

SOME ASPECTS OF THE BEHAVIOR AND ECOLOGY
OF THE SEA OTTER, ENHYDRA LUTRIS,
IN MONTAGUE STRAIT, PRINCE WILLIAM SOUND, ALASKA

By Donald G. Calkins

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A
THESIS

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MASTER OF SCIENCE

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ABSTRACT

Distribution, feeding habits, and territoriality and general behavior of the sea otter (Enhydra lutris) were studied in Montague Strait, Prince William Sound, Alaska during May through September, 1971.

Otters were found associated with certain features of the habitat such as: kelp beds (Nereocystis luetkeana), a lagoon, a favored feeding area, and a sheltered area. No otters were seen hauled out on land nor were any areas used exclusively by males or females seen.

Montague Strait otters feed primarily on three groups of prey animals: pelecypods, decapods, and asteroids. The most important species in each of these groups are Saxidomus giganteus, Telmessus cheiragonus and Evasterias troschelii, respectively. The otters expended 81% of their feeding effort on pelecypods, 7% on decapods, and 0.8% on asteroids. Clams were dug from the bottom by the otters, and opened with the aid of stones. Sea urchins and fishes appear to be of minor importance.

Territoriality was manifested in two sea otters in Montague Strait by territorial defense, fighting, border patrolling and territorial invasion. A female with a large pup joined one of these territorial males and completed the breeding sequence with him. The male devoted only 8.5% of his time to feeding during one day as compared to 52% for a breeding male reported by Kenyon (1969).

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TABLE OF CONTENTS

	Page
INTRODUCTION	1
DISTRIBUTION	5
Study Area	5
Methods	5
Results	7
Discussion	10
FEEDING HABITS	13
Study Area	13
Methods	13
Results	20
Kinds of Organisms Eaten	20
Feeding Behavior	22
Discussion	31
TERRITORIALITY AND GENERAL BEHAVIOR	39
Study Area	39
Methods	41
Results	42
Territorial Behavior	42
Territorial defense	42
Fighting	43
Border patrolling	45
Breeding Behavior	46
Routine Activities	46
Discussion	49
LITERATURE CITED	53
PERSONAL COMMUNICATIONS	55

LIST OF TABLES

	Page
Table 1. Numbers of sea otters sighted during surveys from a boat off Montague and Green Islands from June through August, 1971, with locations of largest groups sighted on each survey	8
Table 2. Comparison of otters counted from aircraft versus from boat during the summer of 1971	9
Table 3. Comparison of habitats of the feeding areas	14
Table 4. Bottom dwelling invertebrates of the Montague Strait area and the percent of occurrence in the diet of sea otters . . .	21
Table 5. Results of 673 timed dives listed according to depth	24
Table 6. Average feeding times for individual food items measured in seconds	30
Table 7. Qualitative comparison of food of sea otters	32
Table 8. Percent frequency of occurrence of major food items in the diet of sea otters . . .	33
Table 9. Time spent in each of four activities by Male 1, the female, and the pup in Ookshilk Lagoon on July 9, 1971	48

LIST OF ILLUSTRATIONS

	Page
Figure 1. The coastline of Montague, Green and Little Green Islands which was included in the study area	3
Figure 2. Ookshilk Lagoon study area	15
Figure 3. Study area outside Ookshilk Lagoon	16
Figure 4. Study area near Port Chalmers	17
Figure 5. Ookshilk Lagoon showing territories used by two male otters during July and August 1971	40

INTRODUCTION

The sea otter Enhydra lutris, after being hunted to near extinction by 1911, is steadily reoccupying its former range. Several areas are being repopulated naturally, while others have been restocked with otters transplanted from Amchitka Island in the Aleutians or from southcentral Alaska (Kenyon, 1969). In some areas of the Aleutian Islands sea otters have become so abundant that the Alaska Department of Fish and Game has initiated a limited harvest of the mammals. Populations in Prince William Sound also have become large enough to have permitted the capture and transplantation of a small number of animals. Despite the recovery of the species, large gaps still exist in our knowledge of the biology and life history of the otters. Sea otter studies have dealt primarily with populations in California and at Amchitka Island. No comprehensive study of sea otters in Prince William Sound has been undertaken; in fact, the only published information on sea otters of that area is concerned with either transplanting activities or population counts. No ecological or behavioral work has been attempted on sea otters in Prince William Sound prior to this study.

The lack of information on sea otters in Prince William Sound plus the impending development due to take place in the form of oil transportation and exploration, dictated

the necessity for this study.

This thesis is concerned with three aspects of sea otter biology: distribution, feeding habits, and territoriality and general behavior. Each topic is treated in a separate section with separate methods, results, and discussion for each section.

The investigation took place in Montague Strait, Prince William Sound, Alaska. One week was spent in the field in September 1970, and four months, from May through August, in 1971. In May, 1971, a field camp was established on a small cove on the northwestern end of Montague Island (60 deg. 15 min. 54 sec. N., 147 deg. 12 min. 18 sec. W.).

The study area comprised the northwestern end of Montague Island, from the north side of Stockdale Harbor to the log camp about 19 km southwest of it (Fig. 1). Green Island, Little Green Island and the intervening waters also were included.

The entire area is characterized by rugged coastline with boulder beaches, the boulders ranging from 10 to 50 cm in diameter. There are only two sand beaches 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. These mud flats provide habitats for eel grass (Zostera sp.) and in many areas support populations of clams of the

