringe. Instead there are areas of only *L. longipes* stipes and holdfasts or of bare rock and areas containing *T. clathrus* and *L. groenlandica*. (*T. clathrus* and *L. groenlandica* occur only subtidally or in tide pools on Amchitka.) *Hedophyllum sessile* is heavily grazed in the lower midlittoral region and is absent or heavily grazed in channels and tide pools. The upper midlittoral region and the landward end of the bench contain *H. glandiforme*, *I. cornucopiae*, and *F. distichus* and are not heavily grazed. *Thalassiophyllum clathrus* occupies areas of several square meters in this zone (Fig. 15). All *L. longipes*, *A. crispa*, and *H. sessile* overhanging channels are grazed. Eighty percent of all 0.25-m^2 *L. longipes* plots and 75% of all *H. sessile* plots sampled contained grazed plants (Table 3). The only plants not heavily grazed were coralline algae and *T. clathrus*, which are usually present in channels, tide pools, and the lower intertidal areas.

Dense populations of large sea urchins (*S. polyacanthus*) (Fig. 16) and large chitons (*K.*

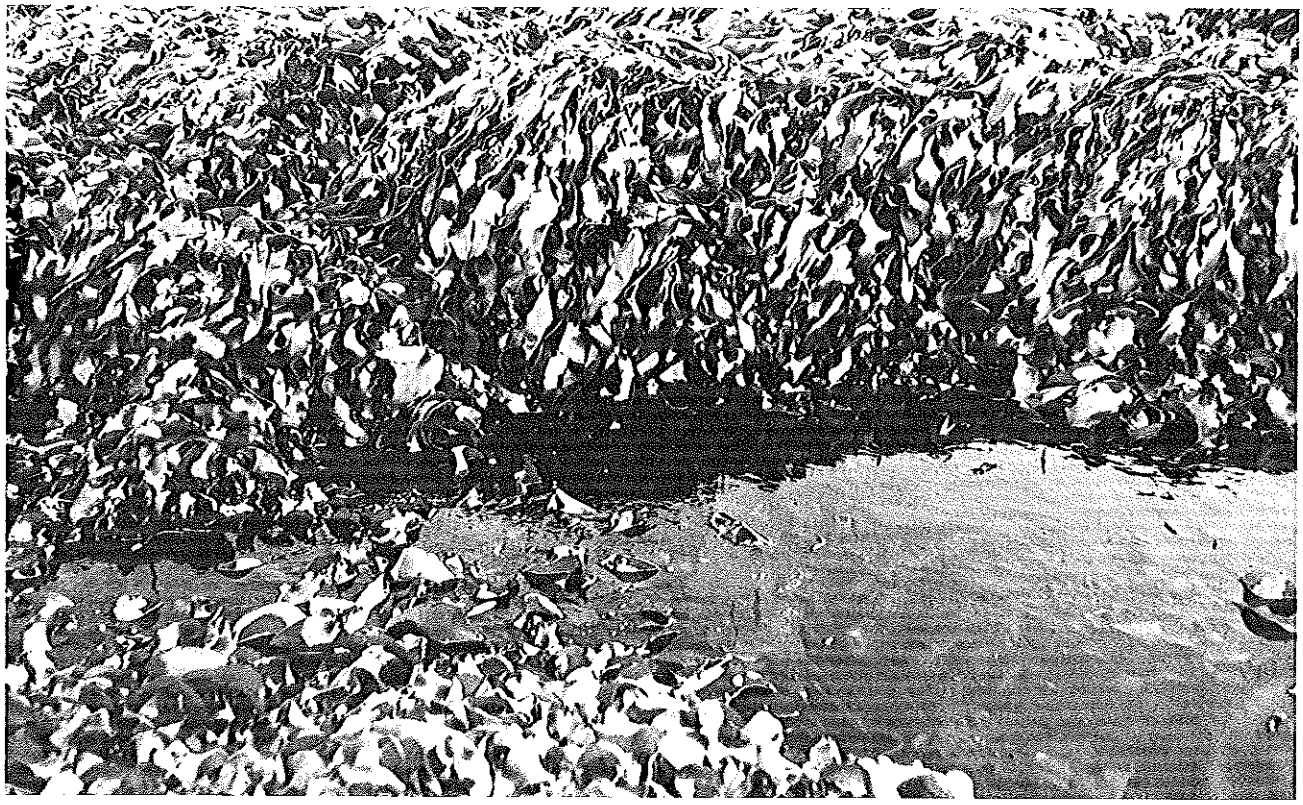

Fig. 11—Ungrazed *Laminaria longipes* on wall and bottom of an intertidal channel at Amchitka Island, Alaska, at low tide (Aug. 7, 1971).

Table 6—Sizes of Intertidal Predacious Sea Stars and Snails in the Western Aleutian Islands*

Area	Size					Weight				
	$\bar{x}$	R	N	SD	CI	$\bar{x}$	R	N	SD	CI
				Leptasterias alaskensis						
Amchitka	14.9	3 to 44	1144	6.0	±11.8	1.5	0.1 to 13.6	571	1.5	±2.9
Shemya	25.6	6 to 55	41	11.3	±22.7	5.3	0.1 to 25.8	33	4.2	±8.6
Growth experiment†										
May 1971	15.4	5 to 26	20	5.6	±11.7	1.3	0.2 to 3.5	20	1.7	±3.6
May 1972	26.9	12 to 49	20	13.5	±28.2	5.9	0.9 to 18.3	20	5.0	±10.5
				Thais lima						
Amchitka										
Intertidal	20.9	10 to 35	98	8.5	±16.9					
Makarius Bay	18.1	15 to 20	8	2.0	± 4.7					
Duck Cove	17.2	10 to 27	57	6.9	±13.8					
Banjo Point	29.6	25 to 35	23	8.0	±16.5					
Constantine Harbor	24.1	14 to 31	10	5.2	±11.8					
Adak										
Kuluk Bay	22.6	11 to 40	330	8.0	±15.7					
Attu										
Chichagof Harbor	42.8	34 to 50	10	6.8	±15.4					

*$\bar{x}$, average individual size in millimeters (arm radius for sea stars, total length of shell for snails) or live weight in grams; R, range of individual sizes in millimeters or live weight in grams; N, number of animals measured; SD, standard deviation; CI, 95% confidence interval.

†Amchitka intertidal sea stars fed at Friday Harbor Laboratories for 1 year.

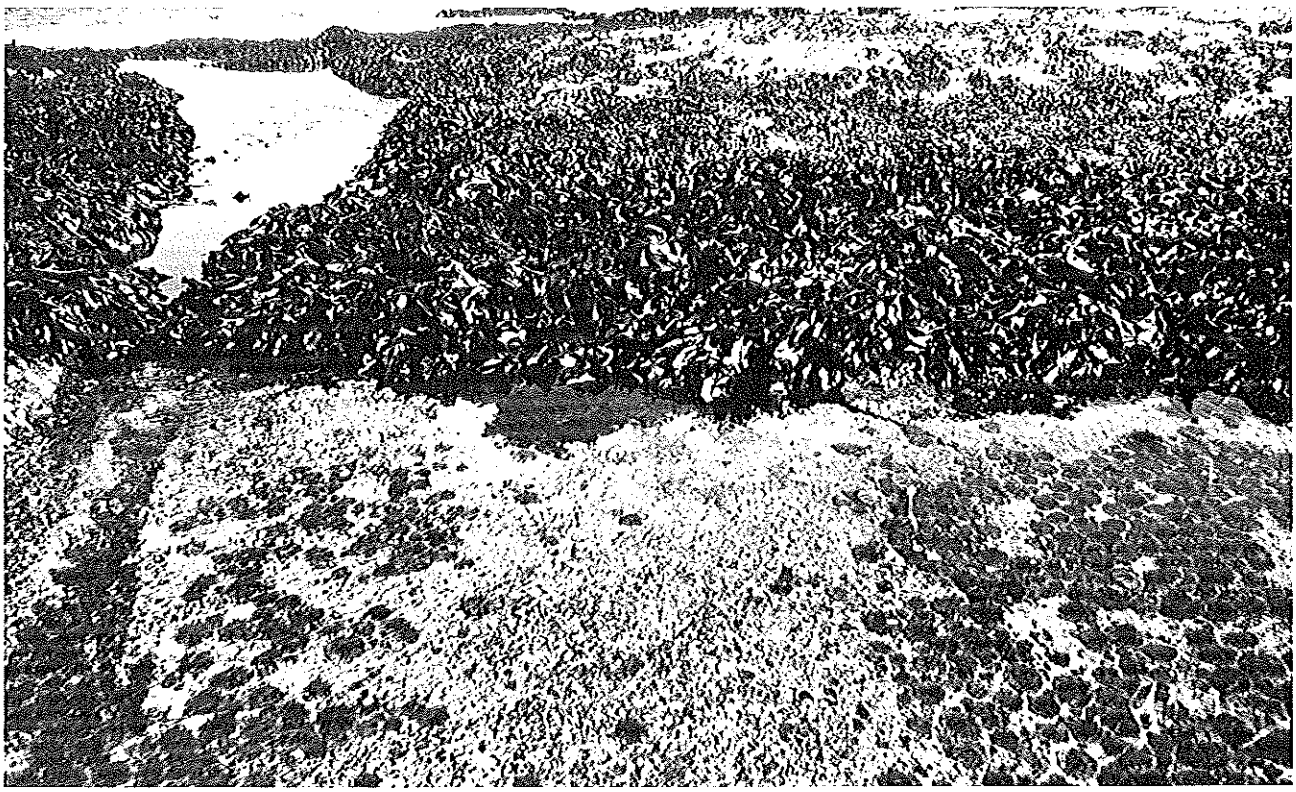

Fig. 12—Heavily grazed algae on intertidal rock benches at Shemya Island, Alaska, at low tide. Note sea urchins in foreground and barnacles (white) in background (Sept. 2, 1971).

Fig. 13—Grazed *Laminaria longipes* on wall and bottom of an intertidal channel at Shemya Island, Alaska, at low tide. Note density of sea urchins in channel (Sept. 2, 1971).

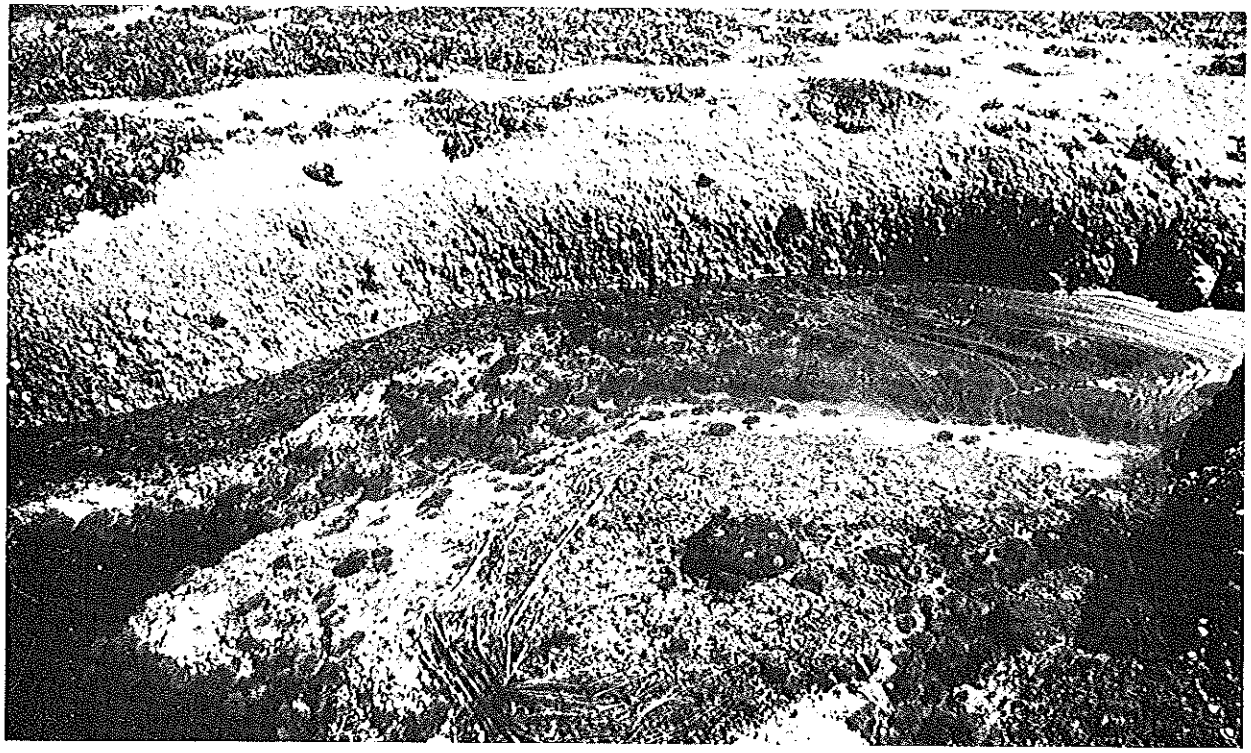

Fig. 14—Tide-pool wall and bottom devoid of algae at Shemya Island, Alaska, at low tide. Note sea urchins beneath water surface and limpets (white ovals) on tide-pool wall (Sept. 2, 1971).

Fig. 15—Large area of *Thalassiophyllum clathrus* in *Laminaria* zone at Shemya Island, Alaska, at low tide (June 29, 1972).

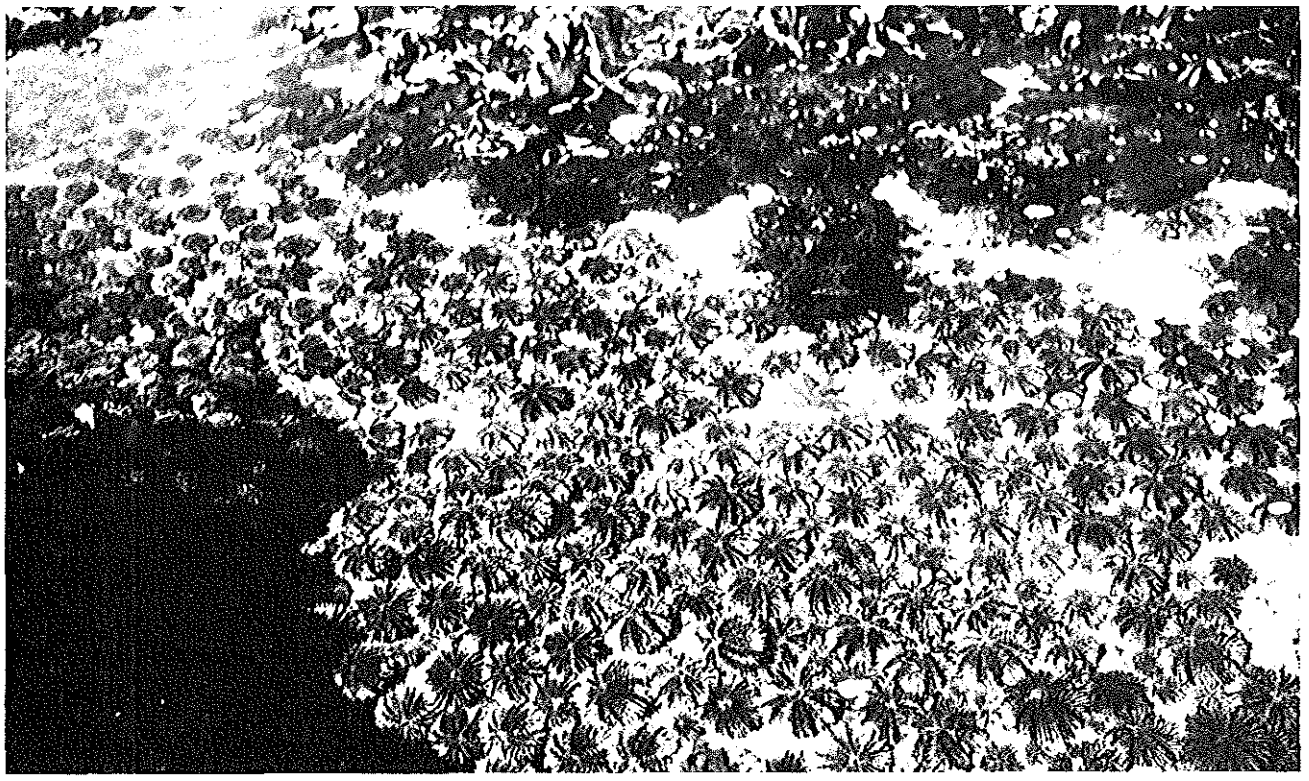

Fig. 16—Dense concentrations of large ($\bar{x}$, about 70 mm in diameter) sea urchins in lower intertidal zone at Shemya Island, Alaska, at low tide. Note large sea star (arm radius, 55 mm) to right of center (Sept. 2, 1971).

tunicata) and extensive beds of mussels (*M. edulis*) and barnacles (*B. glandula* and *B. cariosus*) (Table 4) occur on the intertidal benches at Shemya. Sea urchin density and size are greater in channels and tide pools than in the lower and higher intertidal regions (Tables 4 and 5). Chitons are present only in the *Hedophyllum* and *Laminaria* zones. *Balanus glandula* is most abundant in the upper midlittoral region (Fig. 12), but *B. cariosus* is most abundant in the sublittoral fringe and lower midlittoral region where it occurs with *L. longipes* (Fig. 17) and *H. sessile*. Mussel beds are most abundant on the seaward edge of the bench in the high midlittoral region. Predacious sea stars (*Leptasterias alaskensis*) are larger here than at Amchitka (Table 6). Hermit crabs (*Pagurus* sp.) are abundant on the bench, in tide pools, and in channels in the upper midlittoral region. Amphipods and isopods are not as abundant here as at Amchitka. Fewer than 20 individual amphipods and isopods were present under small rocks at low tide. Limpets (*C. pelta*) are large and abundant on tide-pool walls and in the lower intertidal area (Tables 4 and 5 and Fig. 14).

Sea urchins were observed grazing primarily *L. longipes, H. sessile, A. crispa,* and *Ulva* sp. Only rarely were they observed grazing *T. clathrus*. Gut analyses of over 100 sea urchins (range of 10 to 75 mm in diameter) showed that kelp was most abundant followed by *Ulva* sp. and diatoms. *Leptasterias alaskensis* and *T. lima* were observed preying on mussels and barnacles. One *L. alaskensis* was observed scavenging a sea urchin.

Attu. The algal association at Attu is heavily grazed in the lower intertidal area, in channels, and in tide pools and is very similar to the association at Shemya. *Thalassiophyllum clathrus* occurs in the lower intertidal area, in tide pools, and in channels and is virtually ungrazed.

The invertebrate association at Attu also is similar to the association at Shemya. Dense populations of sea urchins (*S. polyacanthus*), chitons (*K. tunicata*), mussels (*M. edulis*), and barnacles (*B. glandula* and *B. cariosus*) occur on the bench. Densities of hermit crabs (*Pagurus* sp.) and crustaceans (amphipods and isopods) also are similar to those at Shemya. Littleneck clams (*Protothaca* sp.) occur in gravel beds in the midlittoral region, and the large chiton (*Cryptochiton stelleri*) was noticed in the sublittoral fringe.

The food habits of sea urchins and predacious sea stars and snails were similar to those at Shemya.

