FEEDING HABITS AND FEEDING GROUNDS OF THE NORTHERN ELEPHANT SEAL

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ABSTRACT.—Prey species consumed by northern elephant seals were identified from the stomach and throat contents of dead seals and from observations of prey captured. Their diet is catholic, consisting of a variety of pelagic, deep water squid, Pacific hake, sharks, rays, and ratfish. Feeding grounds of elephant seals were inferred from sightings of tagged elephant seals at non-rookery locations. Feeding areas extended from northern Baja California to northern Vancouver Island. Juveniles of both sexes and adult males moved north from their haul out sites in search of food, travelling furthest north during the summer. A few sightings suggested that adult females remain in the vicinity of the rookeries where they breed.

Northern elephant seals, *Mirounga angustirostris,* breed and molt in large aggregations on land in Baja California and California, but spend the majority of the year feeding at sea. The large breeding aggregations are easy to observe and a great deal is known about the elephant seal's reproductive behavior (Le Boeuf, 1974; Reiter et al., 1981). In contrast, the animals are rarely observed at sea and little is known about their feeding biology.

Existing information on the food habits of the northern elephant seal comes from the examination of stomach contents of only nine specimens (Huey, 1930; Freiberg and Dumas, 1954; Cowan and Guiguet, 1956; Morejohn and Baltz, 1970; Antonelis and Fiscus, 1980; Jones, 1981). The remains of sharks, ratfish, squids, and bony fish were identified. Albro (1980) observed an elephant seal feeding on a dogfish shark at sea.

The elephant seal's distribution while feeding is also poorly known. Individuals have been seen on shore away from rookeries, on rare occasions, from California to Alaska and in British Columbia (Willett, 1943; Freiberg and Dumas, 1954; Cowan and Guiguet, 1956; Morejohn and Baltz, 1970; Antonelis and Fiscus, 1980; Jones, 1981). They have also been seen or captured at sea off California, Oregon, and Washington (Huey, 1930; Brown and Norris, 1956; Scheffer, 1964; Albro, 1980).

The purpose of this paper is to document feeding habits and feeding sites of northern elephant seals. We present data from prey remains found in dead seals and observations of seals feeding. These data were gathered opportunistically and are only a qualitative description of the seal's diet. We also present reports of tagged seals sighted away from rookeries, data which suggest where the animals feed.

METHODS

Food habits.—Information on the food habits of 27 elephant seals was obtained. Data were collected from northern Baja California to Oregon between 1953 and 1982. Most of these data came from specimens collected on San Miguel Island in southern California and Año Nuevo Island and the nearby mainland in central California between 1976 and 1982.

We examined the stomach contents of 18 seals, adults and juveniles of both sexes. Sixteen of them died on rookeries during the breeding season and two of them washed up dead away from a rookery. When a dead seal was discovered, we removed the stomach after tying off the esophagus and intestine. The stomach was transported to the laboratory where it was examined immediately or frozen. Stomach contents were examined by cutting the stomach longitudinally and turning it inside out. In many cases, fragments of prey remains could be seen and were picked off the stomach lining. When sand and rocks were present, all stomach contents were washed in a tray and sifted through cheese cloth. Organic items, mainly cephalopod beaks and teleost fish otoliths, were picked out macroscopically, stored in 70% ethanol, and sent to experts for identification (see Clarke, 1962, 1966; Fitch and Brownell, 1968; Romer, 1970).