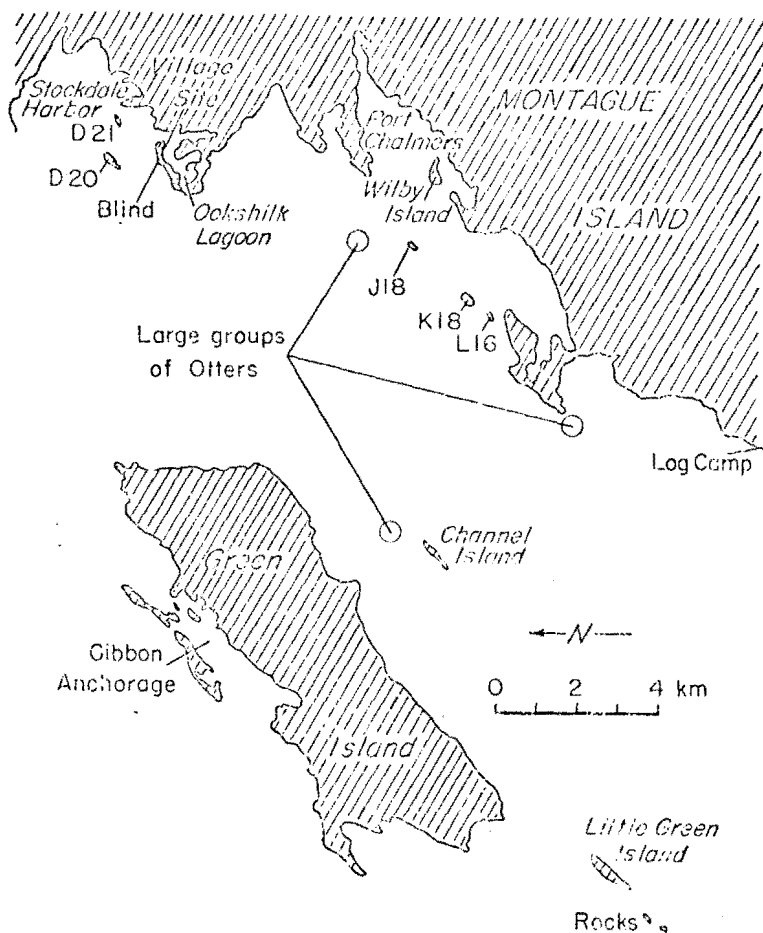


Figure 1. The coastline of Montague, Green and Little Green Islands which was included in the study area. Designation such as D20, J18 etc. indicate unnamed small islands.

genera Macoma, Saxidomus, and Protothaca.

Approximately 55 km of coastline were included in the study area. Kenyon (1969:57) says 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, at least 50 of the 55 km of the coast within the study area are suitable for sea otters. The animals did not frequent the areas with sandy beaches, nor were they seen in shallow estuaries.

DISTRIBUTION

THE STUDY AREA

The entire area was used in the investigation of distribution of the sea otters in Montague Strait (Fig. 1).

METHODS

Surveys were made by means of both boat and airplane. The boat was a 16 foot aluminum craft with an 18 hp. out-board engine. One man operated the engine while the other, using 6 x 30 binoculars, counted otters. The study area was divided into two parts when the boat was used for surveys: the northwestern coast of Montague Island was surveyed the first day, and Green and Little Green Islands were examined the next day, weather permitting.

Aerial surveys were made from a Grumman Goose and Supercub aircraft. The survey altitudes ranged from 100 to 500 m for both aircraft. When the Grumman aircraft was used, one observer sat in the co-pilot's seat and counted otters sighted, while another sat between the pilot and the first observer and counted animals sighted from the pilot's side of the aircraft. The pilot also assisted with the counting. All sightings by the two observers and the pilot were recorded on a single map. Only one survey was accomplished from the Supercub aircraft. In the Supercub the observer sat behind the pilot. When otters were

sighted in large groups, they were circled and counted individually when possible. Sea otters often show alarm and dive in the presence of low flying aircraft, therefore accurate counts of groups containing more than 10 individuals were usually not feasible. All other otters, singles and small groups, were counted individually.

Weather was recorded daily. Temperatures were monitored with a maximum/minimum thermometer; wind direction and velocity were estimated, and height and direction and type of cloud cover were recorded.

RESULTS

The results of surveys from the boat are shown in Table 1. Certain of these, in which the entire area was surveyed within a four day period are compared with the results from the aerial surveys (Table 2). The four day period was considered the longest reasonable time in which the distribution of the otters would not change significantly. The mean of the counts from the aerial surveys was 152, while the mean from the boat surveys was 164. Figure 1 shows the location of all groups that contained more than 10 otters sighted during the summer, from both boat and plane. With the exception of the otters in Stockdale Harbor, large groups were usually associated with large kelp beds (Nereocystis luetkeana). The largest group consistently sighted was situated north of Channel Island, though it was not sighted initially. Conceivably, my inexperience as an observer (my first aerial survey) contributed to missing this group on the first flight.

I found no evidence of discrete areas in which only males congregated, as described by Kenyon (1969) for otters in the Aleutian Islands. Single males and females without pups were seen throughout the area, and, in one case, a large pup without its mother was identified.

Table 1. Numbers of sea otters sighted during surveys from a boat off Montague and Green Islands from June through August, 1971, with locations of largest groups sighted on each survey.

Date	Island	No. of otters sighted		Location of Largest Group
		Total	Largest Group	
June 18	Montague	45	3	Ookshilk Lagoon
June 28	Green	122	60	Channel Island
July 1	Montague	46	17	S of Port Chalmers
July 10	Montague	79	46	Port Chalmers
July 12	Green	154	54	Channel Island
July 15	Montague	120	35	S of Port Chalmers
July 29	Montague	55	14	Near Island J18
Aug. 4	Green	71	30	Channel Island
Aug. 5	Montague	118	20	S of Port Chalmers
Aug. 15	Green	37	13	Channel Island
Aug. 19	Montague	80	17	Near Island J18
Aug. 25	Montague	64	14	Stockdale Harbor
Aug. 26	Green	49	14	Channel Island

Table 2. Comparison of otters counted from aircraft versus from boat during the summer of 1971. Of the surveys from the boat, only those in which the entire area was surveyed within a 4-day period are included.

Date	Survey Type	No. sighted Total	Location of largest Group from Air
May 7, 1971	Aerial	107	NW end of Little Green Island
June 16	Aerial	176	SW side of Stockdale Harbor
June 28/July 1	Boat	168	
July 10/12	Boat	233	
August 2	Aerial	176	Channel Island
August 4/5	Boat	189	
August 15/19	Boat	117	
August 25/26	Boat	113	
Averages	Aerial	152	
	Boat	164	
	All	160	

DISCUSSION

The survey work was accomplished to give information on distribution and not to estimate the total population; estimating the total population would not be practical with the information gathered in this study. The area has no natural barriers to sea otter emigration and immigration; therefore the total population could be changing continuously. Karl Schneider (pers. comm.) considers aerial surveying of sea otters to be only of marginal value as a method of counting exact numbers of otters in a given area.

Sea otters were found to be distributed irregularly throughout the study area. Distribution is directly related to suitability of the habitat: some parts of the area, seemed to be favored, for otters were sighted there during each of the surveys, while other areas seemed to be unfavorable in that otters were never seen there. For instance, Ookshilk lagoon (Fig. 1) provided an excellent place for territoriality to develop. This area was taken over by two otters that established and defended separate territories throughout the study period. Another area, around Islands D20 and D21 (Fig. 1), appeared to be a favored feeding area; otters were seen there very frequently. The area northwest of Channel Island contained a large kelp bed, approximately 300 to 400 m long and 100 m wide,

and a pod of 50 to 100 otters could be found there at nearly all times. Otters were usually seen also in Gibbon Anchorage, a well protected area.

In all cases where large groups were sighted they were found to include females and pups. Males might have been present in these groups, but it was usually not possible to determine the sex of individual adults in these groups, other than those accompanied by a pup.

The fact that I was unable to identify areas occupied only by males suggests that this phenomenon does not occur in Montague Strait; conceivably it is uncommon anywhere in Prince William Sound. Karl Schneider, who has worked with otters in Montague Strait, told me that he also found no evidence of sexual segregation in the area.

