FEEDING BEHAVIOR AND MAJOR PREY SPECIES OF THE SEA OTTER, *ENHYDRA LUTRIS*, IN MONTAGUE STRAIT, PRINCE WILLIAM SOUND, ALASKA

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ABSTRACT

Food habits and feeding behavior of sea otters were studied in Prince William Sound, Alaska, from May through August 1971. Otters fed primarily on clams, crabs, and sea stars: *Saxidomus gigantea*, *Telmessus cheiragonus*, and *Evasterias troschelii*, respectively, were the most important prey species identified in the major groups. Mean times for feeding dives were 67 s for females (mean water depth = 9.6 m) and 59 s for males (mean water depth = 11.9 m). Clams were dug from the bottom and opened with the aid of stones. Sea urchins and fishes were not identified as dietary components.

The sea otter, *Enhydra lutris*, hunted to near extinction by 1911 in Alaska, is steadily reoccupying its former range. Several areas are being repopulated naturally (Kenyon 1969), while others have been restocked with otters translocated from Amchitka Island in the Aleutians or from south central Alaska (Burris and McKnight 1973). In some areas of the Aleutian Islands, sea otters have become so abundant that an experimental harvest has been conducted by the Alaska Department of Fish and Game. Populations in Prince William Sound have become large enough to permit capture of a small number of animals for restocking areas of former abundance.

Large gaps still exist in our knowledge of the biology and life history of the sea otter. Past studies have dealt primarily with populations along the California coast and off Amchitka Island. No intensive study of sea otters in Prince William Sound has been completed, and the only available information from that area concerns restocking activities and population counts (Pitcher and Vania[2]). The lack of information on the biology of the sea otter in Prince William Sound and the impending development of oil reserves along the Alaska coast motivated this study.

STUDY AREA

This investigation took place in Montague Strait, Prince William Sound, Alaska (Figure 1). One week was spent in the field in September 1970. In May 1971, a camp was established at the northwestern end of Montague Island (lat. 60°15'54"N, long. 147°12'18"W). Observations were made from May through August 1971. The study area included the northwestern end of Montague Island, from Stockdale Harbor to a logging camp 19 km southwest. Green Island, Little Green Island, and the adjacent waters were also included (see Figure 1).

The area was selected as a location where sea otter populations have always existed. Although the population is still expanding, there has always been some sea otters in this area (Karl Schneider, Alaska Department of Fish and Game, pers. commun.).

The area is characterized by a rugged coastline with rocky shores. Two sand beaches occur in the area, one south of Port Chalmers and one on the south side of Green Island. Several streams empty into the Sound from Montague Island: mud flats and small estuaries are common. The mud flats support stands of eel grass, *Zostera* sp., and provide habitats for populations of clams—*Macoma* spp., *Saxidomus gigantea*, and *Protothaca staminea*.

Approximately 55 km of coastline was included in the study area. Kenyon (1969:57) stated that "generally sea otters favor waters adjacent to rocky coasts near points of land" and that "coasts adjacent to extensive areas of underwater reefs are particularly attractive." Using these criteria,

[1]Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.

[2]Pitcher, K. W., and J. S. Vania. 1973. Distribution and abundance of sea otters, sea lions and harbor seals in Prince William Sound. Unpubl. manuscr., 18 p. Available Alaska Department of Fish and Game, Anchorage, Alaska.

Manuscript accepted June 1977.
FISHERY BULLETIN: VOL. 76, NO. 1, 1978.

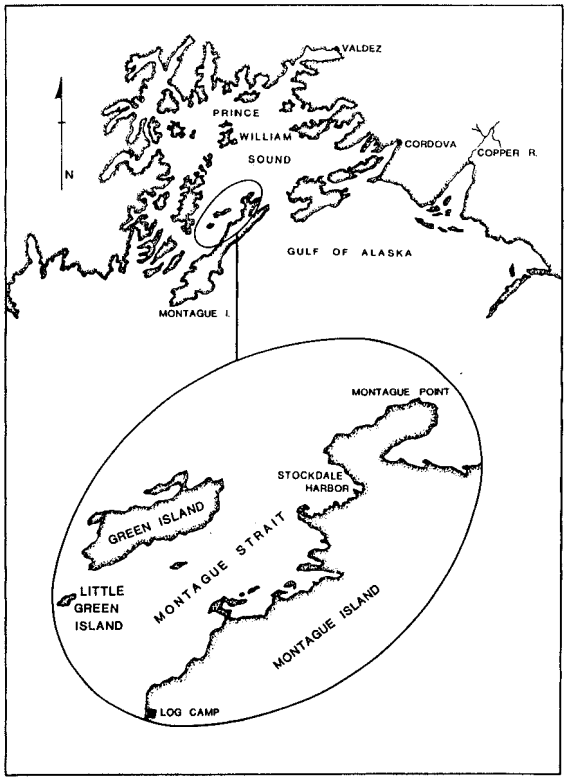

FIGURE 1.—Montague Strait sea otter study area located in Prince William Sound, Alaska.