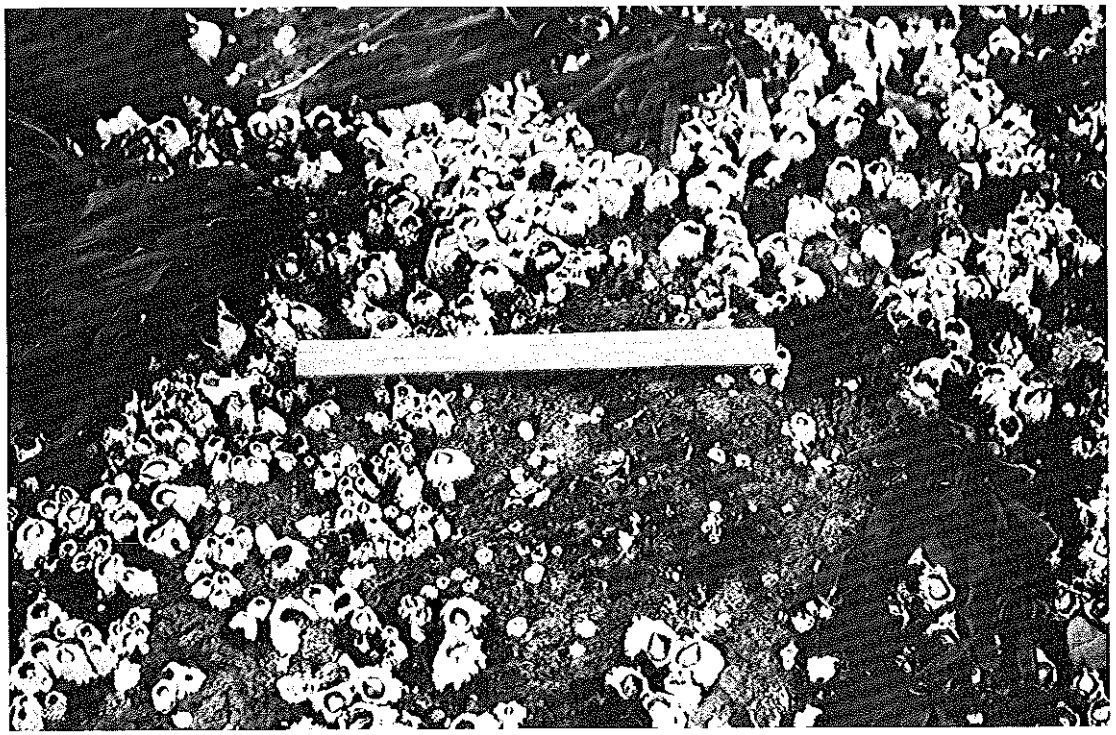

Fig. 17—Abundant *Balanus cariosus* in *Laminaria* zone at Shemya Island, Alaska, at low tide [ruler is 30.5 cm (12 in.) long] (June 28, 1972).

Sea urchins at Massacre Bay and Murder Point on Attu are larger than those at Shemya (Table 5). Sea urchins in Chichagof Harbor appeared to be smaller (although no measurements were made) than those at the other two study areas at Attu.

Subtidal Communities

Amchitka and Adak. The subtidal macrophytic association at Amchitka extends from the intertidal area and covers most of the solid-rock substrate to depths of 20 to 25 m (66 to 82 ft) (Figs. 18 to 20). Major contributors to this association are *Alaria fistulosa, Laminaria longipes, L. groenlandica, L. yezoensis, L. dentigera, Agarum cribrosum, Thalassiophyllum clathrus, Desmarestia* sp., and various Rhodophyta. *Laminaria* and *Agarum* are the most abundant forms.

Sea urchin population densities increase with increasing depth at Amchitka (Fig. 19). At the sublittoral fringe, sea urchins are seen infrequently unless they are associated with algal holdfasts or protective cracks and crevices in the substrate. Openly exposed sea urchins are rarely seen in water shallower than 10 m (33 ft). Below about 15 to 20 m (50 to 66 ft), high-density sea urchin populations are openly exposed in some areas.

Phillip A. Lebednik (personal communication) reported that the rocky subtidal community (algal associations and sea urchin size, density, and distribution) at Adak appears to be comparable to that at Amchitka. He made only a single dive at Adak in 1972 [at 7, 13, 20, 27, and 34 m (23, 43, 66, 89, and 112 ft) depths], but he made 62 dives at Amchitka and 4 dives at Shemya.

Shemya and Attu. Subtidal macrophytes are generally absent from solid-rock substrate in the Near Islands (Figs. 19 and 21). They occur only in small isolated patches, frequently located on submarine pinnacles, and often in a state of destruction from sea urchin grazing.

Sea urchin densities at Shemya and Attu decrease with increasing water depth (Fig. 19). Immediately below mean water level, sea urchin populations frequently completely cover the entire rocky substrate.

Vegetation. No data on vegetation coverage were collected at the Near Islands. Subtidal macrophytes are absent from most areas at the Near Islands, and thus a coverage of zero percent is inferred from our general observations (Fig. 19).

At Amchitka *L. longipes* extends from the sublittoral fringe to a depth of 3 to 10 m (10 to 33 ft). This species possesses a stipe that allows it flexibility in an area where wave action is maximum. The association of three species (*L. groenlandica, L. yezoensis,* and *L. dentigera*) begins at mean water level and extends out to a depth of

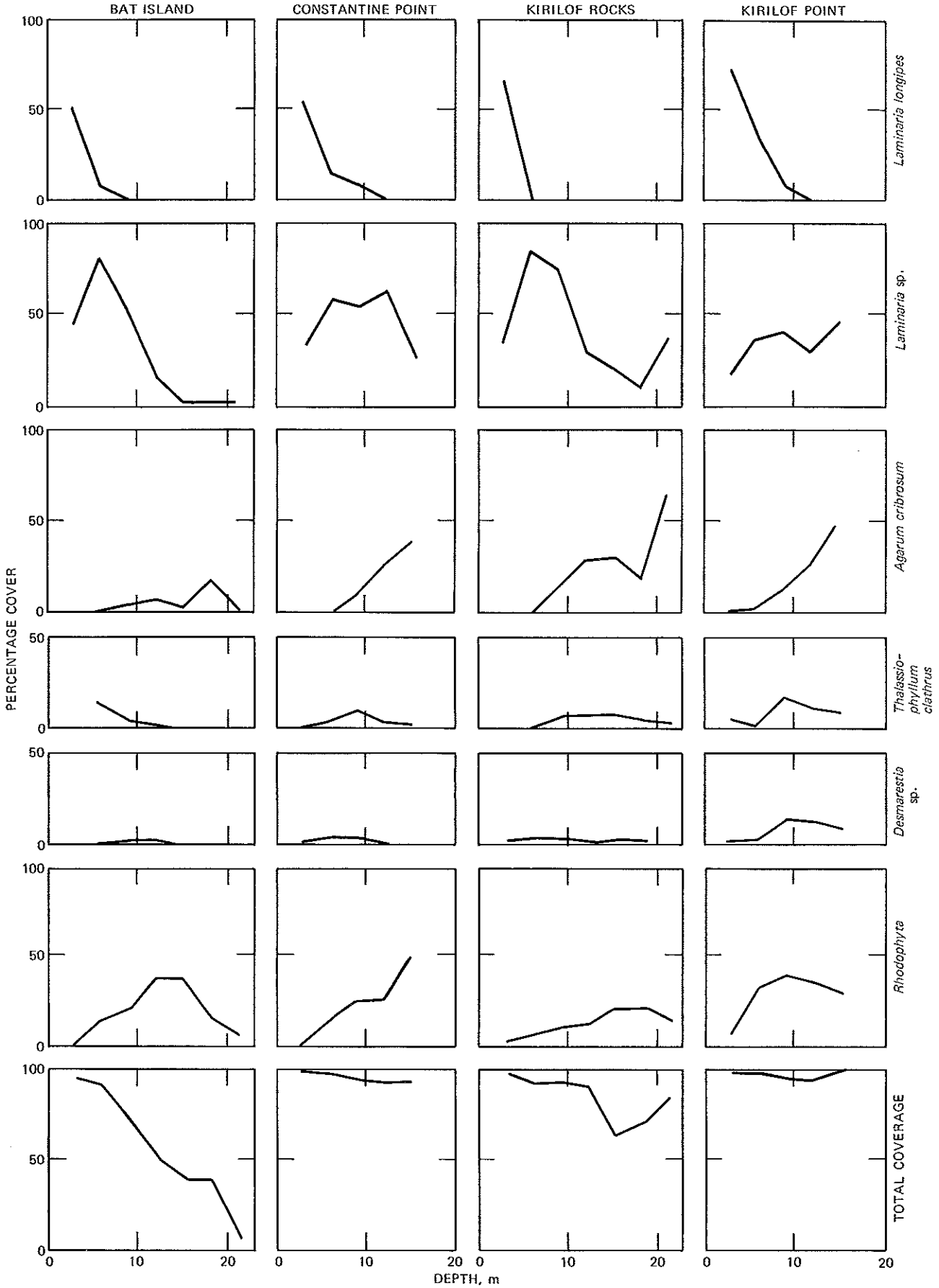

Fig. 18—Vegetation coverage as a function of depth at the four Amchitka Island, Alaska, study areas.

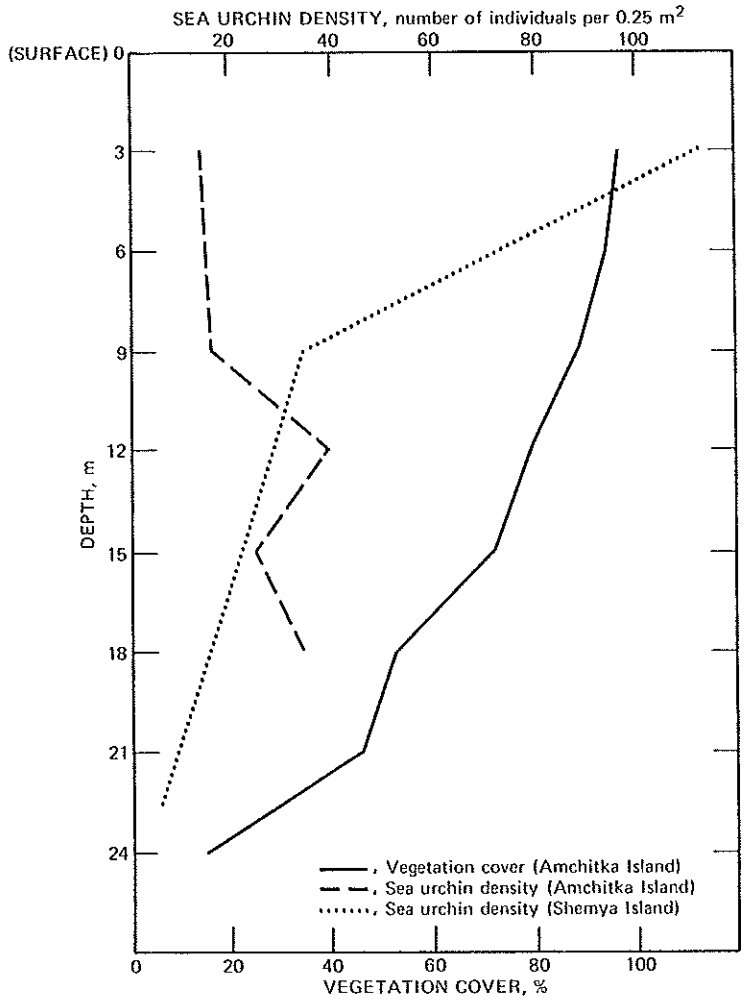

Fig. 19—Total macrophyte coverage and sea urchin density as a function of depth at Amchitka and Shemya Islands, Alaska.

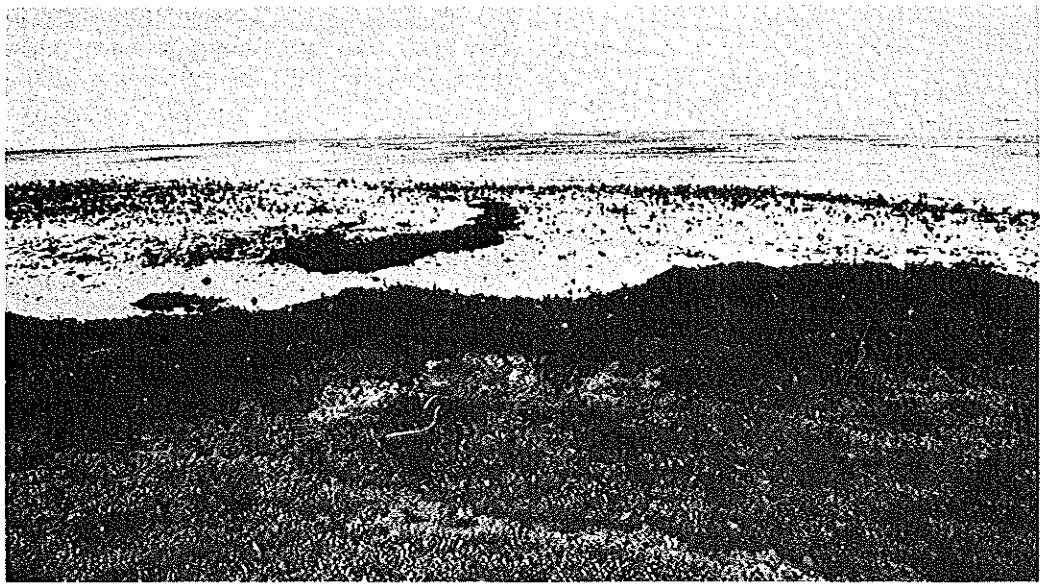

Fig. 20—Dense ungrazed subtidal kelp beds in nearshore community of Amchitka Island, Alaska (*Laminaria longipes* in foreground and *Alaria fistulosa* in background) (Aug. 5, 1972).

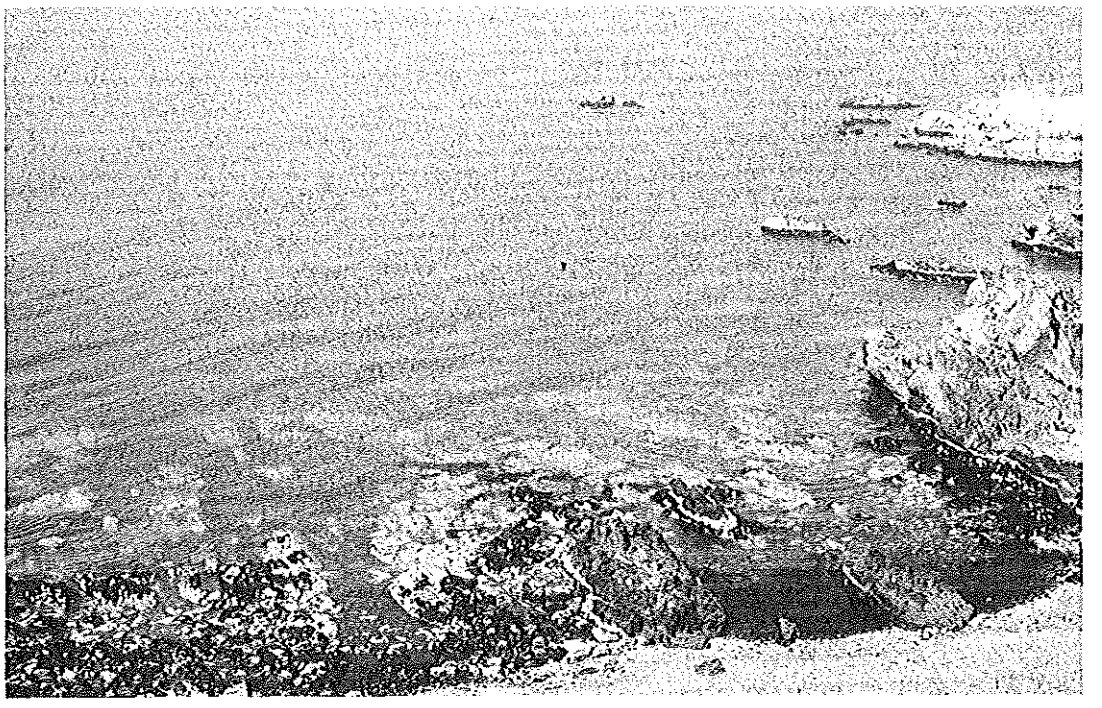

Fig. 21—Nearshore community of Shemya Island, Alaska, showing a virtually complete absence of subtidal kelp. Note light-colored rock bottom (June 30, 1972).

23 to 25 m (75 to 82 ft). This association of species is dominant between about 3 and 12 m (10 and 40 ft). *Agarum cribrosum,* which begins at a depth of about 6 m (20 ft) and extends out to a depth of at least 23 to 25 m (75 to 82 ft), is most abundant between 16 and 20 m (52 and 66 ft). *Thalassiophyllum clathrus* and *Desmarestia* sp. are only relatively minor contributors to the sublittoral macrophyte association and seldom cover more than 10% of the rocky substrate. *Thalassiophyllum clathrus* ranges in depth between 3 and 20 m (10 and 66 ft) and is most abundant at a depth of about 10 to 12 m (33 to 40 ft). *Desmarestia* sp. also ranges in depth between 3 and 20 m (10 and 66 ft) but shows no distinct pattern of maximum abundance. Foliose Rhodophyta occur from the sublittoral fringe to beyond 25 m (82 ft) in depth. Near the surface Rhodophyta grow beneath the *Laminaria* canopy as well as epiphytically on the Phaeophyta. Abundant space is available on the rock substrate in the shallow subtidal region because blades of *L. groenlandica, L. dentigera,* and *L. yezoensis* are extended a meter or more toward the surface on thick inflexible stipes. Rhodophyta are abundant continuously from the surface to beyond 25 m (82 ft), perhaps showing a slight increase in abundance with increased depth (see Chap. 17, this volume, for distribution of *A. fistulosa*).

Sea Urchin Populations. The size class distribution of a typical high-density sea urchin population at Amchitka is shown in Fig. 22a. These data indicate that the maximum test diameter of subtidal sea urchins at Amchitka Island is about 35 mm. Biomass distribution (as a function of size class) is also given in Fig. 22a. Biomass density probably is more indicative than numerical density of resource exploitation by various size classes.

The size class distribution of a typical high-density sea urchin population at Shemya, from water about 2 to 3 m (7 to 10 ft) in depth and immediately adjacent to the intertidal area, is shown in Fig. 22b. Apparently two peaks are in this distribution, one at 10 to 15 mm in diameter and another at 60 to 65 mm in diameter. The maximum size of sea urchins from this sample is about 87 mm, although individuals over 100 mm in diameter were found while we were specifically searching for large animals. The biomass of sea urchins also is shown in Fig. 22b. A total biomass density of 12,328 g/m^2 was estimated for the Shemya subtidal sea urchin population in areas of high population density. The biomass of the Amchitka sea urchin population in areas of maximum density was estimated at 1496 g/m^2. Of total sea urchin biomass density at Shemya, 11,672 g/m^2 (95%) is contributed by that segment of the population that is larger than the largest sea urchin observed from the Amchitka samples.