I did not see otters leave the water at any time, though I observed them several times as they slept in the water during dusk and even in darkness, several hours after sunset. Kenyon (1969) reported that the otters at Amchitka Island haul out on a daily basis to sleep, although they sleep in the water also. Karl Schneider (pers. comm.) believes that sea otters do not haul out in Prince William Sound or California to the degree that they do in the Aleutians, and that several factors, including air temperature and suitable hauling out places influence their hauling out. I observed harbor seals (Phoca vitulina) hauled out regularly on several rocks in the Montague

Strait area, but the sites utilized by the seals are not necessarily suitable for the otters. I think that if hauling out does occur in Prince William Sound, it must occur very infrequently.

In summary, sea otters seem to distribute themselves in response to environmental conditions. Where food and suitable resting places are available, sea otters can be found on a regular basis. If weather or sea conditions make it necessary, the otters may come out on land, but where conditions are more favorable, the sea otters may spend their entire life in the water.

FEEDING HABITS

STUDY AREA

The feeding habits of sea otters were studied in three main areas: inside Ookshilk Lagoon, on the south side of Stockdale Harbor (Fig. 2), the area just outside Ookshilk Lagoon (Fig. 3), and the Port Chalmers area (Fig. 4). Table 3 shows a comparison of the habitats in these three areas.

Observations in Ookshilk Lagoon were made from the village site, and outside of Ookshilk Lagoon at a blind site (Fig. 3). The majority of the feeding observations in the Port Chalmers area were made from a small island (J18, Fig. 4). The majority of observations were from the north side of the island, because this was the only place that provided a good observation post; distribution of feeding appeared to be random throughout the area.

METHODS

Probably the most effective method of studying feeding habits of sea otters would be a combination of analysis of stomach contents of a large number of animals, analysis of a large collection of scats from the area, and long-term visual observations of the animals feeding. No study to date has combined all three of these methods. Kenyon (1969) has presented the most comprehensive work on feeding habits,

Table 3. Comparison of habitats of the feeding areas.

Area	Water Depth	Substrate of Beach	Substrate of Subtidal	Beach and Subtidal Flora	Favored Feeding Locations in Area
Ookshilk	5 to	Muddy		eel grass	Middle of central
Lagoon: (Fig. 2)	7 m	To Rocky	sand	(<u>Zostera</u> sp.)	area to shore.
				Rockweed	Point west of Island.
				(<u>Fucus</u> sp.)	Entrance area.
Outside	5 to	Rocky.	Sand with	Rockweed	2/3 of the way
Ookshilk	16 m	Boulders	reefs and	(<u>Fucus</u> sp.)	along a line from
Lagoon (Fig. 3)		average	shoals		the blind to the
		about			center of Island D20.
		15 cm			
Port Chalmers	14 to	Rocky	Sand with	Rockweed	No favored location.
(Fig. 4)	26 m		reefs and	(<u>Fucus</u> sp.)	
			shoals	Kelp	
				(<u>Nereocystis</u>	
				<u>luetkeana</u>)	

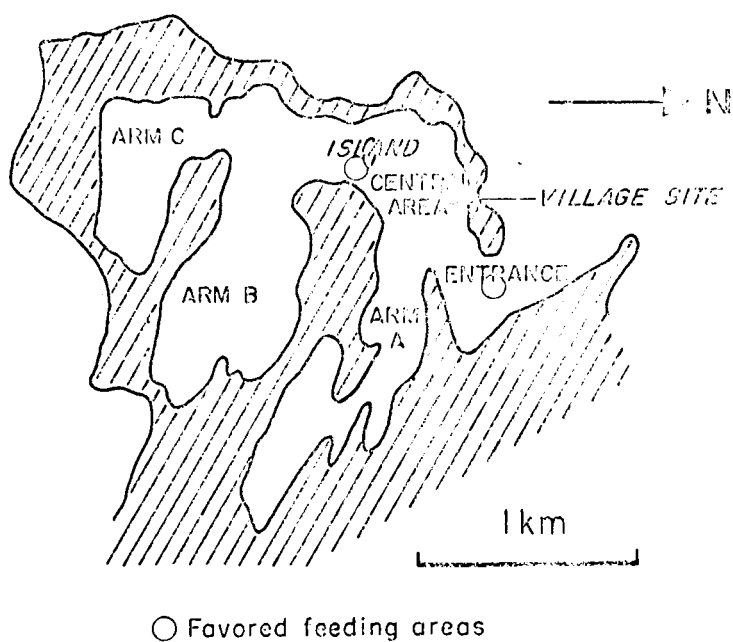


Figure 2. Ookshilk Lagoon study area.

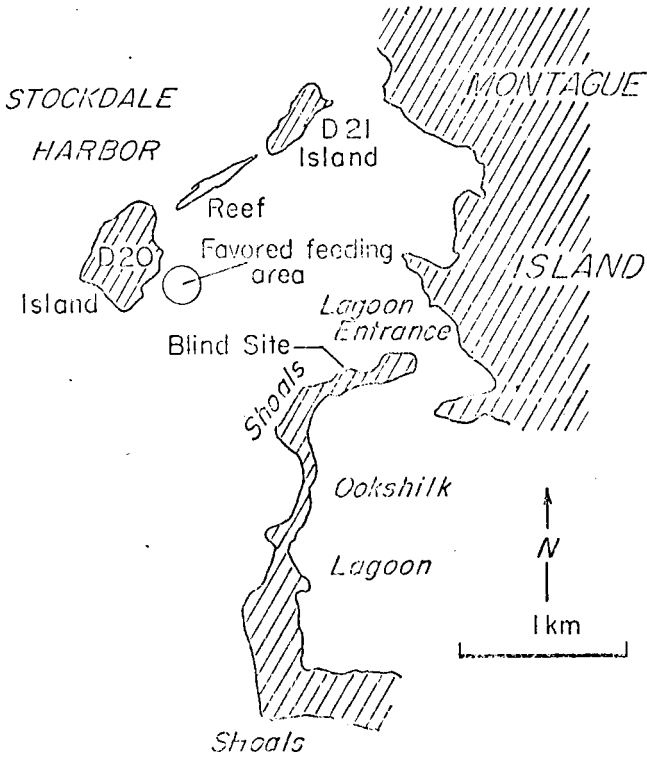


Figure 3. Study area outside Oakshilk Lagoon.