at least 50 km of the coast within the study area seemed suitable for sea otters. The animals did not frequent the areas with sandy beaches or shallow estuaries.

Feeding habits were studied at three main locations at Montague Island: a small lagoon (Ookshilk Lagoon, see de Laguna 1956) on the south side of Stockdale Harbor, the area outside Ookshilk Lagoon to the north and west, and Port Chalmers south of Stockdale Harbor. Ookshilk Lagoon had water depths from 5 to 7 m and rock and mud beaches grading to subtidal sand which supported stands of eel grass, *Zostera* sp., and rockweed, *Fucus* sp. The area outside Ookshilk Lagoon was characterized by water depths of 5 to 16 m, rock beaches and sand with reef shoals subtidally, and *Fucus* sp. beach and subtidal flora. Port Chalmers had water depths of 14 to 26 m with rock beaches and subtidal sand with reefs and shoals. Beach and subtidal flora in the Port Chalmers area consisted of *Fucus* sp. and kelp, *Nereocystis lutkeana*.

METHODS

All observations on feeding habits were made from advantageous locations on land. Spotting telescopes with magnification of 15 to 60× were used to identify food organisms. Observation distances ranged from 20 to 500 m. The dimensions of the organisms were estimated relative to the otters paws, which were estimated to average 4 cm wide. Dimensions of octopuses were estimated across the tips of the tentacles, relative to the otter's body, and all sizes are reported in this manner. No identification of organisms was attempted beyond 100 m, but it was often possible to classify food items by categories such as clam, crab, sea star, etc., up to 500 m away. Dive and surface feeding times for a total of 14 feeding periods were measured with stopwatches. Timing of feeding periods began when other activities ceased and the otter dived for food and ended when the last bit of food was eaten and some other activity began.

Prey species were collected at low tide, and taken to the University of Alaska for identification. Clams were collected on a gravel beach in Ookshilk Lagoon where otters fed. Work was confined to 1 h before until 1 h after low tide (−0.86 m). Ten transects were dug 25 m apart with each transect running from the extreme high-tide mark to the water's edge. Sample holes of approximately 0.25 m^3 were dug at 5-m intervals along each transect. Sample holes were dug to a depth of 25 cm.

In areas where extensive observations were made, water depths were measured using a weighted line graduated at 25-cm intervals.

RESULTS

Types of Organisms Eaten

All food organisms were bottom-dwelling invertebrates from three major groups of organisms: molluscs, crustaceans, and echinoderms. The percentage occurrence of prey organisms in the diet is shown in Table 1. Five species of clams are found in this area (Table 1), and all were eaten. Empty shells and observations of feeding otters suggest that *Saxidomus gigantea* is the clam most commonly eaten by otters.

Several species were present in the area but never observed to be eaten by otters (Table 1). Each had been previously identified as food of sea otters (Barabash-Nikiforov 1947; Kenyon 1969).

TABLE 1.—Bottom-dwelling invertebrates of Montague Strait, Alaska, and the percent of occurrence in the diet of sea otters.

Food organism	No.of times consumed	Percent of occurrence in diet
Arthropoda:		
Crustacea:		
Telemessus cheiragonus	43	7
Mollusca:		
Gastropoda:		
Nucella(=Thais) lamellosa	0	0
Pelecypoda:		
Saxidomus gigantea[1]		
Protothaca staminea[1]		
Mya truncata[1]	481	81
Macoma inquinata[1]		
Macoma incongrua[1]		
Mytilus edulis, mussel[2]	2	0.3
Pododesmus macroschisma	0	0
Clinocardium nuttalli	0	0
Cephalopoda:		
Octopus sp.	4	0.6
Echinodermata:		
Asteroidea:		
Evasterias troschelii	5	0.8
Echinoidea:		
Strongylocentrotus drobachiensis	0	0
Holothuroidea	2	0.3
Unidentified	60	10
Total	597	100

[1]Each of these pelecypods was identified as a dietary item one or more times, but the relative frequency of use was not determined.
[2]Observations were made on two different occasions of otters feeding on mussels. The small mussels averaged around 2 to 3 cm each. This plus the fact that the observation distance was up to 100 m made it impossible to get an exact count.