At Shemya, at depths of 10 to 15 m (33 to 50 ft), the peak of small animals in the size class

distribution is reduced, and the peak of larger individuals is absent. The biomass density also is reduced to 824 g/m^2. At these depths 65% of the biomass is contributed by animals larger than the maximum size at Amchitka (Fig. 22c).

At depths of 20 to 25 m (66 to 82 ft), population densities are further reduced, and there are no apparent peaks in the size class distribution. Here the biomass density is reduced to 208 g/m^2, 39% of which is contributed by animals larger than the maximum size at Amchitka (Fig. 22d).

RESULTS

Intertidal Community

Grazing Studies. At Amchitka sea urchin grazing experiments in *L. longipes* and *H. sessile* zones demonstrated that dense populations of sea urchins could reduce algal cover. Twenty 19-mm-diameter sea urchins grazed 80% of all encaged plants and reduced algal cover by 60 to 70% within 9 months whereas control cages maintained 100% algal cover.

At Shemya both tide pools cleared of sea urchins in September 1971 had a 90% cover of *Ulva lactuca* by June 1972. The larger tide pool contained three *H. sessile* plants and five large sea urchins (about 75 mm in diameter). The smaller tide pool contained no sea urchins. There were no noticeable changes in algal species or in percentage of cover in the two control tide pools from which sea urchins had not been removed.

Limpet grazing experiments conducted in dog dishes on newly denuded rock surfaces in the midlittoral region at Duck Cove and in the midlittoral region and sublittoral fringe at Makarius Bay showed that after 1 year dishes without limpets had 100% algal cover (mostly *U. lactuca* and *H. glandiforme*) whereas dishes with three 30-mm-long limpets had between 2 and 10% cover of the same algal species. Within 1 year after limpets had been removed from the *Halosaccion* zone at Makarius Bay, previously grazed (bare) areas became completely occupied by small red algae (*Rhodymenia* sp. and *I. cornucopiae*). Similar areas where limpets had not been removed remained bare.

Pieces of subtidal and intertidal drift algae placed in small cups containing seawater and either amphipods or isopods were noticeably grazed after 2 days. These algae remained intact when placed in cups containing only filtered seawater.

Field observations showed that drift kelp on the shoreline (composed mostly of subtidal species, such as *A. fistulosa*) provides food and shelter for amphipods (*Orchestia*) and kelp flies (Coelopidae). As kelp decomposes it accumulates around algal holdfasts in calm areas, in small depressions and tide pools, and around and under rocks. Here many species of abundant amphipods and isopods (often hundreds of individuals per square meter) and sea urchins feed on this algal debris and detritus.

About 5000 Emperor Geese (*Philacte canagica*) spend the winter at Amchitka (Williamson, Emison, and White, 1971) where they feed in the intertidal area during low tide. Field observations and stomach analyses from six adult birds showed that *Ulva* sp. and small red algae (*Porphyra* sp. and *Rhodymenia* sp.), but not kelp, were eaten (Palmisano, 1975). Similar findings were made by Williamson, Emison, and White (1972).

Growth and Feeding Studies. Five intertidal sea urchins from Amchitka doubled in size within 1 year after they were transferred to the marine laboratories at Friday Harbor and kept in a water table containing a constant supply of kelp (Table 5).

The food-preference tests conducted at Amchitka showed that sea urchins from Amchitka and Shemya prefer *L. longipes, A. crispa,* and *H. sessile* to *T. clathrus.*

Mussels [*M. edulis* ($\bar{x}$, 18 mm long)] from Puget Sound that had been transferred to Amchitka tripled their size ($\bar{x}$, 58 mm long) in 18 months.

At Friday Harbor, intertidal sea stars from Amchitka, which were fed opened live clams, mussels, and barnacles for 1 year, increased more than one and one-half times in size and more than four times in weight (Table 6). Field observations at Amchitka on 35 feeding sea stars (*L. alaskensis*) showed that small unattached prey, such as crustaceans (amphipods and isopods) and mollusks (clams and snails), comprised over 90% of their diet (by number).

Thais lima from intertidal benches at Amchitka preyed on live barnacles at the University of Washington in Seattle. Field observations on 106 feeding snails (*T. lima*) showed that small littorine snails (*Littorina*) comprised over 93% of their diet (by number). *Thais lima* also preyed on barnacles, where barnacles were abundant in the intertidal region (e.g., Constantine Harbor), and on mussels that had been transferred from Puget Sound to the intertidal region at Makarius Bay.

Siltation Studies. Of 10 dishpans placed in the intertidal area in July 1972, only those enclosing *Hedophyllum* and *Halosaccion* (in high and protected areas) contained silt. The silt averaged 8 cm (3 in.) in depth, and there were no sessile animals or macrophytic plants inside the pans. Pans enclosing *L. longipes, C. vancouveriensis,* and *A. crispa* (in low and exposed areas) contained healthy attached algae but no measurable silt.

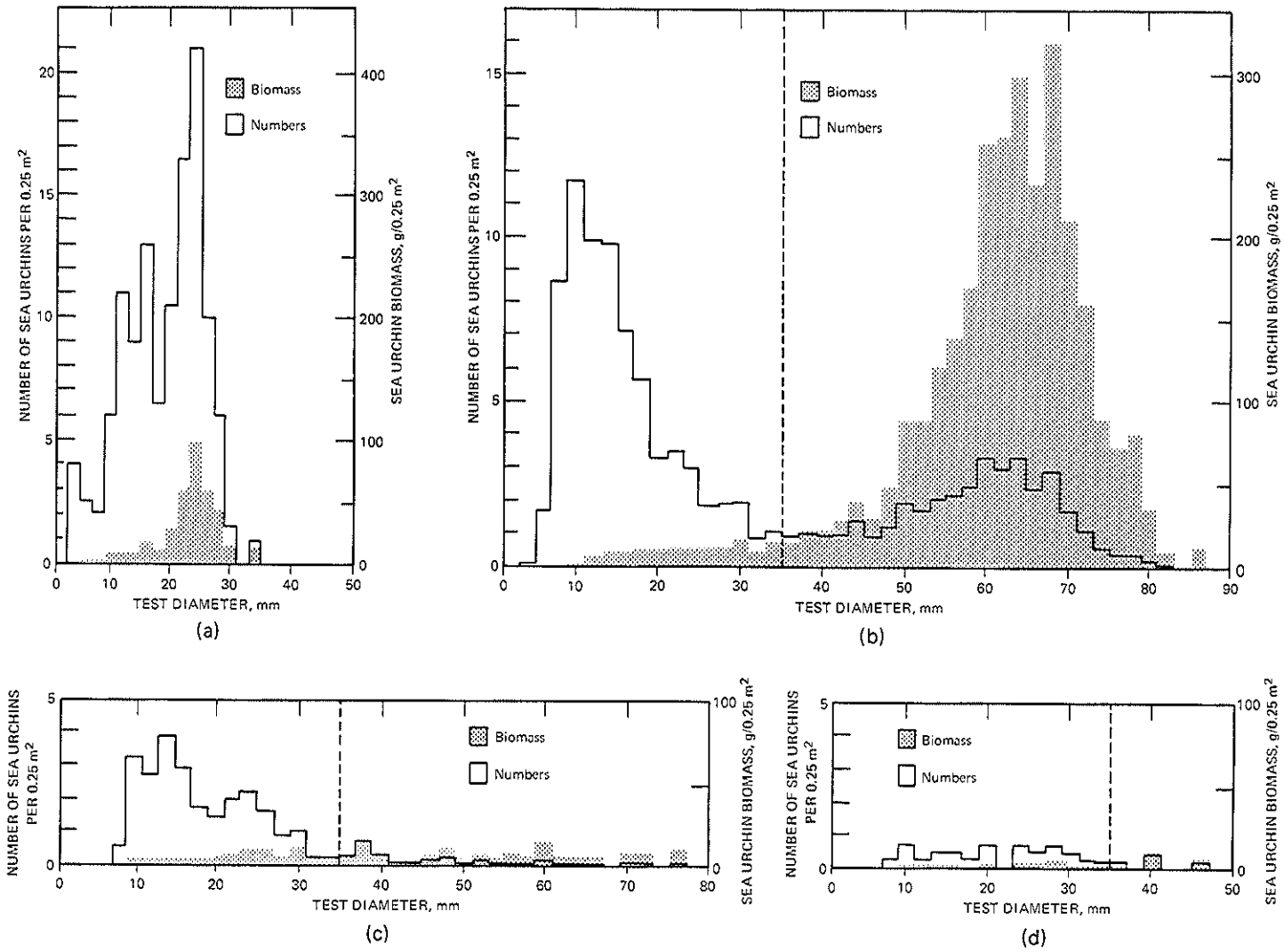

Fig. 22—Sea urchin size class and biomass distribution at depths of (a) 18 to 23 m, Amchitka Island, Alaska; (b) 2 to 3 m, Shemya Island, Alaska; (c) 10 to 15 m, Shemya Island, Alaska; and (d) 20 to 25 m, Shemya Island, Alaska.

Silt 1 to 10 cm (0.4 to 4 in.) deep covers large areas of bays and landward edges of wide intertidal benches. No sessile invertebrates or macrophytes were observed in these areas, although the occurrence of crustose coralline algae beneath the silt suggests that the silt cover is absent during part of the year. (See Lebednik and Palmisano, Chap. 17, this volume.)

Silt also accumulates around algal holdfasts and rocks in sheltered intertidal areas and in higher intertidal zones. Little or no silt accumulates at exposed sites or in lower intertidal zones.

Thirty mussels from Puget Sound (10 to 60 mm long) that had been transplanted to the *Halosaccion* zone (high intertidal region) at Makarius Bay in December 1972 were covered with silt and were dead when examined in April 1973. A similar group of mussels transplanted to the *Laminaria* zone (low intertidal region) were alive and free of silt in April and in August 1973.

Settling Studies. No barnacles or mussels set on oyster shells or in the 1-m^2 denuded rock surfaces at Duck Cove or Makarius Bay. However, a few barnacles (*B. cariosus*) set on the mussels, ropes, and bottles suspended from the dock in Constantine Harbor. Also a few barnacles set at Rifle Range Point in three 0.25-m^2 areas denuded of *C. vancouveriensis.*

Sea Otter Predation. On several occasions small groups (two to six) of sea otters were observed feeding on intertidal benches (sublittoral fringe) during high tide at Makarius Bay, Rifle Range Point, Duck Cove, and Square Bay. Data collected on three adult sea otters (one with a pup) at Makarius Bay during 30-min sampling periods on five consecutive days in August 1973 showed that each adult averaged one dive and five sea urchins every 2 min. At this rate one sea otter would eat 150 sea urchins per hour.

During one week in September 1972, sea otters were seen daily at high tide within 1 m (3 ft) of the breakwater at Sweeper Cove, Adak, where the water depth was less than 3 m (10 ft). These animals predominantly fed on sea urchins that were estimated to be 20 to 50 mm in diameter. One adult sea otter was observed for 30 min, during which time it averaged one dive and four sea urchins per minute. At other areas at Adak, sea otters were observed feeding on unidentified food items, although their scats along the rock and cobble shoreline provide evidence that crab, clam, and mussels are consumed.

Approximately 25 sea otters were seen at Chichagof Harbor on Attu. Several of these otters were observed feeding on sea urchins and mussels within 100 m (325 ft) of shore. No other sea otters were seen at Attu. On subsequent visits to Attu in 1975 and 1976, more than 250 and 340 otters, respectively, were counted.

We saw no sea otters during either trip to Shemya. No otters were observed in 1975 or 1976 at Shemya.

Blade Width of *Laminaria longipes*. The blade width of ungrazed *L. longipes* was greater in protected areas than in exposed areas at each of the four islands studied (Table 7).

DISCUSSION

The direct and indirect consequences of sea otter predation on intertidal communities and the effect of predation by sea otters on subtidal

Table 7—Mean Blade Width (mm) of Ungrazed Intertidal *Laminaria longipes* in Areas Subjectively Considered Exposed or Protected (from Wave Shock) in the Western Aleutian Islands, Summer 1972*

	Exposed					Protected				
Island	N	$\bar{x}$	R	SD	CI	N	$\bar{x}$	R	SD	CI
Amchitka	100	34.3†	20 to 45	7.3	±14.4	100	91.1‡	50 to 140	18.8	±37.2
Adak	100	35.4§	22 to 46	6.9	±13.7	100	88.2¶	48 to 140	16.9	±33.5
Shemya	100	24.6**	15 to 38	6.1	±12.1	100	45.8††	28 to 60	13.3	±26.3
Attu	100	23.3§§	15 to 38	5.2	±10.3	100	88.2¶¶	51 to 138	18.0	±35.6

*N, number measured; $\bar{x}$, average individual size in millimeters; R, range of individual sizes in millimeters; SD, standard deviation; CI, 95% confidence interval.

†Rifle Range Point.

‡Makarius Bay.

§Cape Adagdak.

¶Kuluk Bay.

**Urchin Point.

††There were no protected intertidal benches at Shemya; this value came from *L. longipes* plants in a drainage channel near the shoreward portion of the Urchin Point bench.

§§Murder Point.

¶¶Massacre Bay.

communities are discussed, and this information is integrated with theoretical concepts of community organization in an attempt to elucidate the role of sea otters in the nearshore community at Amchitka.

Intertidal Community

Predation can influence the structure of intertidal communities by preventing competitive exclusion or by directly affecting local extinction (Connell, 1961a; Paine, 1966). Wave shock (Ricketts and Calvin, 1968) influences community structure in a similar way in addition to reducing silt accumulation and providing moisture to high intertidal zones. Our study suggests that sea otters can influence both of these factors and therefore are an important factor in determining community structure. We believe that four categories of interactions, based on predation, exist between sea otters and the community. These interactions we define in terms of the primary and secondary consequences of a dense population of sea otters on the rocky intertidal community, i.e., sea otter predation and physical changes in the environment caused by sea otter predation. Rather than considering each organism in the community in relation to sea otters, we will discuss only those obviously affected by sea otter predation. We then will show how various interactions affect the size, density, and distribution of other specific organisms.

Interactions. General consequences of sea otter predation on the rocky intertidal community as we see them are as follows:

Category I: Organisms are directly preyed on by sea otters, e.g., sea urchins.

Category II: Organisms are indirectly affected by biological consequences of sea otter predation, e.g., kelp.

Category III: Organisms are directly affected by physical changes in the environment, which in turn are indirectly caused by sea otter predation, e.g., barnacles.

Category IV: Organisms are indirectly affected by physical changes in the environment, which in turn are indirectly caused by sea otter predation, e.g., predacious sea stars.

These categories are neither mutually exclusive nor independent; they simply are an organizational convenience. Also, we have not experimentally proven that these interactions unequivocally are tied to the sea otter. Other possibilities also will be considered in our discussion. For additional details on the effect of sea otter predation on rocky intertidal communities, see Palmisano (1975).

Category I. Sea otters consume 20 to 23% of their body weight in food daily (Kenyon, 1969). Stomach analyses of (Kenyon, 1969; Lensink, 1962; Burgner and Nakatani, 1972), field observations of (Kenyon, 1969; Estes and Smith, 1973; personal observations), and feeding experiments with captive sea otters, all at Amchitka, show that sea otters are opportunistic predators on benthic intertidal invertebrates (sea urchins, chitons, mussels, limpets, etc.) and bottom-dwelling fishes. This suggests that the dense population of sea otters at Amchitka preys heavily on known food items and is responsible for scarce populations of such intertidal animals as the sea urchin.

High densities of intertidal sea urchins and mussels at Amchitka in the 1930s and at Adak in the 1950s, when sea otters were less abundant on both islands (Kenyon, 1969, and personal communication), and high densities of these intertidal organisms at the islands of Attu and Shemya, where presently there are few or no sea otters, are further evidence (although circumstantial) that sea otters influence populations of these intertidal invertebrates.

The high densities of mussels on vertical intertidal faces at Adak (an island with a dense population of sea otters) suggest that (1) sea otters do not prefer mussels at Adak because other food resources, such as crabs and clams, are abundant; (2) these mussels are inaccessible to sea otters; or (3) some other factor affecting mussels is different between Amchitka and Adak (see discussion near end of category III). If sea otters do prey on these mussels, then continued mussel abundance may be due to good recruitment from areas inaccessible to sea otters. The high density of sea urchins in the breakwater at Adak is probably due to the inability of sea otters to get between the rocks where sea urchins are most abundant. Sea urchins eaten by sea otters in this area probably are those which leave the immediate protection of the breakwater.

We believe that the small size of sea otter food items at Amchitka is due to the sustained influence of resource overexploitation by sea otters. Many predators select large prey because this is energetically the most efficient way of feeding. The growth study conducted at Friday Harbor with intertidal sea urchins from Amchitka proved that these sea urchins are not genetically limited to a small size. Also, their small size is not the result of food limitation in view of the extensive kelp association at Amchitka. This association not only provides a food resource but also a refuge from predation for small sea urchins that live within and around the algal holdfasts. When individual sea urchins leave the protection of the algae or become

too large to be concealed by the holdfasts, they become vulnerable to sea otter predation. Thus protection afforded by the kelp association regulates, to some degree, the size and number of sea urchins susceptible to predation and serves to prevent sea otters from completely eliminating sea urchin populations. The observation of larger sea urchins at Amchitka in the 1930s and the remains of larger sea urchins in Aleut kitchen middens suggest that the present small size of intertidal sea urchins at Amchitka is due to overexploitation by sea otters. Sea urchin sizes at Adak, Shemya, and Attu also support this contention as does the apparent larger size of sea urchins at Massacre Bay (no sea otters) compared with Chichagof Harbor (a small population of sea otters) on Attu.

Other predators could contribute to the low density and small size of individuals in the sea urchin population at Amchitka. Common Eiders (*Somateria mollissima*) and Glaucous-winged Gulls (*Larus glaucescens*) are known to feed on sea urchins and are present at Amchitka (Williamson et al., 1972). These birds, however, also are abundant at Attu and Shemya, and thus apparently they are not capable of significantly reducing individual size or population density of sea urchins.

With this wealth of evidence, we suggest that sea otter predation is primarily responsible for the sparse population of small sea urchins in the intertidal area at Amchitka. For similar reasons, sea otter predation also may be responsible for sparse populations and small sizes of other intertidal invertebrates, i.e., chitons, mussels, and limpets.

Category II. The establishment of sea otters as the major predator of sea urchins at Amchitka and overwhelming evidence in the literature on the grazing effects of sea urchins support the hypothesis that extensive intertidal kelp beds at Amchitka are maintained indirectly by sea otter predation. The experiments at Amchitka (caged sea urchins) and Shemya (sea urchins removed from tide pools) further demonstrate that sea urchins inhibit persistence and development of algal associations.

Algae in the lower intertidal area of Shemya and Attu (islands with few or no sea otters, no offshore kelp beds, but benches and climate similar to Amchitka) were heavily grazed, and algae in comparable areas at Adak (an island with many sea otters, few benches, few offshore kelp beds, but with a climate similar to Amchitka) were ungrazed. These observations suggest that the intertidal algal associations in comparable areas at Amchitka are not maintained solely by extensive benches, offshore kelp beds, or climate. Although all these factors may enhance their development, algal communities cannot coexist with dense populations of sea urchins. Therefore we believe that the extensive association of intertidal algae at Amchitka exists primarily because of a sparse population of sea urchins.