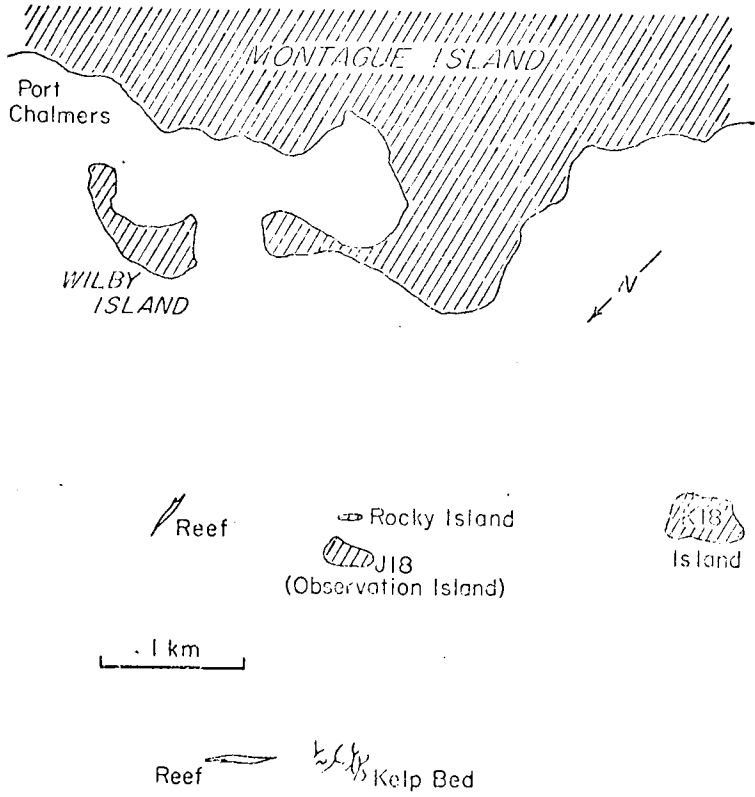


Figure 4. Study area near Port Chalmers.

but does not include quantitative data from field observations.

I used a method similar to that of Hall and Schaller (1964) and Ebert (1968) who relied primarily on visual observations for identification of food items. The fact that sea otters in Prince William Sound do not leave the water precludes fecal analysis. Stomach content analysis was not feasible for this study.

All observations on feeding habits were made by watching the otters from advantageous locations on land. Spotting scopes with magnification of 15-60x 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 I estimated to average 4 cm wide. No specific identifications of organisms were attempted beyond 100 m, but it was often possible to classify the food items by categories such as clam, crab, sea star, etc. up to 500 m away. Dive and surface feeding times were measured with a stopwatch. Whenever underwater and surface times were recorded for the same animal during the same feeding period, time at the surface was clocked by one observer and time underwater was clocked by a second observer.

I collected invertebrates from the beach, attempting to include representatives of each species on which the otters were observed to feed. The specimens from these

collections were returned to the University of Alaska for identification.

Some of the clams I collected were dug from beaches in the Ookshilk Lagoon area (Fig. 2), in the area of the island in the central area of the lagoon. This was accomplished by digging ten beach transects 25 m apart. Each transect ran from the extreme high-tide mark to the water's edge. Sample holes were dug at 5 m intervals along each transect. Digging was accomplished at a tide of -1.9 feet. Work was confined to 1 hour before tide change until 1 hour after. SCUBA gear was used on two occasions for short periods to examine the subtidal areas where otters frequently were observed feeding.

In those areas where extensive observations were made water depths were measured; a weighted line marked off at 25 cm intervals was used.

RESULTS

Kinds of Organisms Eaten

The sea otters in Montague strait used three major groups of organisms as food at the time of this study: mollusks, crustaceans, and echinoderms. Table 4 shows the percentage of occurrence of these prey organisms in the otters' diet as indicated by my observations. Five species of clams are found in this area (Table 4), and each of these seem to be used by the otters. The number of empty shells in the area and my observations on feeding otters suggest that S. giganteus may be the most important clam in their diet. I often observed otters feeding on a large (larger than 10 cm) black-shelled clam usually taken subtidally. Of the five clams commonly found in the area, only S. giganteus is known to grow to this size. Saxidomus giganteus and P. staminea were consumed in large quantities, particularly those of about the size of the otters paws. While watching through a spotting scope, I found S. giganteus and P. staminea to be easily distinguishable from the other clams by their general shape and color but difficult to distinguish from each other.

Several invertebrates listed in Table 4 were present in the area but not specifically identified as being eaten by the otters. Each of these invertebrates has been

Table 4. Bottom dwelling invertebrates of the Montague Strait area and the percent of occurrence in the diet of sea otters. Organisms not identified as part of the diet are indicated by dashes.

Food Organisms	No. of times consumed	Percent of occurrence in diet
Arthropoda		
Crustacea		
<u>Telmessus cheiragonus</u> (crab)	43	7 %
Mollusca		
Gastropoda		
<u>Thais lamellosa</u> (snail)	--	--
Pelecypoda	481 ^{a/}	81 %
<u>Saxidomus giganteus</u>		
<u>Protothaca staminea</u>		
<u>Mya truncata</u>		
<u>Macoma inquinata</u>		
<u>Macoma incongrua</u>		
<u>Mytilus edulis</u> (mussel)	2 ^{b/}	0.3 %
<u>Pododesmus macroschisma</u> (rock oyster)	--	--
<u>Clinocardium nuttalli</u> (cockle)	--	--
Cephalopoda		
<u>Octopus</u> sp.	4	0.6 %
Echinoderm		
Asteroidea		
<u>Evasterias troschelii</u> (sea star)	5	0.8 %
Echinoidea		
<u>Strongylocentrotus dröbachiensis</u> (sea urchin)	--	--
Holothuroidea (sea cucumber)	2	0.3 %
Unidentified	60	10 %
Total	597	100 %

a/ Each of the pelecypods was identified as a dietary item one or more times, but the relative frequency of use was not determined.

b/ 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.

previously identified as food of sea otters (Kenyon 1969, Barabash-Nikiforov 1947). With the exception of sea urchins, each species was found in sufficient quantities to be considered as potentially important food source for the otters. Shells of the snail (Thais sp.), cockle (Clinocardium sp.), and the rock oyster or jingle (Pododesmus sp.) were commonly found on most of the beaches in the study area, but tests of sea urchins were rare.

All of the octopuses consumed by otters seemed to be of one species and ranged in size from 30 cm to 1 m across the tips of the tentacles (approximate measurement made during feeding activity). The crabs eaten ranged in size from 5 to 15 cm across the carapace. The clams Mya sp. and Macoma sp. were approximately 2 to 3 cm long, Protothaca sp. and Saxidomus sp. ranged from 2 to 10 cm in length and the mussels were about 2 to 3 cm long. The two sea cucumbers were about 15 cm long and the sea stars were 20 to 30 cm across the rays.

From the thirty stations along the intertidal transects, I collected a total of 4 clams (2 Macoma sp. and 1 S. giganteus and 1 P. staminea) and 56 Blue Mussels (Mytilus edulis), after digging for two hours.