Shells of the snail *Nucella (=Thais) lamellosa*; cockle, *Clinocardium nuttallii*; and the rock oyster or jingle, *Pododesmus macroschisma*, were abundant in the study area. Tests of sea urchins were rare.

Octopuses consumed by otters ranged from 30 cm to 1 m across the tips of the tentacles. Crabs (*Telmessus cheiragonus*) eaten ranged from 5 to 15 cm across the carapace. The clams consumed (*Mya truncata, Macoma inquinata,* and *M. incongrua*) were approximately 2 to 3 cm long, with *Protothaca staminea* and *S. gigantea* ranging from 2 to 10 cm long. Mussels (*Mytilus edulis*) were 2 to 3 cm long. Sea cucumbers measured 15 cm long and sea stars (*Evasterias troschelii*) 20 to 30 cm across the rays.

From the 30 stations occupied along the intertidal transects, a total of four clams (two *Macoma* spp., one *S. gigantea,* and one *P. staminea*) and 56 mussels were collected.

Feeding Behavior

Otters usually rose vertically so that the shoulders were above the water surface before diving (also see Limbaugh 1961). In water depths <4 or 5 m otters usually sank to shoulder level before rolling forward into a dive. In deeper water they ordinarily dove from the highest position of emergence, presumably to provide greater downward thrust. During the beginning of a dive, the forelimbs were kept close to the body. One otter often dove backward from a supine floating position by kicking its hind flippers and arching its back. The duration of feeding dives (average 66 s; Table 2) was approximately the same as that observed for sea otters in California (60-90 s; Limbaugh 1961).

Otters in Montague Strait ate crabs as described by Fisher (1939) for California otters and by Kenyon (1969) for Aleutian otters. Otters removed the legs with one paw while clasping the crab to the chest with the other paw. Kenyon (1969:116) reports that "in the Aleutians the carapace was not among the stomach contents," whereas Fisher (1939:28) noted for California otters "when the legs are finished, the body is eaten." While holding otters in captivity prior to translocation from the Montague Strait area during 1965 and 1966, the animals were fed commercially available crabs (*Cancer magister*) (Ed Klinkhart, Alaska Department of Fish and Game, pers. commun.). The otters consistently ate the chelipeds first and then the walking legs. Next the carapace was removed and the body eaten. Finally the carapace was generally licked prior to discarding. Unconfined sea otters occasionally bit the carapace but usually discarded it after finishing the legs. Two crabs were often taken during one dive.

Otters dug out clams with their forepaws while maintaining a head downward position (see Limbaugh 1961 for similar shallow-water feeding behavior of California otters). Holes or craters from 15 to 45 cm across and up to 50 cm deep, made by

TABLE 2.—Results of 673 timed feeding dives of sea otters in Montague Strait, Alaska, listed by depth.

	Sex	No. of dives observed	Mean diving time (s)	Approx. water depth (m)
1	F	20	3	4
2	M	80	47	4.8
	F	60	49	
3	M	3	108	10.6
	F	14	83	
4	M	14	83	13.3
	F	406	73	
5	M	6	118	13.3
6	F	26	83	16.3
7	M	44	69	17.6
Total F		526	67	[1]9.6
Total M		147	59	[1]11.9
Total both sexes		673	66	[1]11.9

[1]Average depths for combined observations.

the otters in this process, were abundant in intertidal and subtidal areas with gravel or sand bottoms.

A male otter was observed feeding on clams about 3 to 5 cm long; 38 clams were consumed in 35 min (1.08/min). A female and a large pup, observed at the same location, fed on clams of the same size range as those eaten by the male. Only the female successfully brought up clams although the pup dove with her. Together, they consumed 56 clams in 65 min (0.86/min). Both adults brought up as many as three clams per dive.

Generally, clams 3 to 5 cm long were eaten intact including the shell. The otter pushed each clam into its mouth, crushed the shell, and swallowed the entire clam immediately. Larger clams (5 to 10 cm long) were cracked with the cheek teeth, usually breaking one valve in half (see Miller et al. 1975). This has also been observed in Monterey Bay (H. Feder pers. commun.). Valves were then forced open by a rotating motion or were pulled apart with the paws, and the soft parts scooped or bitten out with the incisor teeth.