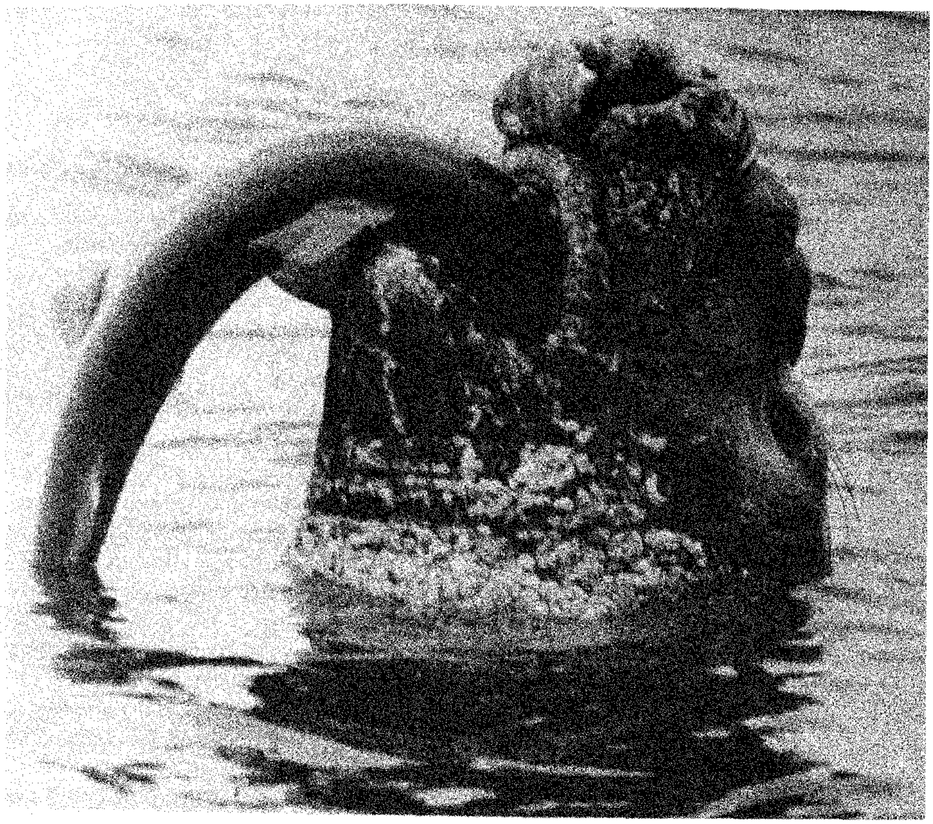

FIG. 1.—An adult bull elephant seal feeding on a dogfish, *Squalus acanthis*, near the San Juan Islands, Washington. (Photo by R. Hoelzel).

We also report information gathered by other biologists (see Acknowledgments). We were given descriptions of prey remains found in stomachs from four elephant seals which washed ashore dead on non-rookery sites. Five more dead or moribund seals were found with prey remains trapped in their mouth or throat and four seals were observed feeding on recognizable prey at sea (Fig. 1).

To analyze diet as a function of age and sex, we placed the animals into one of three categories. Juveniles were females less than 3 years and males less than 5 years old, mature males were age 5 and older, and adult females were age 3 and older. Untagged seals (see below) of unknown age were placed in one of the above categories based on length and estimated weight.

Distribution away from rookeries.—Elephant seals breed at six major rookeries and seven minor ones from central Baja California to central California (Le Boeuf et al., 1974; Le Boeuf, 1981). They depart these rookeries to feed twice annually for long periods (Le Boeuf et al., 1974). We assume that seals seen away from rookeries were feeding in the area or were enroute to or from feeding locations. Thus, concentrations of sightings are likely to represent feeding grounds.

We assembled all sightings of tagged animals made away from rookeries from 1968 to 1982. Tagging operations are described in Le Boeuf et al. (1974) and Reiter et al. (1978). Le Boeuf and colleagues have tagged pups every year since 1968 on one or several rookeries. Until June 1982 tag reading effort away from rookeries depended on scientists' and other people's interest in reporting tagged pinnipeds. In June 1982 we conducted a research expedition for the purpose of obtaining sightings of tagged and untagged elephant seals from central California to Vancouver Island. We also made inquiries with biologists throughout the area, seeking reports of elephant seal sightings.

Most tag sightings were of beached seals, so these data reveal only latitudinal distribution of feeding

TABLE 1.—*Prey species found in northern elephant seals. The frequency of occurrence of a prey species is the number of seals in which that prey species was identified. Subtotals add up to more than 27 because any seal that had more than one species in its stomach appears more than once in the table (R = rookery, NR = non-rookery; S = identified in stomach contents, M = identified trapped in mouth, O = observed eaten).*