Feeding Behavior

All identifiable food items consumed by the otters of Montague Strait were bottom-dwelling invertebrates. Thus,

the otters must dive to the bottom and remain there long enough to search for and capture their prey. Preparatory to a feeding dive, each otter usually rose vertically so that its shoulders were above the surface of the water (Limbaugh, 1961), then glanced around, surveying the surroundings. When the otter surfaced after each dive, he again examined his surroundings, this time from a supine position. If something had changed on the shore nearest to him, such as my position, he would dive immediately and swim away underwater. This suggests a short term memory. Where the water was less than 4 or 5 m deep, the otter usually sank to the level of the top of the shoulders before rolling forward into a dive. Where the water was deeper, the otter ordinarily dove from the highest position of emergence, to provide greater downward momentum. As the otters dove, they kept their forelimbs close to their sides. One otter often dove backward from a supine floating position by kicking his feet and arching his back.

The duration of dives tended to be slightly longer in deeper water (10-18 m) than it was in shallow (3-5 m) water (Table 5). The diving time of sea otters in California (60-90 seconds, Limbaugh, 1961) is approximately the same as that noted for otters in Montague Strait. There was no indication of a sex-related difference in the duration of feeding dives.

Table 5. Results of 673 timed dives listed according to depth.

	Sex	No. of dives observed	\bar{X} Diving times (in sec.)	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	9.6*
Total	M	147	59	11.9*
Total both sexes		673	66	11.9*

* Average depths for combined observations.

On returning to the surface with the food "stored for transportation . . . in folds of loose skin which extend from the axilla across the chest" (Kenyon, 1969:111), the otters immediately began to consume their food.

The otters in Montague Strait ate crabs in a manner similar to that described by Fisher (1939) for otters in California and by Kenyon (1969) for otters in the Aleutians. On arriving at the surface with the crab clasped to the chest with one paw, the otter then removed the crab's legs with the other paw and ate them. Kenyon (1969:116) reports that "in the Aleutians the carapace was not among the stomach contents", whereas Fisher (1939:28) says that "when the legs are finished, the body is eaten" by the California otter. The sea otters in Montague Strait occasionally took a bite out of the carapace but usually discarded it after finishing the legs. Two crabs were often caught during a single dive.

The otters of Montague Strait fed mainly on clams at the time of this study (Table 4). For example, on July 2, 1971, I watched a male otter in Ookshilk Lagoon feeding on clams about 3 to 5 cm long, of which he consumed 38 individuals in 35 minutes (1.08 per min.). On July 8 I observed a female and a large pup in the same location feeding on clams of about the same size 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

minutes (0.86 per min.). One, two, and occasionally three clams were brought up per dive.

The otters obtained the clams from the bottom by digging them out with their forepaws, while maintaining an inverted position, head downward, and paddling with their hind feet. Limbaugh (1961) describes similar shallow-water feeding behavior for otters in California. I observed otters feeding in this manner on two occasions in water less than 2 m deep. Holes or craters, from 15 to 45 cm across and up to 50 cm deep, made by the otters in this process, were abundant in the intertidal and subtidal zones. The holes were common in sand or gravel bottom but not in rock or mud bottom.

Generally, clams that were equal to or smaller than the otters' paws were eaten entirely, including the shell. The otter pushed each small clam into its mouth, crushed the shell with its teeth, 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. The valves were forced open by a rotating motion of the paws or were pulled apart with the paws, and the viscera was scooped out or bitten out with the incisor teeth.

Large male otters were occasionally able to crack open clams larger than 10 cm with the cheek teeth and then pull the valves apart with their paws. Typically otters fed

upon the larger clams by pounding them against each other or against a rock until the shell was fractured and could be forced open. There seemed to be no specific preference as to the size or shape of rocks used in this manner, for they ranged in size from 7 to about 15 cm long and in shape from nearly round to flat.

Generally the otters used stones in the same manner described by Fisher (1939), Limbaugh (1961) and Hall and Schaller (1964) for California otters. With the stone lying on the otter's chest, the clam was struck against it with several quick, hard blows until the shell itself or the hinge was broken. Generally otters appeared to be non-selective when striking the clam against the rock, although one otter consistently struck the hinge area which usually separated with three or four blows. None of the otters that I have observed used the same rock on more than one occasion; they usually discarded each rock as soon as the clam was opened. The rock was discarded by allowing it to slip off the chest while the animal was eating.

Mussels were obtained from the bottom by pulling up the holdfasts of Laminaria sp. to which they were attached in clusters. The otter then lay on the surface with the algal frond draped across its body, and picked individual mussels off with its forepaws, and ate them directly. At

no time did the otters eat any part of the algae; the plant was quickly discarded as soon as the mussels were eaten.

Octopuses were eaten completely. I agree with Kenyon (1969:118) who states that they are "eaten with particular enthusiasm and wild otters appear to relish them". On August 6, 1971, I observed a female catch and eat an octopus that was about 60 cm from tip to tip across the tentacles. The otter took more than six minutes to consume it entirely. Any scraps or pieces dropped during the process were usually retrieved. The otter held the body of the octopus in his paws and bit into an arm or the body while pulling away with its head and pushing away with its paws. This left a long stringy piece of octopus in the otter's mouth, which was then stuffed into the mouth with the paws, while the rest of the octopus was held in the axilla or against the chest with an elbow. This procedure was repeated until the entire octopus was eaten.

Sea stars did not appear to be a preferred food. According to Kenyon (1969:119), "the otter usually tears off and eats one or two arms of a sea star, then loses interest and discards the remainder". The otters in Montague Strait reacted in much the same way. Although Kenyon (1969) found evidence that several species of sea stars are eaten by the Aleutian otters, I found evidence of only one species (Evasterias troschelii) being eaten in Montague Strait,

though others (Dermasterias imbricata and Pycnopodia helianthoides) were present.

Sea cucumbers were rarely eaten by the otters of Montague Strait, and are apparently of minor importance to the Aleutian otters also (Kenyon, 1969). The usual procedure for eating sea cucumbers was to tear them open, select a portion of the viscera and part of the body wall, and discard the rest.

A total of 14 feeding periods was timed. Each began when other activities ceased and the otter dove for food; each ended when the last bit of food was eaten and some other activity was begun. These feeding periods ranged in length from 25 to 147 minutes and averaged 84.5 minutes. Elapsed times for eating at the surface during these 14 feeding periods ranged from 17 seconds for a clam to 6 minutes for an octopus, with a mean of 38 seconds (Table 5 for diving times). Table 6 shows the average times for consumption of each kind of food item.

Table 6. Average feeding times for individual food items measured in seconds.

Food Item	No. of Observations	Range	\bar{X} Surface Time in Seconds
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. Generally they feed on bottom-dwelling invertebrates, but will select fishes if the invertebrate supply is depleted (Kenyon, 1969 in Table 7). In Table 8 we see that mollusks comprised the most important single group of food items used in California and Prince William Sound, echinoderms were apparently most important in the Commander Islands and fishes were the most important in the Aleutians (Table 8). Crustaceans were second in importance at Pico Creek, California and in Montague Strait: mollusks were second in the Aleutians, and echinoderms were second at Point Lobos, California.