Large males were occassionally able to crack clams >10 cm with their cheek teeth and pull the valves apart with their paws. However, they typically opened larger clams by pounding them against each other or against a rock until the shell was fractured and the valves forced open. The size of the rocks ranged from 7 to 15 cm long but there was no preference for shape.

Otters often used stones as tools for opening hard shelled invertebrates such as clams (Fisher 1939; Limbaugh 1961; Hall and Schaller 1964). With the stone lying on the otter's chest, the clam was struck against it with several quick, hard blows until the shell or the hinge was broken. Otters were typically nonselective when striking the clam against a rock; however, one otter consistently struck the hinge area which usually separated after three or four blows. A rock was not used more than once. Each rock was always discarded immediately by allowing it to slip off the chest.

Otters obtained mussels by pulling up holdfasts of *Laminaria* sp. to which the bivalves were attached. The animal then floated with the algal frond across the body and picked individual mussels off with its forepaws and ate them whole. Otters never consumed algal material.

Octopuses were eaten completely. One female consumed an octopus (60 cm across the tips of the tentacles) in slightly more than 6 min. The otter held the body of the octopus in its paws and bit into an arm or the body while pulling away with its head and pushing away with its paws. This left a piece of octopus in the mouth, which was pushed in while the remainder was held in the otter's axilla or against the chest. This procedure was repeated until the entire octopus was eaten. Pieces dropped during the feeding process were retrieved.

Sea stars were not a preferred food. According to Kenyon (1969:119), "the otter usually tears off and eats one or two arms of a sea star . . . and discards the remainder." Otters in Montague Strait fed in a similar manner. Kenyon (1969) reported several species of sea stars are eaten by otters in the Aleutians. Only one sea-star species (*Evasterias troschelii*) was taken by otters in the present study, although others were available (*Dermasterias imbricata* and *Pycnopodia helianthoides*).

Sea cucumbers were rarely eaten and were also apparently of minor importance to Aleutian otters (Kenyon 1969). Sea cucumbers were torn open, a portion of the viscera and part of the body wall eaten, and the remainder discarded.

Feeding periods ranged from 25 to 147 min, averaging 84.5 min. Elapsed times for eating at the surface during the 14 feeding periods ranged from 17 s for a clam to 6 min for an octopus, with a mean value of 38 s for all foods (see Table 2 for diving times and Table 3 for average consumption times of each food item).

TABLE 3.—Range and mean of feeding times for individual food items measured in seconds for sea otters in Montague Strait, Alaska.

Food item	No.of observations	Surface feeding time	
		Range	Mean
Clam	81	17-64	38.6
Crab	2	30-39	34.5
Sea star	4	25-41	30
Octopus	1	—	380
Unidentified	5	17-53	34
No food brought up	52	10-54	24.5

DISCUSSION

The sea otter is an opportunistic feeder throughout its range. It generally feeds on bottom-dwelling invertebrates, but may select fishes if the invertebrate supply is depleted (Kenyon 1969 in Table 4). Mollusks were the most important food of otters in California and Montague Strait, echinoderms are apparently most important in the Commander Islands, and fishes most important in the Aleutians (Table 5). Crustaceans were second in importance at Pico Creek, Calif.,

TABLE 4.—Qualitative comparison of food of sea otters in Montague Strait, Alaska.