Prey species	Frequency of occurrence	Collection site	Collection method
Teleost fish			
Pacific hake, *Merluccius productus*	4	NR	S
Pink rockfish, *Sebastes eos*	1	NR	M
Rockfish, *Sebastes* sp.	2	NR	S, M
Cartilaginous fish			
Brown catshark, *Apristurus brunneus*, eggcase	1	NR	S
Ratfish, *Hydrolagus colliei*	3	NR	M
Stingray, *Urolophus halleri*	2	NR	M, O
Blue shark, *Prionace glauca*	1	NR	O
Angel shark, *Squatina californica*	1	NR	O
Cephalopods			
Commerical squid, *Loligo opalescens*	2	NR, R	S
Onychoteuthis borealjaponicus	5	R	S
Moroteuthis robusta	1	NR	S
Histioteuthis sp.	3	NR	S
Gonatopsis sp. (probably *borealis*)	5	NR, R	S
Taningia danae	1	R	S
Octopoteuthis deletron	7	R	S
Chiroteuthis calyx	1	R	S
Cranchidae, two unidentified genera	4	R	S
Octopoda, two unidentified species	2	R	S
Total fish (3 species)	8		
Total cartilaginous fish (5 species)	8		
Total cephalopods (12 species)	14		
Grand total (20 species)	27		

grounds, not distance from shore or depth at which the seals feed. Some information on these subjects, however, is provided by nine seals caught at sea in fishing gear. Five ships reported the depth of their fishing gear and their distance from shore when a seal was captured.

Sighting distribution was analyzed as a function of a seal's birthplace by dividing the tag sightings into three groups: the three major Mexican rookeries, the two major southern California rookeries, and the two central California rookeries. Age and sex classes were separated as described above. Except when stated otherwise, statistical significance was tested using the Kruskal-Wallis test.

RESULTS

Elephant seal diet.—Eighteen of the 22 stomachs examined contained identifiable prey remains. Twelve of sixteen stomachs collected from animals found on rookeries contained squid beaks and no other prey remains, but sometimes sand. The other four stomachs contained no prey remains, but did contain sand and broken shells. Many of the seals which died on rookeries had not entered the water for as long as 35 days yet still had squid beaks in their stomachs. All six stomachs from animals collected away from rookeries contained prey remains. One contained only a badly worn otolith. The others had squid beaks, fish otoliths, numerous tiny gastropod and bivalve shells, rocks, and sand.

We identified 15 prey species in these stomachs; 12 of them were squids (Table 1). The two most frequently occurring prey were *Octopoteuthis deletron* and *Onychoteuthis borealjaponicus*, large, abundant, pelagic squid found in deep, offshore waters (Roper and Young, 1973). One bony fish species, the Pacific hake, was found frequently. It is an abundant, pelagic, offshore

TABLE 2.—*Frequency of tagged elephant seals sighted away from rookeries by age and tagging location. Except for mature males, tagging location is synonymous with birthplace.*

	Tagging location							
	Mexico			Southern California		Central California		
Age	Isla Cedros	Isla San Benito	Isla de Guadalupe	San Nicolas Island	San Miguel Island	Año Nuevo	Farallons	Total
<1 year	0	1	10	7	18	40	2	78
1–2 years	1	1	15	2	10	61	0	90
2–4 years	0	0	2	1	3	11	0	17
Adult female	0	0	0	1	0	1	1	3
Mature male	0	0	2	0	0	7	0	9
Total	1	2	29	11	31	120	3	197

species that can grow up to 85 cm in length (Nelson and Larkins, 1970; Miller and Lea, 1972; Fiscus, 1979). One rockfish and one eggcase from a shark also were identified.

Four species of cartilaginous fishes and two more bony fishes were identified from remains caught in a seal's mouth and from observations of seals feeding (Table 1). The most frequent prey identified from these techniques were ratfish and rockfish.

The kind of prey species identified varied with the technique used (Table 1). Squids were identified only in stomach contents, whereas sharks and rays were found only in cases where a seal was observed feeding or was found with prey spines trapped in its mouth. However, these comparisons are based on small sample sizes.

The sample size was too small to demonstrate a relationship between prey size and the size or age of the predator. However, all three cases in which a seal was observed attacking a large shark or ray (Fig. 1) involved an adult male elephant seal, and only juvenile seals were found with ratfish and stingray spines caught in their mouths. Animals of all ages and both sexes fed on fish and squid.

Distribution away from rookeries.—Of the 190 seals seen at non-rookery locations, five seals were seen twice and one was seen three times, yielding a total of 197 tag reports. Seals of all ages born at several rookeries were included (Table 2). The majority of tagged seals sighted had been born at Año Nuevo (61%) and the age group most commonly observed were juveniles (94% of sightings). Twenty-five of these seals were resighted later at a rookery.