It is apparent that throughout most of their range, sea-otter populations are expanding (Kenyon, 1969). Along with this expansion, bottom communities are rapidly changing (Kenyon, 1969; Ebert, 1968; McLean 1962). A well known example of otters having an effect on bottom communities is the competition which exists between sea otters and abalone (Haliotis sp.) fishermen in California. Ebert (1968:41) says "evidence at Pico Creek and along the Monterey Peninsula indicates that as the sea otters move onto commercially valuable abalone beds south of Pico Creek, they will deplete these beds to such an extent that they will no longer support a commercial fishery".

Table 8. Percent frequency of occurrence of major food items in the diet of sea otters. Organisms from the Commander Islands study are shown according to relative abundance as indicated by plus signs.

Food item	Amchitka Isl. Pico Creek, Aleutian Isls. Calif. 1968)		Point Lobos Commander State Park, USSR Calif. (Barabash- Hall- Nikiforov, Schaller, 1933)		Montague Strait Alaska (This study)	
	By %	By %	By %	By %	By %	By %
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		0.4				
Total for Group	37	66.1		51.1		81.9
Crustaceans						
Crabs	Present	25.9		14.5	++	7
Spiny Lobster				0.6		
Total for Group		25.9		15.1		7
Echinoderms						
Sea Urchins	Present			32.8	+++	0.8
Sea Stars	Present			0.6		0.3
Sea Cucumbers	Present					1.2
Total for Group				33.4		
Fishes	50			0.2	++	.
All Others	13					10.8
Total	100	100		100		100

McLean (1962) found that a herd of California otters nearly exterminated a population of sea urchins (Strongylocentrotus franciscanus), while Kenyon (1969:128) noted that "small green sea urchins are abundant", although it is "impossible to find large individuals in the intertidal zone" at Amchitka Island. Kenyon (1969) presents evidence that suggests that large sea urchins were abundant prior to the expansion of the sea-otter population at Amchitka.

Sea urchins seem to be a relatively minor part of the otters' diet in Montague Strait also. I found no living sea urchins in the intertidal zone and only occasionally found a test, each of which was less than 3 cm across. Kenyon (1969:111) says 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 that I found on the beaches of Montague Strait, none showed this diagnostic purple stain. I conclude from these findings that sea urchins are of little importance to the sea otters in Montague Strait.

Fishes represent an important food source in the Aleutians when invertebrates become depleted. Kenyon (1969:110) says that "at Amchitka it appears that the otters fall into two groups -- those eating mostly fish and those eating mostly invertebrates". Since I did not see otters eating fishes in Montague Strait, I feel that fishes are not

important to these otters at this time. However, I was unable to determine whether the apparent lack of fishes in the otters' diet was due to preference or to their being unavailable. Certainly preference is an important factor. Vania (1966) found that otters captured in Montague Strait and held for transport refused to eat chum salmon (Oncorhynchus keta) and pink salmon (Oncorhynchus gorbuscha) for a period of 24 hours. During the latter part of the summer chum and pink salmon became abundant in my study area. After spawning began dead chum and pink salmon littered the beaches, however I did not see the otters eat either the living or dead salmon.

Relatively little use of rocks as tools for opening hard-shelled invertebrates has been observed in Alaska. Kenyon (1969) failed to observe this phenomenon in the wild, but saw a captive otter from Alaska pound a clam against the side of its cement pool. Perhaps the reason that rock pounding has not been observed in the Aleutians but has been observed in Montague Strait, can be attributed to the fact that, in the Aleutians, otters do not feed extensively on hard-shelled invertebrates, and do not need a rock. I agree with Kenyon (1969:84) who likens rock-pounding behavior in the sea otter to "the use of gravity by gulls and ravens". Kenyon (1969:84) felt that tool-using behavior is derived from "chest pounding, frustration behavior". I often

observed an otter pounding a clam on his chest when the clam appeared particularly difficult to bite open.

Limbaugh (1961) noted that otters used the same rocks on successive dives in California. I did not see otters use the same rock on successive occasion; when a rock was brought up on successive occasions it was different each time. Perhaps the best reason the otters of Montague Strait did not use the same rock on successive occasions was that the otter would probably find it impossible to hold a rock and dig for clams at the same time.

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, my observation show that the otters in Montague Strait frequently and successfully dig clams. According to Fitch (1953), S. giganteus and P. staminea are found at depths of 25 to 45 cm along the North Pacific coast, although Feder and Paul (pers. comm.) never found them deeper than 8 cm in Northern Prince William Sound.

It is my opinion that otters in general fed on clams in areas where they had been successful in the past, but had no specific means for determining the precise location of the bivalves. I think, rather, they dove to the bottom and started digging at random. If digging was unsuccessful and a sea star was available, the otter would take it in lieu of coming up without food. Once the otter started digging

he probably located the clam by touch. Paul Marhenke dove in the area where otters had fed and attempted to dig but visibility was obscured by a cloud of sediment and debris, thus negating the use of visual clues. Kenyon (1969) has shown that otters are capable of locating food by relying on tactile sense only. He demonstrated this by feeding captive otters. One otter fed by Kenyon was blind and another, using only its forepaws, selected a preferred food (Mytilus edulis) from a bucket which also contained small crabs (Pachygrapsus), pebbles of various sizes, and turbid water.

Although low clam densities were indicated by limited intertidal sampling where otters fed extensively on clams, I do not consider the results of my sampling efforts adequate to draw comparisons or conclusions at this time. It is difficult to understand how the otters can take large numbers of clams in view of the fact that it may take as long as seven years for these clams to reach the size which would make them of value as food items for the otters (Feder and Paul, pers. comm.). Two possibilities exist which may explain the otters' ability to take such large numbers of clams: either they do not do this over long periods of time or a much higher growth rate is found in this area than in Northern Prince William Sound by Feder and Paul.

I feel that the possibility exists that the present situation with the sea otters in California allows them to exploit a particular invertebrate they favor in one area and then move on to another area when that food source is depleted. This type of exploitation is especially possible in such areas as California where great expanses of empty habitat are found on either side of the populations. Kenyon (1969) has shown how otters can move out and occupy new adjacent habitat as the population grows.

It is apparent that sea otters are able to subsist on a wide variety of bottom-dwelling invertebrates and fishes. They seem to have local preferences but are able to take advantage of and exploit whatever is available in their area to satisfy their food needs. As the otter populations increase they cause drastic changes in bottom communities, but can be expected eventually to reach an ecological equilibrium with their food supply as they must have done in the past.