Experiments conducted at Amchitka showed that grazing by limpets (*C. pelta*) can prevent the development of algal sporelings in small areas. This effect is confirmed by the well-documented results of Shotwell (1950), Jones (1948), and Dayton (1971). Thus it appears that the scarcity of limpets at Amchitka contributes to the development of algal communities.

Although sea otters do feed on limpets, Black Oystercatchers (*Haematopus bachmani*) may depredate this mollusk more severely because limpets are the preferred food of the approximately 300 oystercatchers at Amchitka (Williamson et al., 1972). However, because sea urchins potentially are more destructive to algal communities than are limpets (limpets are slow moving and feed primarily on sporelings and small algae) and because sea otters are more abundant and consume more food, Black Oystercatchers probably are not as important as sea otters in maintaining the association of intertidal algae at Amchitka.

The absence of sea otters and oystercatchers at Attu and Shemya (Sekora, 1973) almost certainly accounts for the dense population of limpets there.

The grazing effect of Emperor Geese on the intertidal kelp beds is negligible because the only plants eaten by geese are small red and green algae.

The wide expanse and dense canopy of *L. longipes* at Amchitka appear to prevent other kelp species from settling and persisting in the sublittoral fringe. *Thalassiophyllum clathrus* is restricted to the subtidal area and tide pools at Amchitka. However, it occurs intertidally at Attu, Shemya, and Adak where *L. longipes* is less abundant than at Amchitka. In the sublittoral fringe at Attu and Shemya, *T. clathrus* settles in the bare patches caused by the grazing of sea urchins. *Thalassiophyllum clathrus* apparently persists here because sea urchins prefer not to graze it (demonstrated by food-preference studies). The short irregular boulder-strewn intertidal bench at Adak probably does not permit *L. longipes* to develop extensive continuous beds and thus to competitively exclude other intertidal kelps, such as *T. clathrus.*

Thalassiophyllum clathrus did not settle in experimentally denuded rock areas at Amchitka, but *C. triplicata,* a subtidal alga at Amchitka, did settle there (Palmisano, 1975). *Cymathere triplicata* was also present in the intertidal area at Adak. Another subtidal kelp, *L. groenlandica*, also

was present in the intertidal area at Shemya and Attu, although not at Adak. Thus it appears that one subtidal kelp occurs intertidally at Attu and Shemya but not at Amchitka because of an indirect effect of sea otter predation, and it occurs intertidally at Adak because of the heterogeneity and narrowness of the bench.

Low-intensity herbivory at Amchitka may enable intertidal algae to outcompete barnacles and mussels for space. Lewis (1964) observed that algae outcompete sessile invertebrates along protected rocky coasts in Great Britain. Dayton (1973) found that algae are competitive dominants over sessile invertebrates in the high intertidal area along the open coast of Washington. Although algae have overgrown some invertebrates at Amchitka, settling experiments showed that neither barnacles nor mussels settle on experimentally denuded horizontal rock surfaces or on oyster shells in protected areas, such as Makarius Bay (areas with few or no barnacles and mussels). Some barnacles did settle on denuded rock in exposed areas, such as Rifle Range Point, on material suspended subtidally from the dock at Constantine Harbor, and on experimentally denuded horizontal rock surfaces at Shemya (areas with moderate to high densities of barnacles). These results suggest that recruitment of sessile invertebrates is closely related to the size and proximity of existing populations. Thus sea otter predation indirectly may cause the dominance of algae and the scarcity of barnacles and mussels on the intertidal bench. On the other hand, those species whose food webs originate from macrophyte productivity, such as the crustaceans (which feed on attached and drift kelp) and the fish they support at Amchitka (Simenstad, 1971; Burgner and Nakatani, 1972; Isakson, Simenstad, and Burgner, 1971), will be absent or scarce where kelp beds have been destroyed or severely reduced by intensive grazing pressure (Simenstad et al., Chap. 19, this volume).

Category III. Many intertidal organisms depend on wave shock to create bare areas needed for larval settling or to prevent accumulation of smothering silt (Ricketts and Calvin, 1968). These organisms are rare in protected environments. Lewis (1964) observed that along the rocky coasts of Great Britain sessile invertebrate associations predominate in areas exposed to direct wave action whereas algal associations occur in more protected areas. Extensive offshore kelp beds can absorb wave energy and thus reduce wave shock to the intertidal area (Moore, 1958; Lewis, 1964; MacGinitie and MacGinitie, 1968).

Weinmann (1968) observed that *L. longipes* have wider blades in protected areas than in exposed areas. The blades of *L. longipes* are wider at the seaward edge of the benches at Amchitka than they are at similar areas at Attu and Shemya (Table 7). This suggests that the intertidal benches at Amchitka are more protected by extensive offshore kelp beds than are similar areas at Attu and Shemya where offshore kelp beds are absent. Blade width is not related to geographical isolation in this situation because *L. longipes* has wide blades in protected areas at Attu (Palmisano, 1975; personal observation) and narrow blades in exposed areas at Amchitka.

At Amchitka barnacles and mussels are most abundant along exposed shorelines. Our experiments show that more silt accumulates in protected areas and higher intertidal zones than in exposed areas and lower intertidal zones. Furthermore, mussels transplanted into known areas of siltation at Amchitka were smothered and eventually died, and barnacles were killed by natural and man-induced increases of siltation at Square Bay and Duck Cove. Therefore the abundant kelp beds at Amchitka, which protect the intertidal area, facilitate siltation and probably, at least in part, are responsible for relatively low densities of barnacles and mussels.

Factors other than offshore kelp beds may be responsible for the depauperate mussel–barnacle association at Amchitka. For example, well-developed intertidal benches also may reduce wave exposure and thus increase siltation. However, there are dense populations of barnacles at Attu and Shemya where benches similar to those at Amchitka exist but where offshore kelp beds are absent.

Mussel and barnacle associations also could be poorly developed at Amchitka because of competition for space, predation, or lack of food. Algal competition may be partially responsible for the scarcity of mussels and barnacles; however, because algae and these invertebrates coexist in the intertidal area at Attu and Shemya, we consider reduced wave shock at Amchitka to be the more important factor.

Mussels and barnacles coexist abundantly with dense populations of predacious snails and sea stars at Attu, Shemya, and Adak. This suggests that predation by mollusks and sea stars, which are less dense and take other prey at Amchitka, is not responsible for the low abundance of barnacles and mussels.

Food is probably not a limiting resource to the growth of mussels or barnacles at Amchitka. Individual large mussels and barnacles occur at Rifle Range Point, Banjo Point, and Constantine Harbor. Also, mussels introduced to Amchitka from Puget Sound tripled their lengths within 18

months. Therefore reduced populations of barnacles and mussels on intertidal benches at Amchitka apparently are more closely related to reduced wave shock than to these other factors.

Barnacle and mussel densities may be high at Adak because of physical factors unrelated to the presence of sea otters. These invertebrates occur there on vertical surfaces not subject to accumulation of silt. Also, although the convoluted coastline is protected by its very physical nature at Adak, there are few offshore kelp beds (because of unsuitable substrates) to absorb wave energy and no wide benches to reduce wave shock.

Thus, although purely physical factors, such as bays, islets, and reefs, do affect intertidal communities by reducing wave shock, the evidence suggests that sea otter predation at Amchitka is the major cause of such physical changes and thus in turn has prevented the development of extensive barnacle and mussel beds in the intertidal community.

Category IV. Organisms limited by barnacle or mussel beds as critical resources may be rare or absent and reduced in size where these beds are absent. For example, at Amchitka *T. lima* prey almost exclusively on small littorine snails and *L. alaskensis* prey on small mollusks and crustaceans. *T. lima* and *L. alaskensis* may be small and scarce on the benches at Amchitka because their individual food resources are small and spatially dispersed (i.e., not clumped); they probably would be larger and more abundant if food resources were large, sessile, densely clumped organisms, such as barnacles and mussels. This hypothesis is supported by the coexistence, at Attu, Shemya, and Adak Islands, of large *T. lima* and large *L. alaskensis* with dense populations of barnacles and mussels. Evidence that these predators at Amchitka are not genetically limited to a small size is provided by the fourfold increase in weight at Friday Harbor of *L. alaskensis* removed from Amchitka and by the occurrence of large *T. lima* in Constantine Harbor and at Banjo Point, areas of relatively high densities of barnacles and mussels.

The abundance and size of *T. lima* may also affect hermit crab (*Pagurus*) populations. Hermit crabs require a shell resource; over 90% of the hermit crabs at Attu, Shemya, and Adak occupied *T. lima* shells. The scarcity of these shells on the intertidal bench at Amchitka apparently is one reason why hermit crabs also are not abundant there. Carl F. Nyblade (personal communication) stated that abundant littorine snails at Amchitka should provide a suitable shell resource for *P. hirsutiusculus* even though these shells are considerably smaller than *T. lima* shells. Palmisano (1975) speculates that this resource is destroyed by marine birds that prey on littorines.

Alternately the sparse hermit crab population at Amchitka could be caused by an inadequate food resource, by unsuitable habitat, or by fish predation. The specific food requirements of hermit crabs are poorly known, but adequate food should be available at Amchitka for these detritus feeders. Shemya has more tide pools than Amchitka or Attu, but Attu and Shemya have comparable hermit crab densities. Thus tide pools apparently are not essential for hermit crab survival. Hermit crabs are also abundant at Adak where there are a few tide pools and an abundant supply of *T. lima* shells but unfortunately an unknown effect of predation by nearshore fishes. Therefore our observations suggest that the sparse population of hermit crabs at Amchitka is caused either by a lack of suitable shells or by predation of fish from the kelp community.

Finally, the small size and low densities of predacious snails and sea stars and the low density of hermit crabs at Amchitka may be physically maintained by low wave shock, which in turn is ultimately caused by sea otter predation on epibenthic invertebrates.

Subtidal Community

Species Diversity in the Nearshore Community. Increased species diversity in both terrestrial and marine environments is a phenomenon generally observed as one progresses from the Arctic to the tropics (Hedgpeth, 1957; Fischer, 1960; Sanders, 1968; MacArthur, 1972). Exceptions to this general pattern are the kelps (Phaeophyta) and red algae (Rhodophyta) and several terrestrial groups (Fischer, 1960). A review of several theories on causal factors responsible for increased species diversity in the tropics in light of his own data on species diversity of the deep-sea benthos led Sanders (1968) to the stability—time hypothesis. Briefly, this hypothesis proposes that physically severe (unstable) environments tend toward an abiotic condition, allowing the existence of only a limited number of species. Stable environments, on the other hand, given sufficient time develop diverse biological communities. Recently this hypothesis was challenged by Dayton and Hessler (1972) who argued that high-species diversity is not necessarily solely the result of competitive niche differentiation but is also caused by predictable disturbances, which reduce the importance of competitive exclusion and thus allow the coexistence of many species who share the same resources.

The importance of disturbance in structuring certain communities is clear. In theory, a pre-

dictable disturbance releases a critical resource, such as light, space, and nutrients, from monopolization by species with superior competitive ability. Thus a diverse community is maintained so long as resources are available to fugitive species. In the absence of disturbance, the tendency of some species toward local extinction is predicted.

The importance of predation as a source of local predictable disturbance was proposed by Paine (1966) and further supported by observations by Paine and Vadas (1969), Connell (1970), Dayton (1971), and others. Paine (1966) found that species diversity is related directly to the efficiency with which predators prevent monopolization of major environmental requisites by competitively superior species in intertidal communities. In his studies predator removal led to local extinction of certain invertebrates and algae. The ecosystem thus became trophically simpler with decreased diversity and decreased primary productivity.

Earlier studies of sea otter food habits in the western Aleutian Islands (Lensink, 1962; Kenyon, 1969; Burgner and Nakatani, 1972) suggest that sea otter predation is an important community interaction. During recent years at Amchitka Island, invertebrates and fish have contributed approximately equally to the sea otter's diet. Studies by Kenyon showed at least 42 species of food items from sea otter stomachs. In the analyses by Burgner and Nakatani, although food items were not reported as individual species, 15 different food items were reported from stomach analyses. Stomachs used in Kenyon's studies were collected from Amchitka in 1962 and 1963, a time when the sea otter population had been at equilibrium density for at least a decade. Stomachs used in the study by Burgner and Nakatani were collected at Amchitka in 1970 and thus also are from a sea otter population at equilibrium density. Lensink (1962) reported analyses of sea otter feces collected at the Komandorskie and Aleutian Islands in the 1930s and 1940s. Only six food items were reported from these observations with sea urchins and mussels composing nearly the entire volume. Lensink's studies indicated that the sea urchin was the dominant sea otter food item at Amchitka and other Aleutian Islands during the late 1930s and 1940s. The later studies of Kenyon (1969) and Burgner and Nakatani (1972) showed an increase in diversity of food items consumed by the sea otter. Of particular interest is the increased amount of fish in the sea otter's diet during recent years. Although techniques used by these various investigators are not strictly comparable, the general pattern of change in sea otter food habits through time is certainly significant. During early stages of population recovery, the sea urchin was apparently the primary food item; later, as the sea urchin population was reduced by sea otter predation, invertebrate community structure and/or sea otter foraging strategies changed. This was reflected as an increased diversity in sea otter forage items, paralleling temporally the development and establishment of high-density sea otter populations.

Similar observations and conclusions have been made on the sea otter in California. A profound decrease in sport and commercial abalone fisheries has been reported following the influx of sea otters into areas of previously unoccupied habitat (Wild and Ames, 1974; Miller, Geibel, and Houk, 1974). A survey conducted in 1967 by the California Department of Fish and Game revealed that, throughout the sea otter's range, preferred forage items were reduced in number and restricted to protected habitat as compared with habitat outside the range (Ebert, 1968). Also, an increased diversity in sea otter forage items has been reported in areas long inhabited by sea otters. This is apparently the result of reduced availability of preferred sea otter forage items (Wild and Ames, 1974).

Thus the role of the sea otter in structuring nearshore marine communities fits nicely into the predation model of Paine (1966). Our observations from Attu and Shemya suggest that the absence of sea otters allows sea urchins to monopolize subtidal communities, and "dominance diversity" (Sanders, 1968, p. 260) is very low. At Amchitka a high-density sea otter population prevents monopolization of subtidal resources by sea urchins so that dominance diversity is higher than at Attu and Shemya. Thus, in addition to general observations on community structure, studies of sea otter food habits in the Aleutian Islands and in California further support the role of the sea otter in maintaining a diverse community.

Sea otter food habits also certainly are affected by food availability (or energy abundance). Schoener (1971) and MacArthur (1972) presented theoretical arguments that relate feeding strategies to food availability. Schoener's model considers species from an energy—time standpoint, and from it he concludes that there is an optimum number of species in the diet of a predator at any given general prey density which will yield a maximum amount of energy per amount of time expended in procuring food. This model predicts that, as prey density increases, there is a decrease in the number of species that should be included in a predator's diet to maximize energy yield. MacArthur's model is based on time economy and prey selection but reaches a conclusion similar to the Schoener model. As prey density decreases, species diversity

in prey selection increases. Numerous examples that support this conclusion are found in the literature, and it is reasonable to expect that the array of food items used by sea otters will increase as exploitation due to predation decreases the general food abundance.

The control of sea urchins by sea otter predation releases algal associations from overgrazing and thus increases vegetational biomass and primary productivity. Species associated with subtidal primary productivity are influenced indirectly. Sea otters, therefore, may influence species diversity through two basic mechanisms: (1) Species diversity may be increased by reduced competition with sea urchins or other epibenthic invertebrates for environmental requisites and (2) species diversity may be increased indirectly by increased primary productivity that results when grazing pressure by an uncontrolled sea urchin population is released. Thus sea otters increase diversity and primary productivity and perhaps lend stability (Sutherland, 1974; but see May, 1973)* to nearshore communities.

This discussion logically leads to the influence of overexploitation of food resources by the sea otter. Paine and Vadas (1969) reported that algal associations of low species diversity are maintained not only by sea urchin overgrazing but also by undergrazing in areas devoid of sea urchins. In the absence of urchin grazing pressure, dominant algal species tend to exclude competitively other species and to monopolize the vegetational association. Intermittent sea urchin grazing provides a release of heterogeneous space, allowing the colonization of fugitive algal species. This process increases the number of coexisting algal species. Maximum algal species richness, therefore, should be approached when the sea urchin population is balanced between overexploitation and underexploitation of the plant association.

Sea otters undoubtedly exploit the Amchitka sea urchin population heavily. Can this, in fact, be considered overexploitation, and, as a consequence, is the macroalgal association monopolized by dominant species? Our data from the shallow subtidal area at Amchitka suggest that in many areas four species of *Laminaria* dominate the epibenthic canopy; sea urchins, other than small individuals associated with haptera or protective crevices, are rare. This observation in itself is open to the interpretation of monopolization by a single species or several species within the genus. Another factor of probable importance as a source of disturbance is the frequent and violent winter storms of the Aleutian Islands. Walker and Richardson (1955) state that *Laminaria* is torn from the sea bed during heavy winter storms around Scotland. Large deposits of vegetation on the beaches of Amchitka following violent storms indicate a similar situation there. Therefore storms also may provide a mechanism for the release of space and thus the colonization of fugitive species.

Sea Otter and Pattern in the Nearshore Algal Association. Hutchinson (1953) stated that community patterns are determined by stochastic processes, physical forces, and biological forces. We will discuss the basic sublittoral community patterns at Amchitka Island according to Hutchinson's scheme. Our tentative opinion as to the causal factors of these patterns is based primarily on the discussion and conclusions from studies of ecologically similar areas. Final acceptance or rejection of these conclusions as they apply specifically to western Aleutian communities depends on direct experimental evidence, which is presently lacking.

Generally, community patterns are similar in coastal north temperate and boreal waters of the Atlantic and Pacific Oceans (Kitching, 1941; Walker, 1947; Jorde and Klavestad, 1963; Kain, 1966; Vadas, 1968; Himmelman and Steel, 1971; Mann, 1972a; and others). Sublittoral macrophyte associations are well developed on rocky substrates throughout this geographic range. Various species of *Laminaria* are dominant in the shallow kelp zone, and *Agarum* frequently is found in slightly deeper water. Sea urchins are the dominant benthic invertebrate in many of these communities.

Connell (1961a) proposed a general theory to explain the rather sharply defined pattern of zonation in rocky intertidal communities; i.e., physical factors limit the upper distribution and biological factors limit the lower distribution of species. Sublittoral communities are apparently less strictly defined spatially (Kitching, 1941) with their upper and lower limits of species distributions not universally defined by physical and biological forces, respectively.

Vadas (1968) stated that the distribution of subtidal algae may be limited by temperature, salinity, light, suitable substrate, exposure, and biological interaction; however, he stressed the importance of predation and competition.

Stochastic Processes. Some variation of sublittoral community structure is undoubtedly the result of stochastic processes. Because large sample sizes are required for adequate analysis of this factor and because we believe the overwhelming

*The dogma that complexity begets stability in ecological systems has recently been challenged (May, 1973). A detailed discussion of diversity–stability arguments is inappropriate here. We only wish to point out that the nature of diversity–stability relationships is conjectural.

evidence points to physical and biological causality in the communities observed, stochastic factors will not be considered here.