Juvenile seals were seen principally in March and April, both in their first year at age 2–3 months and in their second year at age 14–15 months. There was another small peak of sightings in autumn and some sightings in every month.

Most seals trapped in fishing gear were caught around 200 m below the surface (four were caught at 185–231 m, one at 31 m). Two of these were caught at the ocean bottom (both at about 200 m). Four were captured 16–27 km from shore and one 224 km offshore over a seamount.

Two tag reports reveal extraordinary travels by juvenile elephant seals. A 9 month old seal born at Año Nuevo Island was found dead 4,000 km north on Amaknak Island, Aleutian Islands, Alaska (R. Nelson, pers. comm.). A yearling born at San Miguel Island was seen on Midway Island, Hawaii (G. Blazs, pers. comm.), 4,700 km west of its birthplace. Finally, an untagged yearling we observed midway up in the Gulf of California in June represents the southernmost elephant seal record. The fastest long distance movement we documented was by a 2–3 year old male, that was seen in southern California in March and then off the Queen Charlotte Islands in British Columbia in July of the same year. It had travelled 2,500 km in less than 125 days.

Most juvenile seals were seen north of their birthplace (151 seen north, 33 south). This difference is statistically significant ($\chi^2 = 76$, d.f. $= 1$, $P < 0.05$). The pattern was consistent for all rookery areas (Fig. 2).

Juvenile seals from northern rookeries were seen further north than seals born at southern

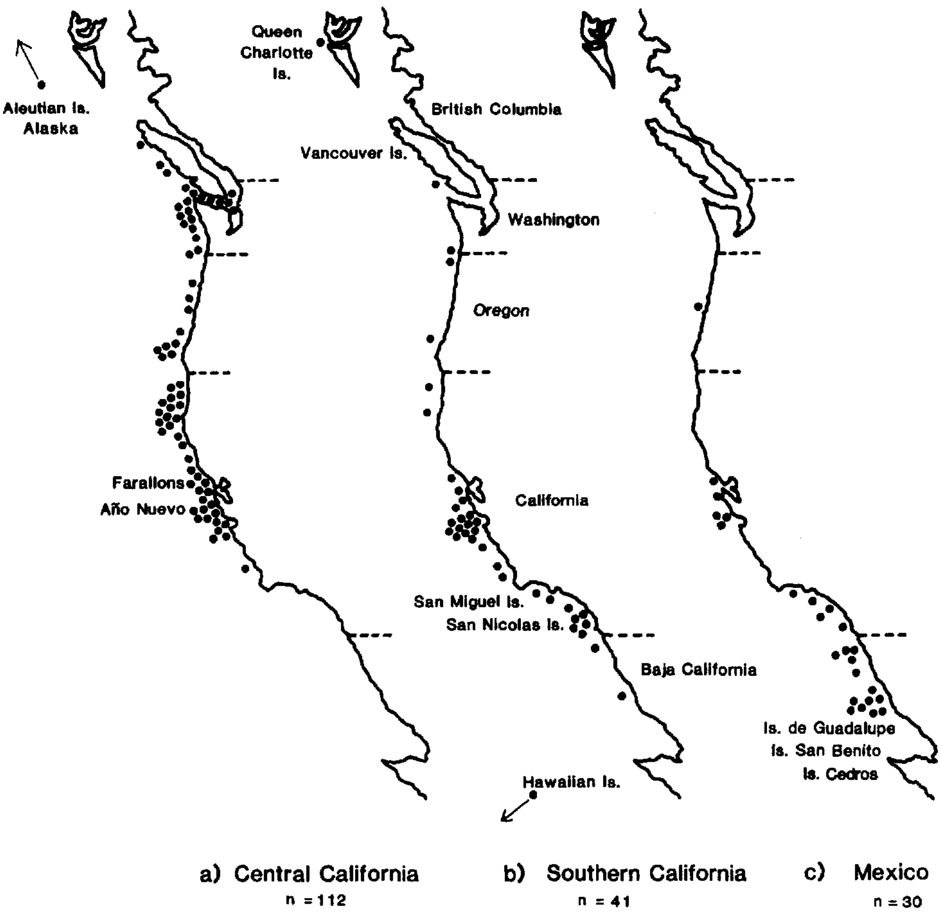

FIG. 2.—Distribution of tag sightings of juvenile elephant seals away from rookeries. a) Juveniles born in central California. b) Juveniles born in southern California. c) Juveniles born at Mexican rookeries. Two sightings in Alaska and Hawaii are indicated with arrows; they both fall well off the map.