Location and reference	Method of analysis	Major food items consumed			
		Molluscs	Crustaceans	Echinoderms	Fishes
Amchitka Island, Aleutian Islands, Alaska (Kenyon 1969)	Stomach and fecal analyses and direct observation	Chiton *Cryptochiton stelleri* Snails *Buccinum* sp. *Argobuccinium oregonensis* Mussels *Musculus vernicosa* *Volsella volsella* Octopus *Octopus* sp. Rock oyster *Pododesmus macroschisma*	Crabs *Cancer* sp. *Placetron wosnessenski*	Green sea urchin, *Strongylocentrotus drobachiensis,*	Globe fish, *Cyclopterichthys glaber,* Red Irish lord, *Hemilepidotus hemilepidotus,*
Pico Creek, Calif. (Ebert 1968)	Direct observation	Red abalone, *Haliotis rufescens,* Gaper clam, *Tresus nuttalli,*	Rock crab, *Cancer antennarius,*		
Monterey Bay, Calif. (Limbaugh 1961)	Direct observation	Red abalone, *Haliotis rufescens,* Purple hinged scallop, *Hinites gigantea,* California mussel, *Mytilus californianus,*		Sea urchin *Strongylocentrotus franciscanus*	
Point Lobos, Calif. (Hall and Schaller 1964)	Direct observation	Mussel *Mytilus californianus* Red abalone, *Haliotis rufescens,*	Crab *Cancer* sp.	Purple urchin, *Strongylocentrotus purpuratus,*	
Commander Islands, USSR (Barabash-Nikiforov 1947)	Direct observation and fecal analysis	Clam *Mya truncata* Mussel *Mytilus edulis*	Crab *Telmessus cheiragonus*	Sea urchin *Strongylocentrotus drobachiensis*	Hexigrammidae
Montague Strait, Alaska (this study)	Direct observation	Clams *Saxidomus gigantea* *Protothaca staminea* Mussel *Mytilus edulis*	Crab *Telmessus cheiragonus*	Sea star *Evasterias troschelii*	

and Montague Strait with molluscs second in the Aleutians and echinoderms second at Point Lobos, Calif.

Sea urchins seem to be a relatively minor part of the diet in Montague Strait. No living sea urchins were found in the intertidal zone and only an occasional test was found. Kenyon (1969:111) indicated that "the bones of those sea otters utilizing sea urchins . . . are stained purple by the biochrome polyhydroxynaphthoquinone (Scott *in* Fox 1953)." Of the six different sets of skeletal remains found on the beaches of Montague Strait during this study, none showed this diagnostic purple stain. Schneider (Alaska Department of Fish and Game, pers. commun.) reports that of the several skulls he obtained from Prince William Sound, none show purple pigmentation.

Fishes are an important food source in the Aleutians when invertebrates become depleted. Kenyon (1969:110) reported that "At Amchitka it appears that the otters fall into two groups—those eating mostly fish and those eating mostly invertebrates." Otters were not observed eating fishes in Montague Strait and fishes are probably not important here. During the latter part of this study pink salmon, *Oncorhynchus gorbuscha,* and chum salmon, *Oncorhynchus keta,* became abundant. Vania[3] found that otters captured in Montague Strait and held for translocation refused to eat chum and pink salmon for a period of 24 h.

[3]Vania, J. 1967. Sea otter. *In* Marine mammal investigations. Alaska Dep. Fish Game, Vol. 7 Annual Project Segment Rep., Fed. Aid Wildl. Restoration, Proj. W-14-R-1 and -2, work plan G, p. 6-13.

TABLE 5.—Frequency of occurrence of major food items in the diet of sea otters in Montague Strait, Alaska, compared with other locations. Organisms from the Commander Islands study are shown according to relative abundance as indicated by plus signs, increasing plus signs indicate increasing abundance.

Location and reference	Amchitka Island, Aleutian Islands, Alaska (Kenyon 1969)	Pico Creek, Calif. (Ebert 1968)	Point Lobos, Calif. (Hall and Schaller 1964)	Commander Islands, USSR (Barabash-Nikiforov 1947)	Montague Strait, Alaska (this study)
Method of analysis	Stomach and fecal analyses and direct observation	Direct observation	Direct observation	Direct observation and fecal analysis	Direct observation
Food item	Percent	Percent	Percent	Abundance	Percent
Mollusks,					
Clams		2.5		++	81
Mussels		0.8	40	++	0.3
Snails					
Chiton		0.4	0.8		
Octopods			0.4		0.6
Abalone		63.4	9.9		
Rock scallop		2.1			
Total	37	69.2	51.1		81.9
Crustaceans:					
Crabs	Present	25.9	14.5	++	7
Spiny lobster			0.6		
Total		25.9	15.1		7
Echinoderms:					
Sea urchins	Present		32.8	+++	
Sea stars	Present		0.6		0.9
Sea cucumbers	Present				0.3
Total			33.4		1.2
Fishes	50		0.4	++	
Others	13	4.9			9.9
Grand total	100	100	100		100

Prior to this study, little use of rocks as tools for opening clams had been observed in Alaska. Kenyon (1969) did not observe this phenomenon in the wild, but saw a captive Alaskan otter pound a clam against the side of its cement pool. Schneider (pers. commun.) observed otters using rocks near Amchitka, but considers this behavior uncommon. Kenyon (1969) compared rock-pounding behavior in the sea otter to the use of gravity by gulls (*Larus* sp.) and ravens (*Corvus corax*). He also suggested that tool-using behavior is derived from "chest pounding, frustration behavior" (Kenyon 1969). Otters will often pound clams on their chest when the clams are particularly difficult to open (also see Hall and Schaller 1964).