Physical Forces. Of the physical factors discussed by Vadas (1968), all but light probably can be discounted as a causal factor dictating patterns in the association of subtidal macrophytes at Amchitka. Temperature and salinity are generally constant throughout the depth range studied. All study areas were located on solid-rock substrates with nearly constant slopes. The four study areas at Amchitka varied in exposure from well protected to heavily exposed, but no consistent pattern can be attributed to this factor. Physical factors also are generally similar in the Rat and Near Islands.

The abundance of vegetation decreases with increased depth in the subtidal area at Amchitka. This observation is consistent with the pattern of other subtidal plant associations over a wide geographical range (Walker and Richardson, 1955; Jorde and Klavestad, 1963; Kain, 1966; Walker, 1947; Aleem, 1956; McLean, 1962; Mann, 1972a). (Light attenuation as depth increases is certainly one factor responsible for this pattern.) Also, red light and blue light are selectively absorbed by clear ocean water, and green light penetrates most deeply. Because the action spectrum of green and brown algae is restricted primarily to blue light and red light, these plants are limited in depth by the shallow penetration of light that they require for photosynthesis. Red algae, which uses the reduced light beneath the lower canopy (Dawson, Neushul, and Wildman, 1960) and the deep penetrating green light (Blinks, 1955) in photosynthesis, are thus abundant throughout the depth range of the brown and green algae and beyond it.

Biological Forces. High-density sea urchin populations have been reported to be responsible for the scarcity of noncoralline algae in many areas (Himmelman and Steele, 1971; Kitching and Ebling, 1961; Vadas, 1968; and others). We believe that the high-density sea urchin population at the Near Islands is responsible for the virtual absence of fleshy macrophytes in subtidal areas.

Conversely, sea urchin densities at Amchitka are extremely variable. However, sea urchins are rare in shallow areas. At Amchitka sea urchin densities increase with increasing depth (Fig. 19), and grazing pressure, therefore, may be partially responsible for the pattern in vegetation abundance.

Vadas (1968) found that *Laminaria* was the climax genus in the absence of grazing in the San Juan Islands. In the presence of moderate grazing pressure on *Laminaria, Agarum* entered the community as a result of reduced competition with *Laminaria* for light. He found that, although *Laminaria* was dominant over *Agarum* in the undisturbed community, *Agarum* was resistant to urchin grazing and became established in the presence of moderate grazing disturbance.

At Amchitka *Laminaria* is apparently able to completely exclude *Agarum* in shallow water [mean water level to about 7 m (23 ft) in depth]. At the lower edge of this shallow zone, *Laminaria* is apparently limited by decreased light and perhaps also by increased sea urchin grazing, thus allowing *Agarum* to enter the vegetation association.

Mechanisms of Sea Urchin Population Regulation. There are two classically understood methods of population regulation. First, populations may be limited by resources, in which instance intraspecific or interspecific competition limits population growth. Requisite resources include nutrients, space, and light. Disturbances also may limit populations. Disturbances operate as biological (predation) forces and/or physical forces, such as catastrophic events and physiological barriers.

The upper distribution of sea urchins at Attu and Shemya appears to be limited by disturbance. At low tide Glaucous-winged Gulls (*L. glaucescens*) are commonly observed feeding on large sea urchins. The upper distribution of sea urchins also is physiologically limited because urchins require almost constant exposure to fresh seawater. At the edge of this area, we frequently observed sea urchins moving up and down with the incoming and outgoing tides. Physiological limitations probably primarily determine the upper limit of sea urchins at the Near Islands.

The lower limit of sea urchins at Attu and Shemya is below depths that we were able to dive with scuba. However, the decrease in population density that we observed at greater depths indicates that the population is more severely limited there than in shallow water. Because there are no apparent sources of disturbance to the sea urchin population at these depths, we believe that the deeper distribution of the population is primarily resource limited, probably by nutrients, such as macrophytes. Drift algae are also probably important to the distribution of sea urchins at Attu and Shemya. After storms, moderate accumulations of algae are observed on the beaches at Attu and Shemya. The majority of this material that is not washed ashore settles in the shallow subtidal area and thus serves as a source of nutrition for herbivores. In support of this idea, Fig. 23 shows sea urchins congregated about a strand of *A.*

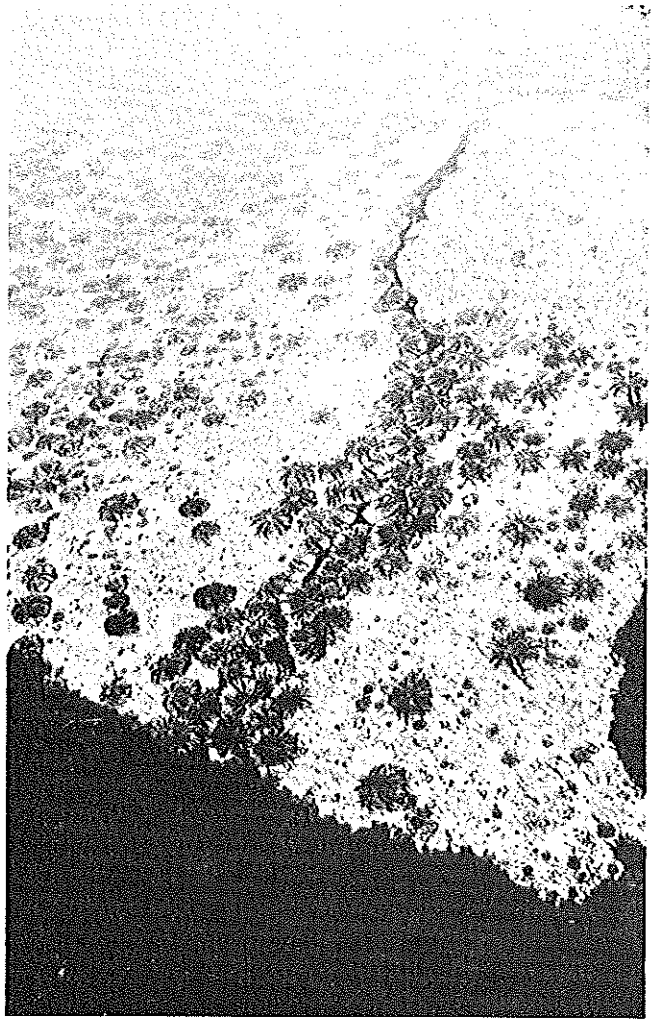

Fig. 23—Sea urchins massing about a strand of *Alaria fistulosa* that has drifted into a large tide pool in lower intertidal area at Shemya Island, Alaska (Sept. 2, 1971).

fistulosa that had drifted into a large tide pool of the lower intertidal area at Shemya. Also, while diving on Attu we encountered several groups of sea urchins massed together in the form of a sphere. We separated one of these spheres and found a small piece of *Thalassiophyllum* blade near its center.

Displacement of nutrients by wave action from the large standing crop of intertidal macrophytes may also be important to sea urchins in the shallow subtidal area at Attu and Shemya. In fact, apparently there is almost no source of nutrient production sympatric with subtidal sea urchin populations. The expected distribution of nutrient input (drifting algae from other areas and nutrients washed from the intertidal area) corresponds closely with observed distribution of sea urchins.

In direct contrast to the distribution of sea urchins at Shemya and Attu, sea urchins at Amchitka are most severely limited in the immediate subtidal area, and population densities increase in deeper water (Fig. 19). We believe that sea otter predation is primarily responsible for this distribution. Certainly the abundant standing crop of algae at Amchitka would preclude sea urchins from nutrient limitation! Competition for space with the well-established algal association also seems unlikely, although the physical and biological configuration of the bottom may influence larval settling (Crisp and Barnes, 1954). Perhaps predation from diving birds, fish, or other invertebrates is of some significance, but the potential impact of sea otter predation is logically the most important limiting factor. As at Attu and Shemya, depth limitations in the use of scuba prevented us from observing the lower distributional limits of sea urchins at Amchitka.

At Attu and Shemya we observed numerous sea urchins with abraded areas on the outer surface of their tests. This was never observed at Amchitka. Himmelman and Steele (1971) noted test abrasions in *S. drobachiensis* which they attributed to cannibalism when insufficient food was available. We have no direct evidence that the bare areas on sea urchin tests at Attu and Shemya were caused by cannibalism, but it seems logical that population crowding is somehow involved.

r- or K-Selection? The concept of r- and K-selection was conceived originally by MacArthur and Wilson (1967) to explain reproductive strategies of species that are closely associated ecologically. In an uncrowded environment, selection preference is extended toward r-strategists or toward species with the highest intrinsic rate of natural increase. The strategy is to convert a maximum amount of food into new members of the population. In a crowded environment, i.e., one in which populations exist near equilibrium density, K-strategists are favored. Efficiency of food use is important in maintaining large populations, and wasteful exploitation of food resources, such as for the production of large numbers of offspring, is selectively unfavorable (Crow and Kimura, 1970). Pianka (1970) summarized some of the correlates of r- and K-selection, a few of which are given in Table 8.

From our prior discussion and from the information given in Table 8, sea urchins at Amchitka appear as r-strategists whereas those at Attu and Shemya appear as K-strategists. This is unlikely because we are dealing with a single species. Thus we expect these populations to be similar genetically and either r- or K-strategists but certainly not both.

We propose that, whereas sea urchins at Attu and Shemya fulfill many requirements of K-

Table 8—Some Correlates of r- and K-Selection*

Item	r-selection	K-selection
Mortality	Often catastrophic, density independent.	Density dependent.
Survivorship	Often type III (Deevey, 1947).	Usually types I and II (Deevey, 1947).
Population size	Variable in time, non-equilibrium; usually well below carrying capacity of environment; unsaturated communities or portions thereof; ecological vacuums.	Fairly consistent in time, equilibrium; at or near carrying capacity of the environment; saturated communities.
Intraspecific and inter-specific competition	Variable, often lax.	Usually keen.

*From E. R. Pianka, On r- and K-Selection, *American Naturalist*, 104: 593 (1970).

strategists, the species has evolved through r-selection. Thus the tendency toward maximum energy exploitation by an uncontrolled r-strategist is incompatible with maintenance of the energy resource (e.g., macrophytes are destroyed).

Sea Otter and Productivity of the Nearshore Community. Benthic macrophytes are of considerable importance to nearshore productivity in temperate waters. Blinks (1955) stated that, although littoral marine algae occupy only a narrow coastal zone as compared with the entire ocean, their productivity may be several orders of magnitude greater per comparable unit than the open sea except in areas of upwelling. Mann (1972b; 1973) found that forests of *Laminaria* and *Agarum*, which characterize the subtidal area of temperate oceans, contribute considerably to the total productivity of coastal waters in the North Atlantic Ocean. He attributed this to the attachment of plants on the rocky substratum and thus to an unusually good supply of nutrients circulated by tides and currents. Significantly the range of feeding habitat of sea otters coincides with, and extends beyond, the area of epibenthic algae. As such the sea otter may indirectly maintain the kelp beds (see earlier discussion).

Some animal species present at Amchitka but scarce or missing at Attu and Shemya may depend on the highly productive macrophytic algae as a nutritional base. Those animal species whose food webs originate from macrophyte productivity certainly could be adversely affected by its removal (Paine, 1966).

The rock greenling (*Hexagrammos lagocephalus*), abundant and commonly encountered while diving at Amchitka, is infrequently seen at Attu and Shemya. This species feeds largely on crustacean invertebrates, which, in turn, are associated with kelp beds (see earlier discussion). Higher trophic forms at Amchitka, which are dependent on fish for some part of their food, probably either use different foraging strategies or maintain smaller populations at Attu and Shemya. Sea otters consume greater amounts of fish at Amchitka than in areas of low sea otter population density (Lensink, 1962). Harbor seals (*Phoca vitulina*) are less common at Attu and Shemya than at Amchitka where groups of over 100 commonly haul out at numerous areas along the coast (Kenyon and King, 1965). Harbor seals feed predominantly on nearshore fishes and cephalopods at Amchitka (Wilke, 1957; Kenyon, 1965).

The Bald Eagle (*Haliaeetus leucocephalus*), although abundant in the Rat Islands, is absent in the Near Islands (Sekora, 1973; personal observations). Bald Eagles in the Aleutians are largely dependent on marine productivity. Fish, marine mammals, and marine birds have been found to constitute the majority of their diet on Amchitka (White, Emison, and Williamson, 1971). Also, drift algal stipes are major constituents of Bald Eagle nests at Amchitka Island (personal observation). The absence of eagles in the Near Islands may therefore be related indirectly to reduced macrophyte productivity.

The Common Eider (*Somateria mollissima*) is by far the most common duck in saltwater areas of Attu Island (Near Islands) (Byrd, 1973). This species probably owes its high density to the sea urchins (Byrd, 1973). Although the Common Eider is present at Amchitka, it is not nearly so abundant there as at Attu, probably reflecting the decreased availability of sea urchins at Amchitka Island.

Sea otters also may contribute to the growth of kelp beds (and associated species of animals) along much of the west coast of North America. McLean (1962) reported that sea otters in California completely remove large sea urchins (*S. franciscanus*) from areas by predation, permitting luxuriant development of the *Nereocystis*—*Pterygophora* association. North (1965) attributed recent kelp bed (*Macrocystis*) reduction to sea urchin grazing and further speculated that an increase in *Macrocystis* density in the Monterey area resulted from sea urchin removal by sea otters. Miller and Geibel (1973), however, point out that recent changes in distribution and abundance of *Macrocystis* and *Nereocystis* in many areas are related to factors other than sea otter predation. Thus, although sea otters clearly reduce benthic invertebrate populations in these areas of the California coast, other interactions are not well understood.

The Aleut has inhabited the eastern Aleutian Islands for at least 8400 years (Laughlin, 1972) and Amchitka for at least 2500 years (Desautels et al., 1970; McCartney, Chap. 5, this volume). Laughlin (1972) believed that the Aleut influenced the sea otter by direct exploitation through hunting and competition for food resources by gathering sea urchins. We doubt that the Aleut was able to compete with sea otters for food, although Aleuts collected sea urchins from the intertidal and very shallow subtidal zones. However, Aleuts certainly were capable of reducing sea otters by hunting, as is evident from the fact that sea otters were driven nearly to extinction by Aleuts after they were enslaved by Russian fur traders. Furthermore, evidence from middens suggest that Aleuts depleted sea otter populations long before the arrival of white men. However, from the standpoint of evolutionary time, the Aleut is recent. Thus his importance as a natural predator in the nearshore community is not yet clear.

Some of the preceding discussion is speculative. However, the sea otter quite obviously is an important species in determining structures and dynamic relationships with nearshore communities, thus fitting the concept of Paine (1969) of a keystone species. Until the recent resurgence of sea otters on the Pacific coast, biologists were unaware of the influence of sea otters on intertidal and subtidal communities within the original range. Our studies indicate that the sea otter was a significant factor in the evolution of the nearshore ecosystem of the North Pacific Ocean.

CONCLUSIONS

That sea otters are capable of reducing both the size and number of sea urchins is indicated by their voracious appetite, analyses of their stomach contents, and feeding observations of wild and captive animals. The overwhelming evidence in the literature and the results of grazing experiments conducted at Amchitka and Shemya clearly demonstrate that marine vegetation flourishes in the absence, but is destroyed in the presence, of dense populations of sea urchins. From further observations of similar areas in the western Aleutians with and without sea otters (both in time and space), we conclude that in the nearshore community at Amchitka sea otters are directly responsible for the reduction of the size and number of sea urchins within their feeding range and indirectly responsible for the resultant development of extensive algal beds and associated communities. Because these kelp beds can alter physical conditions in the intertidal community by reducing wave shock and increasing siltation rates, we further conclude that sea otters are indirectly responsible for the sparse populations of barnacles and mussels and for the small size and low number of predacious snails and sea stars and the small number of hermit crabs.

It is possible that physical factors, such as intertidal benches, coastline features, and climate, or other biological factors, such as other predators and competition resource shortages, are partly or fully responsible for the structure of the nearshore community at Amchitka. However, comparisons of western Aleutian nearshore communities, similar in most aspects except for densities of sea otter populations, and the results of field and laboratory experiments strongly indicate that the sea otter is the keystone species at Amchitka that is primarily responsible for the observed structure of the nearshore community.

ACKNOWLEDGMENTS

Research was supported by AEC contracts AT(26-1)-520 and AT(26-1)-171 through subcontract from Battelle Memorial Institute, Columbus, Ohio. We are indebted to K. Chew, R. Nakatani, and N. Smith for guidance, and to S. Brown, R. Glinski, P. Lebednik, C. O'Clair, C. Simenstad, N. Smith, and G. Tutmark for field assistance. We thank P. Dayton and R. Paine for helpful comments in preparing the manuscript, J. Jackson for assistance with logistic problems, and R. Fernald for providing facilities at Friday Harbor Laboratories. The U. S. Air Force, U. S. Coast Guard, and U. S. Navy provided access to their facilities at Shemya, Attu, and Adak Islands, respectively. Final drafts were prepared by the Fisheries Research Institute and the Auke Bay Fisheries Laboratory. All photographs are by J. F. Palmisano.

APPENDIX: PARAMETER INTERVAL ESTIMATION AND TESTS OF SIGNIFICANCE IN THE LINEAR MODEL $y_i = \mu + \beta(x_i) + e_i$

Variance $(\hat{\mu}) + 1.454 \pm 2$
Variance $(\hat{\beta}) = 1.174$
95% confidence interval $(\mu) = -8.114$ to -7.636
95% confidence interval $(\beta) = 2.924$ to 3.059
t-test of hypothesis $(\mu = 0)$ $t = 65.307^*$ with 111 degrees of freedom
t-test of hypothesis $(\beta = 0)$ $t = 87.310^*$ with 111 degrees of freedom
Analysis of variance for linear regression

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Due to regression	1	289.226	289.226	7623.1*
Residual	111	4.211	0.0379	
Total	112	293.437		

*Significant at 0.01 level.

REFERENCES

Addicott, J. F., 1974, Predation and Prey Community Structure: An Experimental Study of the Effect of Mosquito Larvae on the Protozoan Communities of Pitcher Plants, *Ecology*, 55: 475-492.

Aleem, A. A., 1956, Quantitative Underwater Study of Benthic Communities Inhabiting Kelp Beds off California, *Science*, 123: 183.

Barr, L., 1971, Studies of Populations of Sea Urchins, *Strongylocentrotus* sp., in Relation to Underground Nuclear Testing at Amchitka Island, Alaska, *Bioscience*, 21: 614-617.

Blinks, L. R., 1955, Photosynthesis and Productivity of Littoral Marine Algae, *J. Mar. Res.*, 14: 363-373.

Burgner, R. L., and R. E. Nakatani, 1972, Amchitka Bioenvironmental Program. Research Program on Marine Ecology, Amchitka Island, Alaska, Annual Progress Report, July 1, 1970–June 30, 1971, USAEC Report BMI-171-144, Battelle Memorial Institute.

Byrd, G. V., 1973, Assistant Refuge Manager, U. S. Fish and Wildlife Service, personal communication (from observations made at Attu Island between May 25 and June 1, 1973).

Camp, D. K., S. P. Cobb, and J. F. Van Breedveld, 1973, Overgrazing of Seagrasses by a Regular Urchin, *Lytechinus variegatus, Bioscience*, 23(1): 37-38.

Carlquist, S., 1973, *Island Biology*, Columbia University Press, New York.

——, 1965, *Island Life: A Natural History of the Islands of the World*, Natural History Press, Garden City, New York.