TERRITORIALITY AND GENERAL BEHAVIOR

STUDY AREA

Observations of territoriality in the sea otter were made in a small lagoon on the south side of Stockdale Harbor, Montague Island during the months of July and August, 1971. I have called this lagoon Ookshilk (Fig. 5), after the Chugach Eskimo Village which was once located there. The majority of my observations were made from that village site.

The lagoon is made up of three arms (A, B, and C in Fig. 5) and a large central area with a small island. The total water surface area is about 2 sq. km. Arm A is about 1.5 km long by 0.25 km wide, arm B is about 1 km long by 0.75 km wide, arm C is about 0.75 km long by 0.25 km wide and the central area is about 1 km long by 0.67 km wide. The depth of the lagoon averaged about 4.8 m. The lagoon is completely enclosed by land except the entrance which is about 30 m wide and through which all the water entering and leaving the lagoon must pass. As the water level in the lagoon rises and falls with the normal tidal cycle, the entrance becomes a very swift salt water river, in which the direction of flow changes every six hours.

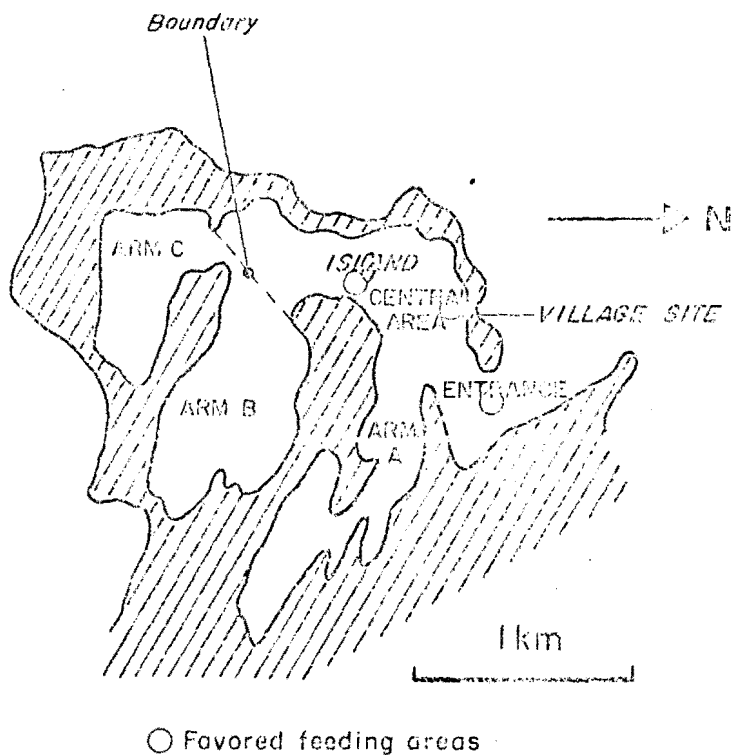


Figure 5. Ookshilk Lagoon showing territories used by two male otters during July and August 1971. Male 1 occupied arm A and the central area, Male 2 occupied arms B and C; the boundary shown separated the two territories.

METHODS

Binoculars and spotting scopes were used to aid in observation. Observation distances ranged from 50 m to 300 m. Observations were made in the lagoon intermittently until July 2, when it was noticed that a male sea otter was occupying the lagoon accompanied by a female and pup. Observations were made continuously, beginning between 6:00 A.M. and 10:00 A.M. and ending between 3:00 P.M. and 9:00 P.M. These intensive observations continued through July 13, when the female and the pup left the lagoon. After this, intermittent observations were again made in the lagoon until September 1.

Otters which were recognized throughout the summer were identified by specific characteristics such as very light head, scars on the nose and general size. Certain behavioral characteristics were also noticed, such as habituation to the boat and individual diving methods. One otter which was seen consistently throughout the summer became habituated to the presence of the boat by allowing it to come closer as time passed while another consistently dove backward from a supine position. This behavior was not noticed in any other otters in the area.

RESULTS

Territorial Behavior

One male otter established, occupied, and defended a territory in the lagoon. This animal was designated Male 1. The territory of Male 1 comprised the entrance, the central area and arm A. A second male, designated Male 2, occupied the rest of the lagoon, i.e. arms B and C. The territories of these animals are referred to hereafter as "territory M 1" and "territory M 2", respectively. Territory M 1 was approximately 1.25 sq. km in area and territory M 2 was approximately 0.75 sq. km.

The territoriality was manifested by the two males by their defense of their respective areas, fighting, border patrolling, and territorial invasion. On July 2 it was noticed that a female and a pup had joined Male 1 in his territory and remained near him most of the time. The female and pup stayed constantly in territory M 1 until July 13.

Territorial defense:

Chasing by Male 1 occurred whenever Male 2 was discovered in territory M 1. When Male 1 saw Male 2 from a distance, he frequently swam under water, and then

surfaced within 2 m of Male 2, whereupon Male 2 dove, then surfaced a short distance away. Male 1 then dove immediately, surfaced just behind Male 2, and the chase then proceeded with a series of short shallow dives. Each shallow dive was followed by a leap, often nearly out of the water, by both males. I subsequently called this behavior "porpoising" although the otters usually came further out of the water than a porpoise would. It was used by otters when chasing or being chased as well as when escaping from a boat or airplane.

The chase was always from territory M 1 to M 2 and usually ended at the border between the territories. After the chase, each animal immediately began to groom himself. One such chase occurred in the central area of the lagoon during ebb tide, when the water was swiftly moving out of the lagoon, causing a strong current along the entire central area. Even under these conditions, Male 2 chose to return to his own territory, rather than leave the lagoon. The only time that Male 2 attempted to escape away from his own territory was when a boat was between him and his territory. In other words, he was in territory M 1 and, faced with the choice of the boat, Male 1, or escape by leaving the lagoon, he chose the latter.

Fighting:

Actual physical contact between Male 1 and 2 was

observed on only two occasions during the observation period. The first was on July 6, when the female, pup and Male 1 were together. A fight between Male 1 and Male 2 took place after Male 2 had invaded Male 1's territory and was chased back to his own territory. After the chase, Male 1 appeared to turn back toward his own territory, when Male 2 started after him. Male 1 turned back and lunged toward Male 2, attempting to bite him on the neck. Following this, both otters remained vertical in the water and lunged at one another. Between lunges, each moved his head rapidly from side to side. Whenever one succeeded in grasping the other with his teeth, much thrashing and splashing occurred as the one apparently attempted to upset the other. Both otters could be heard gasping for air from several hundred meters away. The fight ended as suddenly as it had begun, and each male then vigorously shook his head and shoulders. Male 1 quickly returned to the female and pup, grooming on the way. Male 2 moved out of sight into arm B.

The second fight took place when Male 2 was chased from his territory by a boat and was blocked from returning by the same boat. The only alternatives open to Male 2 were to stay in territory M 1 or to leave the lagoon entirely. Male 2 chose the former. Male 1 discovered him and immediately gave chase. Male 2 "porpoised" a

short distance toward the lagoon entrance, then turned to face Male 1. Each lunged at the other several times; Male 2 then turned and "porpoised" out of the lagoon.