Limbaugh (1961) noted that otters used the same rocks on successive dives in California. This was not observed in Montague Strait.

Although Kenyon (1969:123) felt that "clams which are buried are not dug from the bottom" and that only those exposed to view or with exposed parts are taken by the otters, otters in Montague Strait frequently and successfully dug clams. *Saxidomus gigantea* and *Protothaca staminea* are found at depths of 8 to 45 cm along the North Pacific coast (Fitch 1953: Quale and Bourne 1972: Paul and Feder[4]). Miller et al. (1975) presented evidence which suggests California otters have dug pismo clams, although no direct observations have been made.

When otters dig in soft sediments characteristic of clam habitats, they undoubtedly locate clams by touch due to obscured vision and, in fact, Kenyon (1969) has shown that otters can locate food by tactile sense alone. One blind captive otter located food successfully and another normal individual used only forepaws in the selection of a preferred food (*Mytilus edulis*) from a bucket of turbid water that also contained small crabs (*Pachygrapsus*), and pebbles of various sizes.

It is apparent that sea otters are able to subsist on a wide variety of bottom-dwelling invertebrates and some fishes. Although they seem to have local preferences, they tend to exploit whatever is available. As otter populations increase they can effect drastic changes in bottom communities.

ACKNOWLEDGMENTS

This study was made possible by funds provided under Federal Aid in Wildlife Restoration, Alaska, Project W-17-3, administered through the Alaska Cooperative Wildlife Research Unit. I am extremely grateful to Howard M. Feder, University of Alaska, for his advice and assistance and tireless critical review of the manuscript; I thank

[4]Paul, A. J., and H. M. Feder. 1976. Clam, mussel and oyster resources of Alaska. Univ. Alaska I.M.S. Rep. 76-4. Sea Grant Rep. 76-6, 41 p.

Peter Lent and Francis H. Fay, University of Alaska, for their advice: Karl Schneider, Alaska Department of Fish and Game, for his advice and critical review of the manuscript; Paul Marhenke III, College, Alaska, for his assistance in the field; Matt Dick and George Mueller, Aquatic Collection Center, University of Alaska Museum, for identification of food organisms; and Janet Viale, Anchorage, Alaska, for her encouraging assistance and patient, devoted help throughout the study.

LITERATURE CITED

BARABASH-NIKIFOROV, I. I.
1947. The sea otter (Enhydra lutris L.)—Biology and economic problems of breeding. *In* The sea otter, p. 1-174. (Translated by Isr. Program Sci. Transl., 1962, 227 p., as OTS 61-31057.)

BURRIS, O. E., AND D. E. MCKNIGHT.
1973. Game transplants in Alaska. Alaska Dep. Fish Game, Wildl. Tech. Bull. 4, 57 p.

DE LAGUNA, F.
1956. Chugach prehistory. The archaeology of Prince William Sound, Alaska. Univ. Wash. Press, Seattle, 289 p.

EBERT, E. E.
1968. A food habits study of the southern sea otter, *Enhydra lutris nereis*. Calif. Fish Game 54:33-42.

FISHER, E. M.
1939. Habits of the southern sea otter. J. Mammal. 20:21-36.

FITCH, J. E.
1953. Common marine bivalves of California. Calif. Fish Game, Fish Bull. 90, 102 p.

FOX, D. L.
1953. Animal biochromes and structural colours. Camb. Univ. Press, Lond. 379 p.

HALL, K. R. L., AND G. B. SCHALLER.
1964. Tool using behavior of the California sea otter. J. Mammal. 45:287-298.

KENYON, K. W.
1969. The sea otter in the eastern Pacific Ocean. North Am. Fauna 68, 352 p.

LIMBAUGH, C.
1961. Observations on the California sea otter. J. Mammal. 42:271-273.

MILLER, D. J., J. E. HARWICK, AND W. A. DAHLSTROM.
1975. Pismo clams and sea otters. Calif. Fish Game Mar. Resour. Tech. Rep. 31, 49 p.

QUALE, D. B., AND N. BOURNE.
1972. The clam fisheries of British Columbia. Fish. Res. Board Can., Bull. 179, 70 p.