Connell, J. H., 1972, Community Interactions on Marine Rocky Intertidal Shores, *Annu. Rev. Ecol. Syst.*, 3: 169-192.

——, 1970, A Predator-Prey System in the Marine Intertidal Region. I. *Balanus glandula* and Several Predatory Species of *Thais, Ecol. Monogr.*, 40: 49-78.

——, 1961a, The Influence of Interspecific Competition and Other Factors on the Distribution of the Barnacle *Chthamalus stellatus, Ecology*, 42: 710-723.

——, 1961b, Effects of Competition, Predation by *Thais lapillus*, and Other Factors on Natural Populations of the Barnacle *Balanus balanoides, Ecol. Monogr.*, 31: 61-104.

Crisp, D. J., and H. Barnes, 1954, The Orientation and Distribution of Barnacles at Settlement with Particular Reference to Surface Contour, *J. Anim. Ecol.*, 23: 142-162.

Crossett, R. N., 1967, The Vertical Distribution of Attached Marine Algae in Malta, *J. Ecol.*, 55: 361-371.

Crow, J. F., and M. Kimura, 1970, *An Introduction to Population Genetics Theory*, Harper & Row, Publishers, New York.

Dawson, E. Y., M. Neushul, and R. Wildman, 1960, Seaweeds Associated with Kelp Beds Along Southern California and Northwestern Mexico, *Pac. Naturalist*, 14: 1-81.

Dayton, P. K., 1973, Dispersion, Dispersal, and Persistence of the Annual Intertidal Alga *Postelsia palmalformis* Ruprecht, *Ecology*, 54: 433-438.

——, 1971, Competition, Disturbance, and Community Organization: The Provision and Subsequent Utilization of Space in a Rocky Intertidal Community, *Ecol. Monogr.*, 41: 351-389.

——, 1970, Competition, Predation, and Community Structure: The Allocation and Subsequent Utilization of Space in a Rocky Intertidal Community, Ph. D. Thesis, University of Washington.

——, and R. R. Hessler, 1972, Role of Biological Disturbance in Maintaining Diversity in the Deep Sea, *Deep-Sea Res.*, 19: 199-208.

——, R. J. Rosenthal, and L. C. Mahan, 1973, Kelp Communities in the Chilean Archipelago: R/V *Hero* Cruise 72-5, *Antarct. J. U. S.*, 8: 34-35.

Deevey, E. S., 1947, Life Tables for Natural Populations of Animals, *Quart. Rev. Biol.*, 22: 283-314.

Desautels, R. J., A. J. McCurdy, J. D. Flynn, and R. R. Ellis, 1970, Archaeological Report, Amchitka Island, Alaska, 1969–1970, Archaeological Research, Inc., Costa Mesa, California.

Diamond, J. M., 1973, Distributional Ecology of New Guinea Birds, *Science*, 179: 759-769.

——, 1969, Avifaunal Equilibria and Species Turnover Rates on the Channel Islands of California, *Proc. Nat. Acad. Sci.*, 64: 57-63.

Doty, M. S., 1946, Critical Tide Factors that Are Correlated with the Vertical Distribution of Marine Algae and Other Organisms Along the Pacific Coast, *Ecology*, 27: 315-328.

Druehl, L. D., 1968, Taxonomy and Distribution of Northeast Pacific Species of *Laminaria, Can. J. Bot.*, 46: 539-547.

Ebert, E. E., 1968, California Sea Otter Census and Habitat Survey, *Underwater Natur.*, 5: 20-23.

Estes, J. A., and J. F. Palmisano, 1974, Sea Otters: Their Role in Structuring Nearshore Communities, *Science*, 185: 1058-1060.

——, and N. S. Smith, 1973, Amchitka Bioenvironmental Program, Research on the Sea Otter, Amchitka Island, Alaska. Final Report, Oct. 1, 1970–Dec. 31, 1972, USAEC Report NVO-520-1, University of Arizona.

Fischer, A. G., 1960, Latitudinal Variations in Organic Diversity, *Evolution*, 14: 64-81.

Harper, J. L., 1969, The Role of Predation in Vegetational Diversity, in Diversity and Stability in Ecological Systems, Report of Symposium held May 26–28, 1969, Brookhaven Symposia in Biology, Number 22, USAEC Report BNL-50175, pp. 48-62.

Haxo, F. T., and L. R. Blinks, 1950, Photosynthetic Action Spectra of Marine Algae, *J. Gen. Physiol.*, 33: 389-422.

Hedgpeth, J. W., 1957, *Marine Biogeography*, U. S. Geological Society, Memoir 67(1), pp. 359-382.

Hewatt, W. G., 1937, Ecological Studies on Selected Marine Intertidal Communities of Monterey Bay, California, *Amer. Midland Natur.*, 18: 161-206.

Himmelman, J. H., and D. H. Steele, 1971, Foods and Predators of the Green Sea Urchins *Strongylocentrotus drobachiensis* in Newfoundland Waters, *Mar. Biol.*, 9: 315-322.

Hutchinson, G. E., 1953, The Concept of Pattern in Ecology, *Proc. Nat. Acad. Sci.*, 105: 1-12.

Isakson, J. S., C. A. Simenstad, and R. L. Burgner, 1971, Fish Communities and Food Chains in the Amchitka Area, *BioScience*, 21: 666-670.

Jones, N. S., 1948, Observations and Experiments on the Biology of *Patella vulgata* at Port St. Mary, Isle of Man, *Proc. Trans. Liverpool Biol. Soc.*, 56: 60-77.

——, and J. M. Kain, 1967, Subtidal Algal Colonization Following the Removal of *Echinus*, *Helgolander Wiss. Meeresunters.*, 15: 460-466.

Jorde, I., and N. Klavestad, 1963, The Natural History of the Hardangerfjord. 4. The Benthonic Algal Vegetation, *Sarsia*, 9: 1-99.

Kain, J. M., 1966, The Role of Light in the Ecology of *Laminaria hyperborea*, in Light as an Ecological Factor, British Ecological Society Symposium No. 6, Richard Bainbridge et al. (Eds.), pp. 319-334, Blackwell Scientific Publications Ltd., Oxford.

——, and N. S. Jones, 1965, Algal Colonization After Removal of *Echinus* (abstr.), in 5th International Seaweed Symposium, Dalhousie University, Halifax, Nova Scotia.

Kenyon, K. W., 1969, *The Sea Otter in the Eastern Pacific Ocean*, U. S. Department of the Interior, Bureau of Sport Fisheries and Wildlife, North American Fauna, No. 68.

——, 1965, Food of Harbor Seals at Amchitka Island, Alaska, *J. Mammalogy*, 46: 103-104.

——, and J. G. King, 1965, Aerial Survey of Sea Otters, Other Marine Mammals and Birds, Alaska Peninsula and Aleutian Islands, 19 April to 9 May, 1965, U. S. Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife.

Kitching, J. A., 1941, Studies in Sublittoral Ecology. III. *Laminaria* Forest on the West Coast of Scotland; A Study of Zonation in Relation to Wave Action and Illumination, *Biol. Bull.*, 80: 324-337.

——, and P. J. Ebling, 1961, The Ecology of Lough Ine XI, The Control of Algae by *Paracentrotus lividus* (Echinoidea), *J. Anim. Ecol.*, 30: 373-383.

Laughlin, W. S., 1972, Ecology and Population Structure in the Arctic, in *The Structure of Human Populations*, G. A. Harrison and A. J. Bayce (Eds.), pp. 379-392, Oxford University Press.

Lensink, C., 1962, The History and Status of Sea Otters in Alaska, Ph. D. Thesis, Purdue University, Xerox University Microfilms, Ann Arbor, Mich.

Lewis, J. R., 1964, *The Ecology of Rocky Shores*, English Universities Press, Ltd., London.

Limbaugh, C., 1955, Fish Life in the Kelp Beds and the Effects of Harvesting. University of California Institute of Marine Research, Institute of Marine Research Reference 55-9, pp. 1-158.

Lowry, L. F., and J. S. Pearse, 1973, Abalones and Sea Urchins in an Area Inhabited by Sea Otters, *Marine Biol.*, 23: 213-219.

MacArthur, R. H., 1972, *Geographical Ecology: Patterns in the Distribution of Species*, Harper & Row, Publishers, Inc., New York.

——, and E. O. Wilson, 1967, *The Theory of Island Biogeography*, Princeton University Press, Princeton, N. J.

——, and E. O. Wilson, 1963, An Equilibrium Theory of Insular Zoogeography, *Evolution*, 17: 373-387.

MacGinitie, G. E., and N. MacGinitie, 1968, *Natural History of Marine Animals*, McGraw-Hill Book Company, London.

Mann, K. H., 1973, Seaweeds: Their Productivity and Strategy for Growth, *Science*, 182: 975-981.

——, 1972a, Ecological Energetics of the Seaweed Zone in a Marine Bay on the Atlantic Coast of Canada. I. Zonation and Biomass of Seaweeds, *Marine Biol.*, 12: 1-10.

——, 1972b, Ecological Energetics of the Seaweed Zone in a Marine Bay on the Atlantic Coast of Canada. II. Productivity of the Seaweeds, *Marine Biol.*, 14: 199-209.

May, R. H., 1973, Stability and Complexity in Model Ecosystems, Princeton University Press, Princeton, N. J.

McLean, J. H., 1962, Sublittoral Ecology of Kelp Beds of the Open Coast Area Near Carmel, California, *Biol. Bull.*, 122: 95-114.

Miller, D. J., and J. J. Geibel, 1973, Summary of the Blue Rockfish and Lingcod Life Histories; a Reef Ecology Study; and Giant Kelp Experiments in Monterey Bay, California, California Department of Fish and Game, Fish Bulletin 158.

——, J. J. Geibel, and J. L. Hook, 1974, Results of the 1972 Skindiving Assessment Survey, Pismo Beach to Oregon, California Department of Fish and Game, Marine Resources Technical Report No. 20.

Moore, H. B., 1958, *Marine Ecology*, John Wiley & Sons, Ltd., London.

Morrison, P., M. Rosenmann, and J. A. Estes, 1974, Metabolism and Thermoregulation in the Sea Otter, *Physiol. Zool.*, 47: 218-229.

Nelson-Smith, A., 1968, Biological Consequences of Oil Pollution and Shore Cleansing, in The Biological Effects of Oil Pollution on Littoral Communities, Proceedings of a Symposium held at the Orielton Field Centre, Pembroke, Wales, on Feb. 17–19, 1968, J. D. Carthy and D. R. Arthur (Eds.), Supplement to Volume 2 of Field Studies Council.

Neushul, M., 1967, Studies of Subtidal Marine Vegetation in Western Washington, *Ecology*, 48: 83-94.

——, 1965, Scuba Diving Studies of the Vertical Distribution of Benthic Marine Plants. Botanica Gothoburgensia III, *Marine Biology*, Vol. 5, J. D. Costlow (Ed.), Proceedings of the Fifth Interdisciplinary Conference on Marine Biology, pp. 161-176, Gordon & Breach Science Publishers, Inc., New York.

Newell, R. C., 1970, *Biology of Intertidal Animals*, American Elsevier Publishing Co., Inc., New York.

North, W. J., 1965, An Ecological Study of the Point Loma Kelp Bed, San Diego County, State Water Control Board, Sacramento, Calif.

O'Clair, C. E., and K. K. Chew, 1971, Transect Studies of Littoral Macrofauna, Amchitka Island, Alaska, *BioScience*, 21: 661-665.

Odemar, M. W., and K. C. Wilson, 1969, Population Studies of Sea Otters in California, California Department of Fish and Game, Marine Research Report, Reference No. 70-3.

Ostle, B., 1963, *Statistics in Research*, Iowa State University Press, Ames.

Paine, R. T., 1971, A Short-Term Experimental Investigation of Resource Partitioning in a New Zealand Rocky Intertidal Habitat, *Ecology*, 52: 1096-1106.

——, 1969, A Note on Trophic Complexity and Community Stability, *Amer. Natur.*, 103: 91-93.

——, 1966, Food Web Complexity and Species Diversity, *Amer. Natur.*, 100: 65-75.

——, and R. L. Vadas, 1969, The Effects of Grazing by Sea Urchins *Strongylocentrotus* spp., on Benthic Algal Populations, *Limnol. Oceanogr.*, 14: 710-719.

Palmisano, J. F., 1975, Sea Otter Predation: Its Role in Rocky Intertidal Community Structure at Amchitka and Other Aleutian Islands, Ph. D. Thesis, University of Washington.

Pianka, E. R., 1970, On r- and K-Selection, *Amer. Natur.*, 104: 592-597.

Porter, J. N., 1972, Predation by *Acanthaster* and Its Effect on Coral Species Diversity, *Amer. Natur.*, 106: 487-492.

Powers, H. A., R. R. Coats, and W. H. Nelson, 1960, *Geology and Submarine Physiogeography of Amchitka Island, Alaska*, U. S. Geological Survey, Bulletin 1028-P, pp. 521-554.

Preston, F. W., 1962, The Canonical Distribution of Commonness and Rarity: Part I, *Ecology*, 43: 185-215.

Quast, J. C., 1968, Observations on the Food of Kelp Bed Fishes, California Department of Fish and Game, *Fish. Bull.*, 139: 109-142.

Ricketts, E. W., and J. Calvin, 1968, *Between Pacific Tides*, 4th ed., revised by J. W. Hedgpeth, Stanford University Press, Stanford, Calif.

Sanders, H. L., 1968, Marine Benthic Diversity: A Comparative Study, *Amer. Natur.*, 102: 243-282.

Schoener, T. W., 1971, Theory of Feeding Strategies, *Annu. Rev. Ecol. Syst.*, 2: 369-404.

Sekora, P., 1973, Aleutian Islands Wilderness Study Report. A Study Conducted as a Partial Requirement of the Wilderness Act by the Bureau of Sport Fisheries and Wildlife.

Shotwell, J. A., 1950, The Vertical Zonation of *Acmaea*, the Limpet, *Ecology*, 31: 647-649.

Simberloff, D. S., and E. O. Wilson, 1970, Experimental Zoogeography of Islands, A Two Year Record of Colonization, *Ecology*, 51: 934-937.

Simenstad, C. A., 1971, The Feeding Ecology of the Rock Greenling, *Hexagrammos lagocephalus*, in the Inshore Waters of Amchitka Island, Alaska, M. S. Thesis, University of Washington.

Spight, T. M., 1972, Patterns of Change in Adjacent Populations of an Intertidal Snail, *Thais lamellosa*, Ph. D. Thesis, University of Washington.

Strathmann, R., 1974, The Spread of Sibling Larvae of Sedentary Marine Invertebrates, *Amer. Natur.*, 108: 29-44.

Sutherland, J. P., 1974, Multiple Stable Points in Natural Communities, *Amer. Natur.*, 108: 859-873.

U. S. Department of Commerce, Coast and Geodetic Survey, 1968, *Tide Tables, West Coast North and South America, 1969*, Superintendent of Documents, U. S. Government Printing Office, Washington, D. C.

Vadas, R. L., 1968, The Ecology of *Agarum* and the Kelp Bed Community, Ph. D. Thesis, University of Washington.

Vance, R. R., 1973, On Reproductive Strategies in Marine Benthic Invertebrates, *Amer. Natur.*, 107: 339-352.

Walker, F. T., 1947, Sublittoral Seaweed Survey, *J. Ecol.*, 35: 166-185.

——, and W. D. Richardson, 1955, An Ecological Investigation of *Laminaria cloustoni* EDM (*L. hyperborea* Fosl.) Around Scotland, *J. Ecol.*, 43: 26-38.

Weinmann, F. C., 1969, Amchitka Bioenvironmental Program. Aspects of Benthic Marine Algal Ecology at Amchitka Island, Alaska, USAEC Report BMI-171-115, Battelle Memorial Institute.

——, 1968, Aspects of Benthic Marine Algal Ecology at Amchitka Island, Alaska, M. S. Thesis, University of Washington.

White, C. M., W. B. Emison, and F. S. L. Williamson, 1971, Dynamics of Raptor Populations on Amchitka Island, Alaska, *BioScience*, 21: 623-626.

Wild, P. W., and J. A. Ames, 1974, A Report on the Sea Otter *Enhydra lutris l.*, in California, California Department of Fish and Game, Marine Resources Technical Report No. 20.

Wilke, F., 1957, Food of Sea Otters and Harbor Seals at Amchitka Island, *J. Wildlife Manage.*, 21: 241-242.

Williamson, F. S. L., W. B. Emison, and C. M. White, 1972, Amchitka Bioenvironmental Program. Studies of the Avifauna on Amchitka Island, Alaska. Annual Progress Report, July 1970–June 1971, USAEC Report BMI-171-134, Battelle Memorial Institute.

——, W. B. Emison, and C. M. White, 1971, Amchitka Bioenvironmental Program. Studies of the Avifauna on Amchitka Island, Alaska. Annual Progress Report, July 1969–June 1970, USAEC Report BMI-171-131, Battelle Memorial Institute.

This page intentionally left blank

Sea Otter Metabolism and Heat Economy

P. R. Morrison
M. Rosenmann*
Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska
J. A. Estes†
Arizona Cooperative Wildlife Research Unit, University of Arizona, Tucson, Arizona

In ten 13- to 33-kg sea otters captured and maintained at Amchitka Island, a basal metabolic level of 0.72 cm^3 O_2 g^{-1} hr^{-1} was found in 17 values measured over thermoneutral zones of −20 to 21° C in air and 20 to 33° C in water. Average values of 1.0 and 1.2 cm^3 O_2 g^{-1} hr^{-1} and maximum values of 1.9 and 2.6 cm^3 O_2 g^{-1} hr^{-1} in air and water, respectively, confirm the high food demand of one-fifth to one-fourth their body weight in fish daily. Minimum thermal conductance in air, <0.012 cm^3 O_2 g^{-1} hr^{-1} °C^{-1}, was greater for these mammals than for terrestrial arctic mammals, but it only increased twofold on immersion in water. Water infiltration into the fur above 25° C allowed survival at even 33° C. Body temperature was regulated under neutral conditions at 38.1 ± 0.34° C (mean ± standard deviation), under cold conditions at 36.7 ± 0.45° C, and under warm conditions at 38.5 ± 0.31° C with 44.1° C as a single lethal value.

The sea otter (*Enhydra lutris*) is a species of extraordinary interest both historically and biologically. Its valuable fur and its vulnerability led to its extermination in many areas, and only in recent years through protection and transplanting procedures has it become established in many locations so that it is no longer in danger of extinction (Kenyon, 1969; Estes, Chap. 21, this volume). The sea otter is the largest of the Mustelidae, being rivaled only by the giant Amazonian otter (*Pteronura brasiliensis*), itself threatened with extinction. Among the Mustelidae it is the only truly marine form and as such the most adapted for aquatic life. Although its northern habitat may appear severe and stressful, it is, in fact, of a very constant nature, rivaling or even exceeding the tropical rain forest in its uniformity.

Because of isolated distribution and problems of capture and maintenance, almost nothing is known of its physiological attributes beyond a few body temperatures (Irving and Krog, 1954; Stullken and Kirkpatrick, 1955). Accordingly, such observations are of much interest as comparative physiology and in terms of practical problems in handling and maintaining these animals that have appeared sensitive to thermal adjustment, restraint, disturbance, food requirements, and fouling.