rookeries (Fig. 2). Seals born in central California were commonly seen as far north as British Columbia and concentrated in two areas, northern California and around the southern end of Vancouver Island (mean sighting latitude, 41.6°N). Seals born in southern California were commonly seen in central California and scattered much further north (mean, 36.9°N). Mexican-born seals congregated in southern California (mean, 33.2°N). The mean latitudes for the three rookery groups are significantly different ($\chi^2 = 77.8$, d.f. $= 2$, $P < 0.05$).

Juveniles were seen further north in the summer than in any other season. This pattern was similar for juveniles from all rookeries (Fig. 3). For Año Nuevo and Mexico alone and for all rookeries combined the null hypothesis that seals were seen at the same latitude throughout the year can be rejected ($\chi^2 = 10.6$, 8.5, 21.2 respectively, d.f. $= 3$, $P < 0.05$).

Juvenile males and females were seen equally frequently and at the same latitude. Males from all rookery areas were seen at a mean of 39.5°N ($n = 78$), females at 39.0°N ($n = 77$). Neither the difference in sighting frequency nor latitude is significant ($\chi^2 = 0.07$ and 0.05 respectively, d.f. $= 1$, $P > 0.05$). For Año Nuevo born seals the sample size was large enough

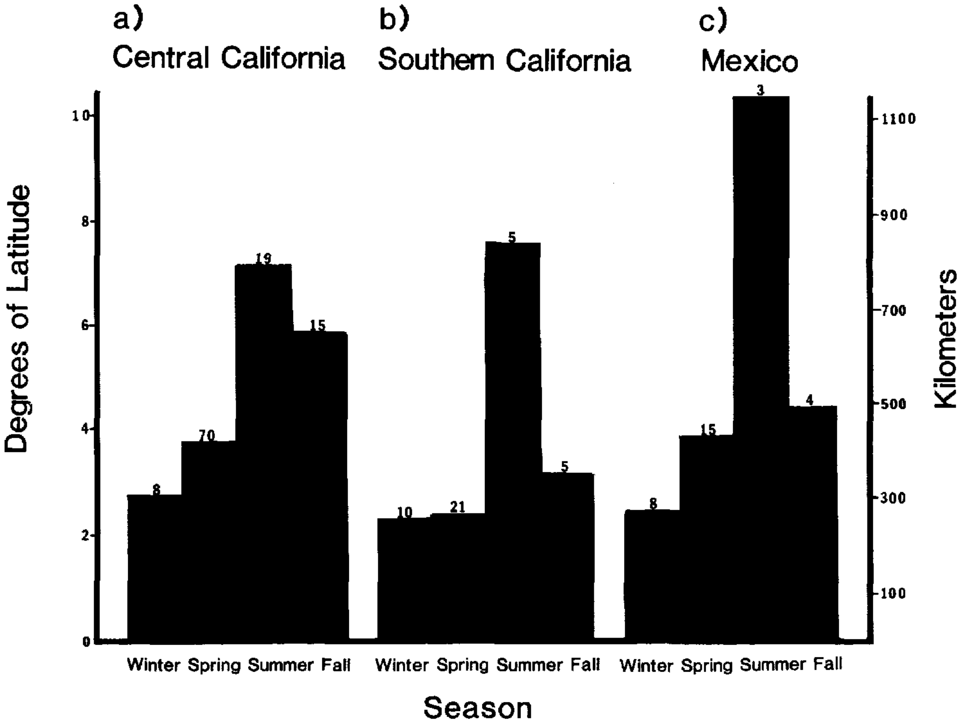

FIG. 3.—Mean latitude of tag sightings of juveniles away from rookeries as a function of season. The latitude is expressed as distance from the birth site, thus aligning the three sets of rookeries with respect to latitude. All averages are above the horizontal axis, or north of the birth site. One degree of latitude is equal to 111 km. Numbers above each bar are the sample size. a) Juveniles born in central California. b) Juveniles born in southern California. c) Juveniles born in Mexico.

to compare seasonal variation in sighting latitude by sex. Male and female patterns were nearly identical and similar to the combined pattern (see Fig. 3).