Border patrolling:

While the female and pup stayed with Male 1, he repeatedly patrolled the borders of his territory. He usually left the female and pup while they were feeding and swam toward the lagoon entrance, then into arm A, then along the boundary between his territory and that of Male 2, then around the island and along the north side of the central area, and towards the entrance. Generally, during the course of this circuit, Male 1 swam on his back, kicking and splashing with his hind limbs more than was normally required for propulsion, and splashing water onto himself with his paws. This splashing action was extremely noisy and highly visible, and I can only interpret it as an acoustic and visual display of territoriality, i.e. as a warning to potential intruders.

While Male 1 patrolled the borders of his territory, Male 2 responded with very cryptic tactics when invading or crossing Male 1's territory. Whenever Male 2 entered or neared Male 1's territory, he did so either underwater or by swimming on his abdomen with only his eyes and nose out of the water. If it became necessary for him to

dive, he simply sank out of sight, seal-like, with a minimum of commotion.

Breeding behavior

Copulation between the female and Male 1 was attempted on July 2, 3, 7, 8, and 9. Each attempt lasted from 3 to 10 minutes and appeared to follow the same sequence of events as described by Kenyon (1969). The pup appeared to be jealous of the female's receptiveness of the male, for it interfered each time copulation was attempted. It did this by climbing over the pair and pushing Male 1 away.

Routine Activities

The daily activities of Male 1, the female, and the pup, were divided into four kinds: feeding, grooming, resting, and swimming. Feeding activities consisted of diving to obtain food, bringing it up and consuming it. This was described fully in the previous chapter. Grooming activity has been well described by Kenyon (1969), and consists of cleaning the fur by rubbing with the forepaws and combing it with the claws. Otters rest by floating on their back with the paws on their chest or muzzle and their hind flippers folded over each other on the abdomen. Often the head is held completely out of the water while resting. Throughout the rest period the otters often awoke, looked

around, and then went back to sleep. They awoke and moved away in response to the slightest noise which I made; even the faint click of my camera shutter disturbed them. Limbaugh (1961) described similar behavior of otters in California.

The otters swam, usually on their back, propelling themselves with their hind flippers. They often turned over on their side in order to see where they were going. Swimming has also been described in detail by Kenyon (1969).

An example of the routine activities of Male 1, the female, and the pup during one day (July 9) is shown in Table 9, the actual and relative amounts of time spent in each activity by these otters is shown.

Often the pup attempted to nurse or to rest in the nursing position with its head on the female's abdomen. Since I could not usually recognize whether the pup was actually nursing or merely resting in the nursing position, I was unable to record the total nursing time. I fully agree with Kenyon (1969) who also had difficulties timing the nursing period since large pups often fell asleep within five minutes in the nursing position. Kenyon (1969) felt that each nursing period lasted from three to five minutes.

Table 9. Time spent in each of four activities by Male 1, the female, and the pup in Ookshilk Lagoon on July 9, 1971. The female and pup carried out all activities simultaneously and are shown together. \bar{X} indicates the mean length of time the activity lasted in minutes.

Activity	Male			Female and Pup		
	Time	\bar{X}	% of Total	Time	\bar{X}	% of Total
Groom	61	10	9.8	44	5.5	7.1
Feed	54	27	8.5	240	80	38.7
Rest	426	61	68.9	280	93	45.8
Swim	79	7.9	12.8	56	7	8.4
Total	620		100%	620		100%

DISCUSSION

Kenyon (1969) concluded that territoriality is but weakly expressed in the sea otter. In general I agree with this and feel that the events that I observed and have described here were made possible by the unusual conditions provided by the restricted area of the lagoon. It would seem to be difficult for an otter to defend a territory along an open coastline.

The motivation for the territorial defense described here appeared to be strengthened by the presence of the female and pup although both males remained in, and defended their territories when no females were present. Also both males continued to feed within their respective territories. Vandevere (1970) found evidence of territoriality in sea otters in California, though the males defending territories seemed to be less successful breeders than those which were not defending territories. Prior to the observation reported here, territoriality has not been reported from Alaska. Karl Schneider (pers. comm.) wrote me:

While Kenyon did not observe it, there is strong evidence that breeding males do exhibit behavior that might be considered territorial, although they usually do not defend a geographical territory. I suspect that it is more a spatial separation with no defined boundaries. This behavior is not obvious but it is sufficiently strong to regulate the number of males in female areas.

Ewer (1968:67) says that "the primary function of territory is to ensure that the holder has at his disposal an area sufficient to provide for his needs in terms of food and shelter", and that mating is a secondary function. My observations indicate that food was equally available in the waters immediately adjacent to the lagoon as well as within the lagoon. This suggests that, for sea otters, food probably plays little if any role in the formation and importance of the territory.

Kenyon (1969) says that it would be difficult for a mother with a pup to engage in the mating period of several days duration due to the extreme demands placed on her by both the pup and the mating cycle which Kenyon describes fully. Barabash-Nikiforov (1947) observed females with newborn and yearling pups indicating that possibly, in the Commander Islands, pups remain with the mother through the breeding cycle and even after the birth of the new pup. Murie (1940) described a situation in which a female engaged in coitus while her pup remained nearby.

Although it may be uncommon for a female with nursing pup to engage in and complete the breeding cycle with a male, my observations indicated that it presented no particular hardship for either the female or the pup. Copulation was attempted on several occasions, and the adult pair and pup remained together for at least eleven days.

However, the pup was quite large, nearly the same size as the female, and was beginning to secure food for himself. In my opinion, the pup was nearly independent and probably became fully independent before the summer ended. I did not see the male take food from the female as described by Vandever (1970).

After the female and pup left the lagoon, Male 1 often left the lagoon for short periods to cruise outside of the entrance. While cruising, he swam on his abdomen, rather than his back, and inspected the anogenital area of each female that he encountered, apparently searching for a receptive female, as described by Kenyon (1969).

The activities summarized in Table 9 represent those of a male and female in the breeding sequence. Kenyon (1969) also recorded the activities of an adult pair in the breeding sequence August 20: he found that the male spent 52% of its time feeding, in contrast to only 3.5% on July 9, in this study (Table 9). Kenyon (1969) also recorded the activities of a captive otter and found that it spent only 9% of the time in feeding activities. He attributed this low feeding activity to the readily available food supply to the otter. This could also explain the low feeding activity in the otters I observed; it is quite likely that food is much easier for the otters to obtain in Montague Strait than at Amchitka Island.

Weather probably plays a part in the daily activities of otters. The data in Table 9 was recorded on a bright, warm, clear day with temperatures reaching 20° to 25°C. This was one of the warmest days to that date, and the otters became somewhat lethargic.

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