These observations emphasized such bioenergetic parameters as basal metabolism (M_b), average metabolic rate (M_{av}) in air and in water, the maximum metabolic rate ($M_{max.}$), the lower critical temperature that calls for thermoregulatory heat production, the upper critical temperatures in air and water above which body temperature (T_b) increases and presents a hazard in maintenance, and the T_b levels that are associated with transition points or with ambient temperature levels (T_a). A more detailed report on these observations has been published (Morrison, Rosenmann, and Estes, 1974).

METHODS

The large size, vigor, behavior pattern, and isolated habitat, which make this species of interest, posed real technical difficulties in handling and instrumentation. The animals, ranging in weight from 13 to 33 kg, were taken in nets near Constantine Harbor or East Cape. They were held outdoors and supplied with running seawater in large (20 by 24 ft) wooden tanks that had been constructed by the Alaska Department of Fish and Game for their transplantation program. Frozen

*Present address: Departamento de Biologia, Facultad de Ciencia, Universidad de Chile, Santiago.

†Present address: U. S. Fish and Wildlife Service, Anchorage, Alaska.

fish filets and squid were supplied twice daily in an amount equal to roughly 20% of the body weight per day. Although some sea otters are sensitive and die outright of shock following netting or handling, once established in tanks most are maintained in excellent condition.

Most experiments were begun in the morning some 15 hr after the last feeding. This is well past the 3-hr period reported by Kenyon (1969) for the passage of food through the gut. No metabolic differences were observed in five runs begun 6 hr and in two runs begun 3 hr after feeding. Animals were lost in two such early experiments (one each in water and air), apparently from shock since there was no other demonstrable cause. No unusual excitement or depression was observed, but the animals suddenly stopped breathing. Thereafter no problems were encountered in some two dozen experiments under conditions ranging from water at 33°C to the equivalent of air below −70°C for durations up to 8 hr. Forceful handling was necessary, especially in measuring body temperature, but our overall view of the sea otter as an experimental animal was very favorable.

Metabolic measurements used a closed-circuit automatic manometric system that recorded the time required to consume successive aliquots of oxygen (Morrison, 1951). In the basic arrangement the subject occupied a wire cage (35 by 35 by 100 cm) within a larger metal box with a Lucite cover. Lateral screened trays filled with barium hydroxide lime absorbed CO_2. A refrigerated bath (to −30°C) maintained the T_a down to −20°C, a modest stress for a large well-furred animal. Greater thermal stress was provided by a 4 : 1 helium–oxygen atmosphere which increased heat transfer by some twofold, giving a thermal equivalent of −70°C in air (Rosenmann and Morrison, 1974).

Alternately, the subjects were enclosed directly in a large water bath (60 by 60 by 120 cm) with the air space above connected to the manometer control (Fig. 1). One external circulation through a barium hydroxide lime canister removed CO_2 from the air phase and a second through particle and charcoal filters removed sediment and organics from the water phase. The temperature of the latter circulation was monitored, and heat was added or removed to maintain the desired T_a. Although the volume of the system was greatly increased, the incompressibility of the aqueous phase allowed the animals to dive and swim freely without compromising the manometric control. Body temperature (T_b) was measured before and after metabolism runs with a thermistor probe with 8- to 12-in. rectal insertions.

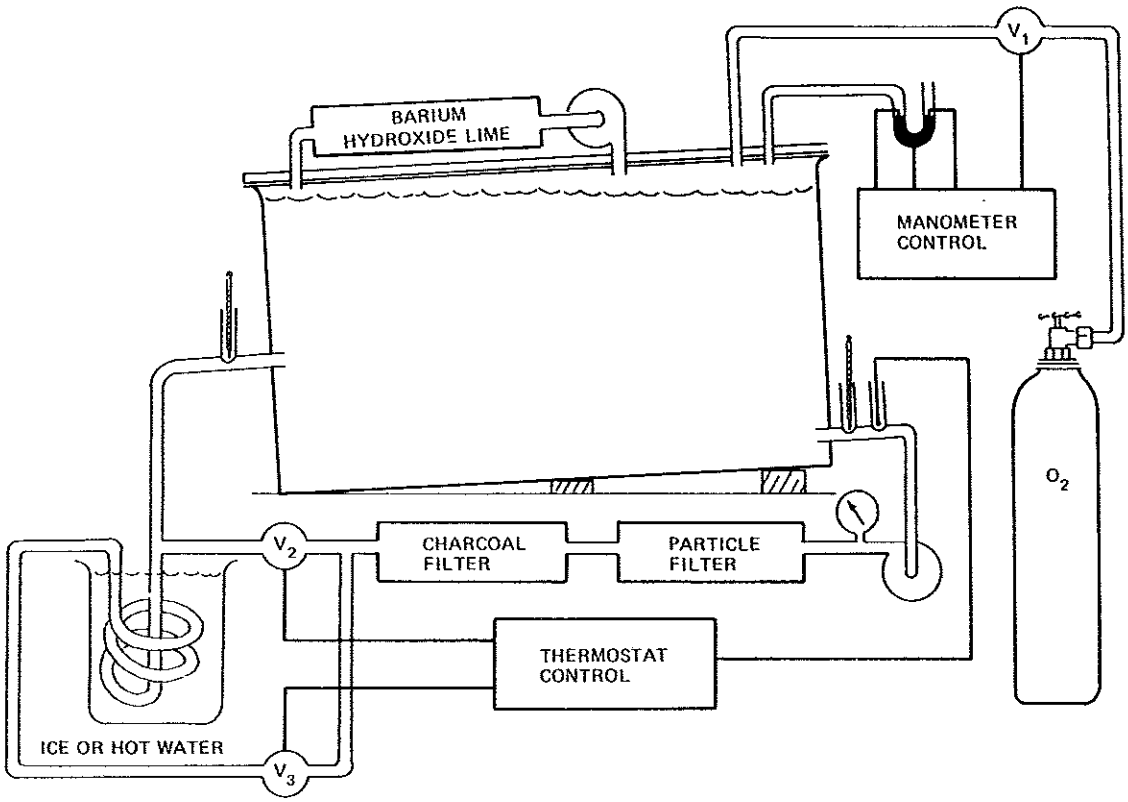

Fig. 1—Diagram of experimental arrangement for metabolic measurements in water.

RESULTS AND DISCUSSION

Basal Metabolism and the Thermoneutral Zone

Metabolism was measured in air in 12 experiments at T_a ranging from 23 to −20°C. Individual experiments reflected bouts of activity with intervening quiet periods (Fig. 2) which provided acceptable values for M_b in 10 cases (averaging the three lowest points in each). These values showed no trend with T_a over the range of −19 to 21°C, which is thus within the thermoneutral zone (Fig. 3). The average of these values, 0.72 ± 0.06 cm^3 O_2 g^{-1} hr^{-1}, lay far above the standard metabolism (M_{st}) of 0.27 cm^3 O_2 g^{-1} hr^{-1} for an 18-kg mammal.*

In 14 experiments the metabolism was measured in water at temperatures ranging from 5 to 33°C. Although the animals responded well, the greater freedom for movement resulted in fewer resting or inactive periods. Overall the minimum three values in 13 runs in water averaged 0.85 cm^3 O_2 g^{-1} hr^{-1}, about 20% higher than in air. However, at higher temperatures the animals appeared sedated, and good periods of sleep were observed in two runs. These values, taken with the four lowest values in air, give a mean of 0.67 cm^3 O_2 g^{-1} hr^{-1}, which may better represent a limiting basal value.

The M_b of 0.67 to 0.72 cm^3 O_2 g^{-1} hr^{-1}, with consistent values measured over a wide range of T_a and in two media, appears to be a very reliable value, and yet it is 2.5-fold higher than the M_{st} for a mammal of this size (i.e., at 2.5 met). To assess the implications of this difference, we must compare other species. The Mustelidae as a family with their vigor and carnivorous mode do show a range of M_b. However, in the Wisconsin least weasel (*Mustela rixosa*), for which more data are on hand, the minimum values were less than 1.2 met, and, in the ferret (*Mustela putorius*) and tayra (*Eira barbara*), values below M_{st} were observed (Morrison and Ryser, 1976). Recently Iverson (1972) reported values on a series of European mustelids ranging in size from the weasel (*Mustela nivalis*) (at near 100 g) to the wolverine (*Gulo gulo*) (at 15 kg). Values in the latter species, which is comparable to our sea otters in weight, were 1.3 to 1.4 met and that in the badger (*Meles meles*), whose weight was 10 kg, was only 0.9 met. Of particular interest were values on river otters (*Lutra lutra*) weighing 7 to 10 kg which ranged rather widely from 1.4 to 2.0 met. Accordingly, the Mustelidae as a group do not show an elevated M_b.

When other marine mammals are compared, we do find a correspondence. Irving (1969) summarized earlier data showing high M_b values of 1.7 to 2.1 met in young seals and 2.3 to 2.9 met in porpoises, and these values have been confirmed in recent studies on both groups (Hampton et al., 1971; Miller et al., 1973; Iverson and Krog, 1973). The last investigators also report a single point (figure only) for a 40-kg sea otter at 2.8 met. Øritsland (1973) recently reported an M_b below M_{st} in a harp seal, but 40% of the 130-kg weight was thought to represent blubber. Thus it is of much interest to find this effect in a marine that is representative of a third mammalian order. This phenomenon has evaded explanation for some time since it does not relate in any obvious way to the primary adaptation to diving and in fact seems a deterrent in a specialization that is directed toward oxygen conservation during dives. Neither does it seem reasonable that the maintenance cost of the biological system should be higher in such marine forms; so one must look elsewhere for explanation.

Another notable example of elevated metabolism is seen in that very small mammal, the long-tailed shrew (*Sorex cinereus*), for which we earlier proposed an explanation that may also apply to the sea otter (Morrison and Pearson, 1946; Morrison et al., 1959). Although the two species differ in mass by some 5000-fold and in metabolic rate and feeding cycle length by some 10-fold, they may both be thought of as "carnivorous grazers" who take food from a restricted local range as needed. Since the diet is largely protein, it must exceed the daily caloric requirement by the amount wasted in nonproductive metabolic conversions [Specific Dynamic Action (SDA)]. Thus, out of an average daily consumption of 1.6 cm^3 O_2 g^{-1} hr^{-1} (6 met), one-fourth, or 1.5 met, might constitute SDA (Brody, 1945). If this SDA were spread throughout the day, it would raise the minimum rate to the observed M_b of 2.5 met. In other words, we would postulate that the SDA is not expended in a metabolic bulge following the meal as in other carnivores but rather is rationed out over the day. We have no information as to how this might be effected. Delayed absorption from the gut would meet the requirements but is hardly compatible with observations of food, including undigested flesh passing within 3 hr (Stullken and Kirkpatrick, 1955).

*The term "standard metabolism" usefully designates the mean basal level for mammals of different size according to the function $M/W = 3.8W^{-0.27}$, or $M = 3.8W^{0.73}$, where M is in cm^3 O_2/hr and W is in grams (Brody, 1945). Basal or other metabolic values are conveniently expressed as multiples of this standard rate (designated "met"), a unit that is thus independent of size.

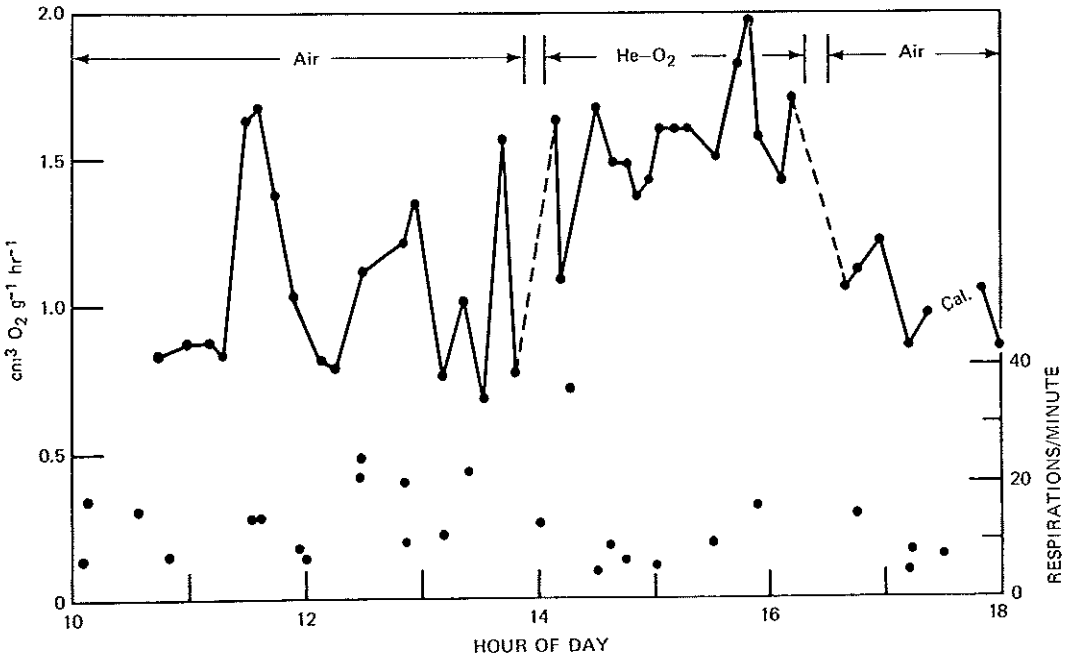

Fig. 2—Representative metabolic experiment in air showing activity cycles and stimulation by He–O_2 (4 : 1) (♀ No. 9, 13.6 kg at −12°C).

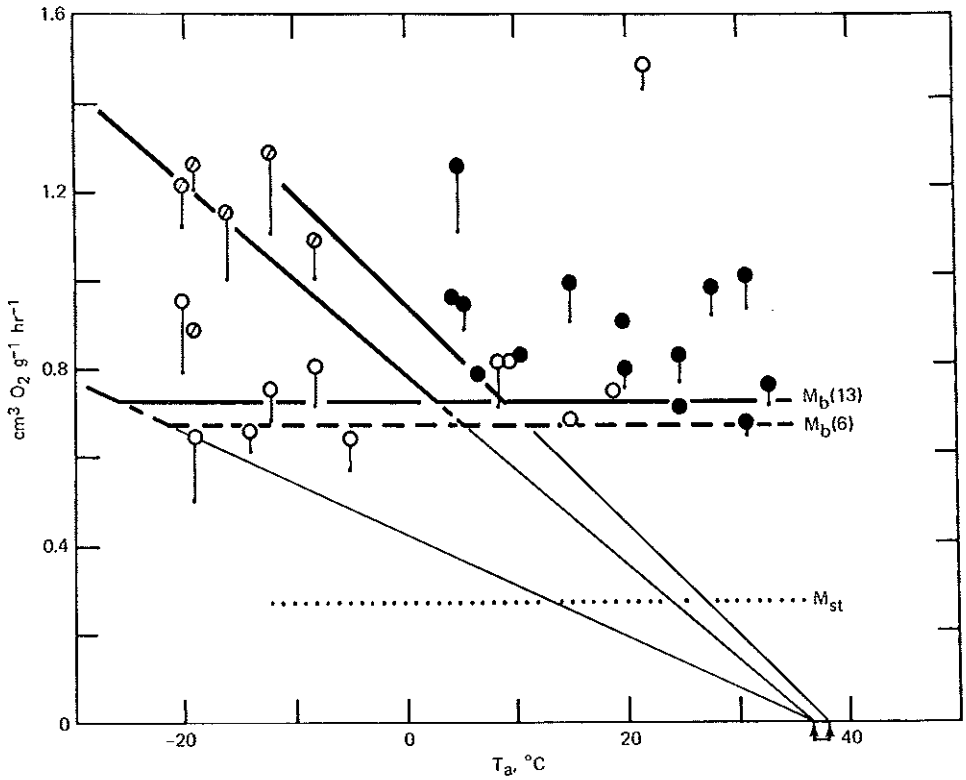

Fig. 3—Sea otter minimum metabolic values in air, He–O_2, and water. Symbols, average of three lowest values; points, lowest value. Horizontal solid line, all values (3 min) in air plus three resting in water; horizontal dashed line, six lowest values in air and water; horizontal dotted line, standard metabolism for an average 18-kg mammal. Diagonal lines show elevated metabolism in air (○), He–O_2 (⊕), and water (●) in 13- to 16-kg animals.

It does seem that each of these species has a special problem in thermoregulation, the shrew because of its very small size and the sea otter because of its cold aquatic habitat. Indeed, were it not for their high M_b, their thermoneutral zones would be much more limited with critical temperatures above their normal T_a rather than below. The use of SDA, representing heat that must be produced and disposed of in any event, would allow thermoregulation by physical means rather than by chemical regulation.

Average Metabolism and Daily Energy Requirements

The M_{av} in air during ten 3- to 5-hr experiments in rather close confinement (Fig. 4) ranged from 20 to 54% above the M_b (average was 0.99 cm^3 O_2 g^{-1} hr^{-1}). In water, which allowed more freedom of movement, the average rate in 13 runs was higher, ranging from 25 to 125% above the M_b (average was 1.21 cm^3 O_2 g^{-1} hr^{-1}), and this may represent a lower maintenance level for sea otters in captivity. Sea otters are known for their voracious appetite and substantial maintenance requirement. Thus Kenyon (1969) measured a consumption of 20 to 23% of the body weight of fish (0.89 kcal/g) per day. This is equivalent to some 1.5 to 1.8 cm^3 O_2 g^{-1} hr^{-1}, a value that corresponds well to our average of 1.4 cm^3 O_2 g^{-1} hr^{-1} for three animals swimming at 5°C when one considers the constraint of our experimental format and the wastage of food during tank feeding..

Maximum Metabolism

Our greatest cold stress, −19°C in He–O_2, did not exceed the sea otter's metabolic capacity. This perhaps is not surprising since in subsequent experiments with mink (*Mustela vison*), a much smaller mustelid, we did not reach the limit of cold tolerance until −60°C in He–O_2. Although the sea otters were rather closely confined in their metabolism chambers, some individuals showed remarkable vigor in attacking the cage or tank lid to briefly sustain $M_{max.}$ as high as 2.8 and 2.6 cm^3 O_2 g^{-1} hr^{-1} in air and water, respectively.

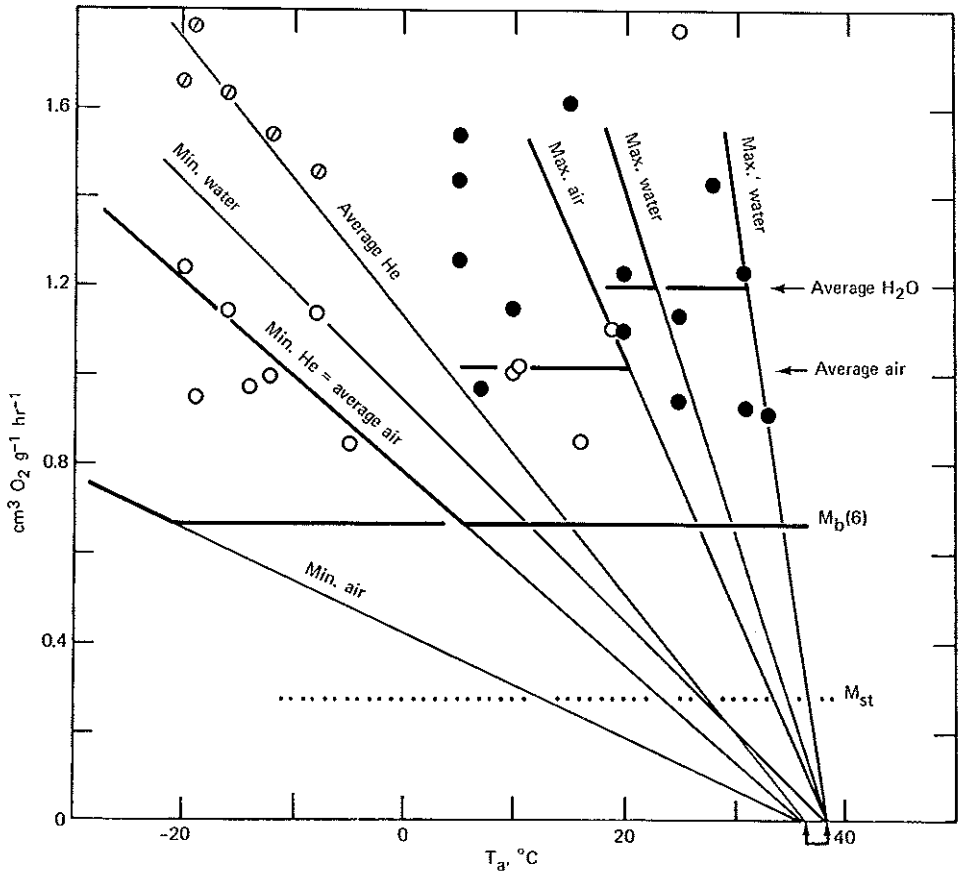

Fig. 4—Sea otter average metabolic values in air (o), He–O_2 (⊘), and water (•). Slopes of diagonals represent thermal conductances in cm^3 O_2 g^{-1} hr^{-1} °C^{-1}. Max.' represents fur infiltrated with water.

This $M_{max.}$ of 10 met is comparable to that found in mink (unpublished observations with K. Doi and L. Peyton) but is higher than values in rodents, which range from 5 to 8 met (Rosenmann and Morrison, 1974). However, in dogs, a species comparable in size to the sea otter, $M_{max.}$ values near 25 met have been consistently reported in treadmill experiments (Young et al., 1959). This difference may relate to a more orderly mode of life in the sea otter without requirements for extreme exertion.

Thermal Conductance

Following Newton's law of cooling, the quotient of metabolism and the ambient-to-deep-body temperature differential ($T_b - T_a$) has been used to describe an overall "thermal conductance." Table 1 gives such values under different conditions in the sea otter. Since the lowest T_a (−19°C) did not raise the metabolism above M_b (i.e., was above the critical temperature), we can only say

Table 1—Thermal Metabolic Increments (Conductance) in Sea Otters

Mode*	Critical T_a, °C	Conductance, $cm^3\ O_2\ g^{-1}\ hr^{-1}\ °C^{-1}$
$C^{air}_{min.}$	<−19	<0.012
$C^{He}_{min.}$	5	0.023
$C^{H_2O}_{min.}$	<7	<0.025
$C^{air}_{max.}$	>19	>0.057
	<23†	0.070
$C^{H_2O}_{max.}$	25	0.084
$C^{H_2O}_{max.'}$	>33	>0.165

*Superscripts indicate medium; subscripts indicate minimum or maximum limiting conductance; max.' designates conditions after infiltration of fur with water.

†Nonequilibrium experiment corrected for heat storage.

that the minimum conductance in air ($C^{air}_{min.}$) was <0.012 $cm^3\ O_2\ g^{-1}\ hr^{-1}\ °C^{-1}$, a value that represents only fair insulation as compared to northern terrestrial mammals that bear longer fur. The sea otter's advantage, of course, lies in the resistance of its pelt to penetration by water (Table 2), which thus retains its integrity during immersion and active swimming. Thus $C^{H_2O}_{min.}$ was <0.025 $cm^3\ O_2\ g^{-1}\ hr^{-1}\ °C^{-1}$, although we suspect that the M_b of 0.67 $cm^3\ O_2\ g^{-1}\ hr^{-1}$ might have maintained the animal at 0°C ($C^{H_2O}_{min.}$ of 0.018). By comparison, we have found that immersion of the snowshoe hare (*Lepus americanus*) increased its conductance

Table 2—Conductance Ratios in Sea Otters*

Effect of medium	$C^{He}_{min.}/C^{air}_{min.}$ = >1.9
	$C^{H_2O}_{min.}/C^{air}_{min.}$ = 2.1
	$C^{H_2O}_{max.}/C^{air}_{max.}$ = 1.3
Range of adjustment	$C^{air}_{max.}/C^{air}_{min.}$ = >4.8
	$C^{H_2O}_{max.}/C^{H_2O}_{min.}$ = >3.4
	$C^{H_2O}_{max.'}/C^{H_2O}_{max.'}$ = >2.0
Overall range	$C^{H_2O}_{max.'}/C^{air}_{min.}$ = >7.0
	$C^{H_2O}_{max.'}/C^{air}_{min.}$ = >13.8

*Coding as in Table 1.

by some 10-fold. Thus the sea otter is maintained at close to its M_b even in icy water. Similarly in air the critical temperature lay below −20°C; so actual environmental conditions on land (Armstrong, Chap. 4, this volume) should never require more than M_b for maintenance.

In contrast to air and water, the increased conductivity of He–O_2 provided conditions below thermal neutrality (critical T_a of 5°C) so that a valid estimate of $C^{He}_{min.}$ = 0.023 $cm^3\ O_2\ g^{-1}\ hr^{-1}\ °C^{-1}$ for 12- to 14-kg individuals could be made for this medium (Fig. 4). This facilitation of heat flow by He–O_2 in the sea otters (>1.9-fold) was slightly greater than the 1.7-fold in the mink (unpublished observations with K. Doi and L. Peyton).

At higher T_a thermal conductance becomes limiting for the dissipation of heat rather than for its retention. Values for $C_{max.}$ are estimated from average metabolism for each T_a. In the warmest equilibrium experiment (T_a of 19°C), $C^{air}_{max.}$ was 0.057 $cm^3\ O_2\ g^{-1}\ hr^{-1}\ °C^{-1}$. In a nonequilibrium experiment at T_a of 22.5°C, which resulted in heat death, a slightly higher value of 0.070 $cm^3\ O_2\ g^{-1}\ hr^{-1}\ °C^{-1}$ was calculated with correction for heat storage. In warm water (>28°C) the animals showed a progressive loss of buoyancy until only the head stayed above the surface, which indicated that water had penetrated the fur. This afforded no inconvenience to the animals in which relaxed behavior and even sleep was observed and clearly facilitated heat transfer during the exposure. Under these conditions $C^{H_2O}_{max.'}$ was 0.165 $cm^3\ O_2\ g^{-1}\ hr^{-1}\ °C^{-1}$ whereas at T_a of 25°C with buoyance retained, $C^{H_2O}_{max.}$ was only 0.084 $cm^3\ O_2\ g^{-1}\ hr^{-1}\ °C^{-1}$.

As overall conductance is increased at higher T_a, heat must be lost from the large flat paws that have an admirable conformation for such dispersal (Table 2). If the integrity of the fur is maintained,

more than two-thirds of the heat load must go through the paws in water at 26°C and perhaps four-fifths in air at 22°C. At 28°C and above, survival appears only possible because of the infiltration of water into the fur with a twofold further increase in conductance, the highest values observed being 7 times the minimum value in water and 14 times that in air. We have subsequently observed a similar tolerance in young harbor seals (Miller et al., 1976).

Body Temperature

The range of values found in some 50 measurements, including exposure to heat and cold and several conditions of confinement, is shown in Fig. 5. A mean T_b of 38.1°C was measured in animals removed directly from the holding pool or after confinement during a metabolic experiment at neutral T_a (Table 3). Since both circumstances include some undefined activity and since these values represent daytime levels in a diurnal species, the basal level may be lower. This average value of 38.1°C under neutral and quiet conditions corresponds to that of 37.9°C by Stullken and Kirkpatrick (1955) on two Nembutalized captives. These values fall below resting levels for smaller mustelids (*Mustela* sp.) but are comparable to those from some genera (*Mephitis* and *Taxidea*) (Morrison and Ryser, 1976). This also corresponds to an overall average of 37.8°C for "all" mammals (Morrison and Ryser, 1952), although a trend toward slightly lower T_b in aquatic mammals as compared to their terrestrial relatives has been noted (Morrison,1962). Stullken and Kirkpatrick's values on six individuals killed in the field varied widely from 35.0 to 40.8°C and may reflect some range of prior activity. However, three middle values (37.5 to 37.8°C) may represent natural inactivity.

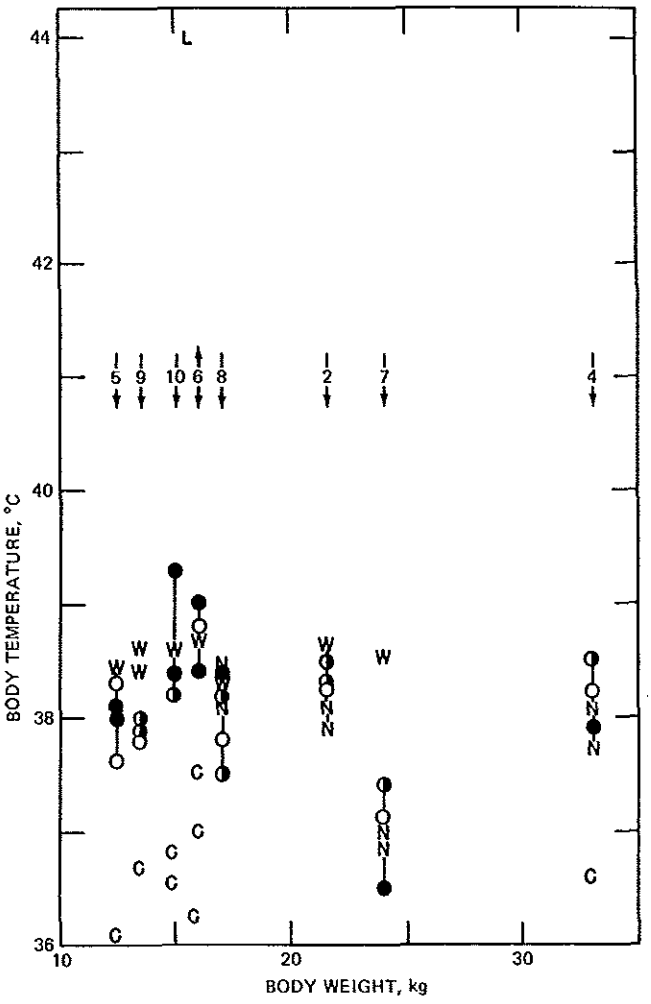

Fig. 5—Body temperatures in sea otters. Previous confinement in metabolic chamber under different thermal conditions: *C*old, *N*eutral, *W*arm, and *L*ethal. Symbols represent animals measured directly from the pool (○), after transport inside holding box (◑), and after drying by fan inside holding cage (●). (See Table 3.)

Table 3—Body Temperatures in Sea Otters According to Previous Condition

Holding pool		T_b,* °C	Metabolism chamber	
Condition	SD (No.)		SD (No.)	Condition
		44.1	(1)	Air 23
Via cage (dried)	0.45(6)†	38.5	0.13(7)‡	Air 14 → 19 H_2O 25 → 33
Via box	0.37(10)§	38.3		
Direct	0.42(7)	38.1	0.25(6)	Air −10 → 12 H_2O 5 → 25
		36.7	0.45(8)‡	Air <−10

*These averages exclude animal No. 7, a grizzled female estimated as the oldest of the group at 6 to 7 years. All her T_b values lay below the range of the other seven individuals and $>4\sigma$ below their mean.

†Confinement in screen holding cage with fan to dry fur for 20 to 30 min; significant vs. direct at 5% level.

‡Significant vs. direct at 1% level.

§Confinement in wooden weighing box for 10 to 15 min; not significant vs. direct.

Confinement before a metabolism experiment resulted in small (0.4°C) T_b increases (Table 3), as did warm exposure during metabolism experiments (25 to 33°C in water and 12 to 19°C in air). Irving and Krog's (1954) value on a captured sea otter is the same as our average of 38.5°C for confined (excited) subjects or ones under warm conditions. The regularity of these values (Table 3) suggests a rather effective control and cooling mechanism for heat regulation.

The one experiment carried to lethal hyperthermia demonstrated the wide thermal margin of 6°C available to this species. Moreover, the devel-

oping stages and even the final critical T_b level did not appear to impair the animal since full vigor was maintained with $M_{max.} > 8$ met. This individual maintained a state of excitement throughout the 2-hr exposure at 22.5°C, with an average metabolic rate of 1.85 cm^3 O_2 g^{-1} hr^{-1}. If all the heat produced (~3.5 cm^3 O_2/g) had been retained, the temperature would have increased some 20°C rather than 5°C; so three-fourths of the heat load was successfully dissipated. Clearly the avoidance of maladaptive behavior (vigorous activity) would have allowed survival, and another individual accepted a 3-hr exposure at 19°C with an average rate of 1.10 cm^3 O_2 g^{-1} hr^{-1} and no T_b increase beyond the normal range.

The T_b response to cold showed greater displacement averaging −1.4°C with considerable scatter. The conditions at −5 to −20°C in He–O_2 were severe, being roughly equivalent to −40 to −70°C in air. However, the low T_b values appeared to be maintained, with no correlation with duration of exposure or with some range of T_a. Neither did the metabolism values show any progressive decline. Thus, although not so precise, regulation to cold was very effective even at T_a below −40°C. Certainly these individuals as maintained under optimal conditions did not confirm Stullken and Kirkpatrick's (1955) impression of the sea otter as a poor thermoregulator.

The tolerance of very warm water was an unexpected finding in view of the normal habitat of these animals, which must only rarely exceed 5°C. Still the range of this species (as *Enhydra lutris nereis*?) (Hall and Kelson, 1959) extended as far south as Baja California, and so it is of much interest that even the northern populations have the physiological flexibility to tolerate the waters of a sun-warmed subtropical lagoon.

SUMMARY

The sea otter has a unique configuration for thermoregulation in terms of its size, aquatic mode, and habitat in the cold but constant Bering Sea. In ten 13- to 33-kg individuals captured and maintained at Amchitka Island under near natural conditions at Constantine Harbor, a basal metabolic level of 0.72 cm^3 O_2 g^{-1} hr^{-1} was found in 17 values measured over thermoneutral zones of −20 to 21°C in air and 20 to 33°C in water. This level, more than 2.5 times the standard (average basal) level for a mammal of this size, is unique among mustelids but conforms to the pattern seen in marine mammals from other orders. Average values of 1.0 to 1.2 cm^3 O_2 g^{-1} hr^{-1} and maximum values of 1.9 and 2.6 cm^3 O_2 g^{-1} hr^{-1} in air and water, respectively, confirm the high food demand of one-fifth to one-fourth their body weight in fish daily. Thermal conductance in air, <0.012 cm^3 O_2 g^{-1} hr^{-1} °C^{-1}, was greater for these mammals than for terrestrial arctic mammals, but it only increased twofold on immersion in water. Water infiltration into the fur at higher temperatures allowed survival at even 33°C, perhaps significant in the far southern distribution of the species. Body temperature was regulated under neutral conditions at 38.1 ± 0.34°C (mean ± standard deviation), under cold conditions at 36.7 ± 0.45°C, and under warm conditions at 38.5 ± 0.31 with 44.1°C as a single lethal value. These observations provide new bioenergetic insights and may allow improved techniques for holding and shipping these remarkable creatures both for transplantation to new habitats and as favored attractions in exhibition of animals.

ACKNOWLEDGMENT

This study was supported in part by National Institutes of Health grant GM-10402.

REFERENCES

Brody, S., 1945, *Bioenergetics and Growth*, Reinhold Publishing Corporation, New York.

Hall, E. R., and K. R. Kelson, 1959, *Mammals of North America*, The Ronald Press Company, New York.

Hampton, I. F. G., G. C. Whittow, J. Szekerczes, and R. Rutherford, 1971, Heat Transfer and Body Temperature in the Atlantic Bottlenose Dolphin, *Tursiops truncatus*, *Int. J. Biometeorol.*, 15: 247-253.

Irving, L., 1969, Temperature Regulation in Marine Mammals, in *Biology of Marine Mammals*, pp. 147-174, H. T. Anderson (Ed.), Academic Press, Inc., New York.

—, and J. Krog, 1954, Body Temperature of Arctic and Subarctic Birds and Mammals, *J. Appl. Phys.*, 6: 667-680.

Iverson, J. A., 1972, Basal Energy Metabolism of Mustelids, *J. Comp. Physiol.*, 81: 341-344.

—, and J. Krog, 1973, Heat Production and Body Surface Area in Seals and Sea Otters, *Norw. J. Zool.*, 21: 51-54.

Kenyon, K., 1969, *The Sea Otter in the Eastern Pacific Ocean*, U. S. Department of the Interior, Bureau of Sport Fisheries and Wildlife, North American Fauna, No. 68.

Miller, L. K., M. Rosenmann, and P. R. Morrison, 1976, Oxygen Uptake and Temperature Regulation of Newborn Harbor Seals (*Phoca vitulina richardi*) in Water, *Comp. Biochem. Physiol., A*, 54: 105-107.

Morrison, P. R., 1962, Body Temperatures in Some Australian Mammals, III: Cetacea (Megaptera), *Biol. Bull.*, 123: 154-169.

—, 1951, An Automatic Manometric Respirometer, *Rev. Sci. Instrum.*, 22: 254-267.

—, and O. P. Pearson, 1946, The Metabolism of a Very Small Mammal, *Science*, 104: 287-289.

—, M. Rosenmann, and J. A. Estes, 1974, Metabolism and Thermoregulation in the Sea Otter, *Physiol. Zool.*, 47: 218-229.

—, and F. A. Ryser, 1976, Body Temperature in Mustelids, in preparation.

——, and F. A. Ryser, 1952, Weight and Body Temperature in Mammals, *Science*, 116: 231-232.

——, F. A. Ryser, and A. R. Dawe, 1959, Studies on the Physiology of the Masked Shrew, *Sorex cinereus*, *Physiol. Zool.*, 32: 256-271.

Øritsland, N., and K. Ronald, Energetics of the Free Diving Harp Seal (*Pagophilus groenlandicus*), *Rapp. P.-V. Réun. Cons. Int. Expl. Mer.*, 169: 451-454.

Rosenmann, M., and P. R. Morrison, 1974, Maximum Oxygen Consumption and Heat Loss Facilitation in Small Homeotherms by He—O_2, *Amer. J. Physiol.*, 226: 490-495.

Stullken, D. E., and C. M. Kirkpatrick, 1955, Physiological Investigation of Captivity Mortality in the Sea Otter (*Enhydra lutris*), *Trans. North Amer. Wildlife Natur. Res. Conf.*, 20: 476-494.

Young, D. R., R. Mosher, P. Erve, and H. Spector, 1959, Energy Metabolism and Gas Exchange During Treadmill Running in Dogs, *J. Appl. Physiol.*, 14: 834-838.

This page intentionally left blank