Mature males, which had been tagged as subadults, were seen on two occasions far north of their breeding site during the spring and late summer. One male tagged at Isla de Guadalupe, Mexico, was seen in central California in April. Another male tagged at Año Nuevo Island was seen near Vancouver Island in September. All other sightings were in winter near the male's rookery.

An untagged adult male was reported to us from southern Alaska in February (D. Waarvik, pers. comm.). In June 1982 we saw two untagged males near the southern end of Vancouver Island. We observed one tagged juvenile (a 4-year-old male born at Año Nuevo) off the Oregon coast. We received 15 reports of untagged males from the San Juan Islands off the southeastern tip of Vancouver Island (reports collected over several years by the Moclips Cetological Society, Friday Harbor, Washington). All were mature males observed between 1 April and 17 May, or 18 August and 28 September, although observations were made throughout the year. We also received several reports of mature males around Barkley Sound on the southwestern side of Vancouver Island (S. Leader, pers. comm.).

Three tagged adult females were seen near the latitude of their rookery during the summer, in June 1968, July 1971, and September 1978. One was on a non-rookery island off southern California, and two more were on the mainland in central California. An untagged female was reported to us in southern California in August.

TABLE 3.—*Prey of northern elephant seals from previous accounts.**

Prey species	Number of reports
Bony fish	
Pacific hake, *Merluccius productus*	1
Rockfish, *Sebastes* sp.	1
Pacific sanddab, *Citharichthyes sordidus*	1
Flounder, Pleuronectidae, unidentified genus	1
Cusk-eel, *Otophidium taylori*	1
Midshipman, *Porichthyes notatus*	1
Cartilaginous fish	
Swell shark, *Cephaloscyllium ventriosum* (=*Catulus ater*)	1
Dogfish, *Squalus acanthis*	2
Skate, *Raja* sp.	1
Brown catshark, *Apristurus brunneus* eggcase	2
Shark or skate, unidentified species, Elasmobranchia	1
Ratfish, *Hydrolagus colliei*	1
Cephalopods	
Commercial squid, *Loligo opalescens*	1
Gonatus, two spp.	1
Gonatopsis sp.	1
Chiroteuthis sp.	1
Octopoteuthis sp.	1
Cuttlefish, *Rossia pacifica*	1
Onychoteuthis borealjaponicus	1
Octopus sp.	1
Jawless fish	
Lamprey, *Lampetra tridentata*	2
Hagfish, *Eptatretus* sp.	1

* Huey (1930), Freiberg and Dumas (1954), Cowan and Guiguet (1956), Morejohn and Baltz (1970), Albro (1980), Antonelis and Fiscus (1980), and Jones (1981).

We checked for differences in distribution between healthy and sick, dead, or wounded juveniles. Healthy juveniles from Año Nuevo were found more than two degrees latitude further north than unhealthy ones (43.1°N versus 40.5°N), a significant difference ($\chi^2 = 8.4$, d.f. = 1, $P < 0.05$). However, the seasonal shift in latitude shown by unhealthy seals was identical to that shown by healthy ones. When juveniles from all rookeries were combined, the difference in distribution between healthy and unhealthy seals in mean latitude vanished (healthy at 38.7°N, unhealthy at 39.0°N, $\chi^2 = 0.4$, d.f. = 1, $P > 0.05$). The seasonal shifts in latitude remained identical. Thus we combined sightings of healthy and unhealthy seals in Figs. 2 and 3. Data were insufficient to make such comparisons for adult sightings.

DISCUSSION

Our results substantiate previous accounts in showing that elephant seals eat squid, fish, sharks, and rays, and that cephalopods are the most frequent prey consumed (Table 3). We identified nine of the species appearing in earlier reports. In addition, we identified seven new squids and three new sharks and rays as elephant seal prey. These were the squids *Moroteuthis robusta*, *Histioteuthis* sp., *Taningia danae*, and an unidentified species in the family Cranchidae, and the angel shark, blue shark, and stingray. At present, 30 species have been identified as northern elephant seal prey.

Caution must be exercised in interpreting these feeding data. Well digested stomach contents might overestimate the proportion of squid in the diet, because squid beaks are more resistant to digestion than fish otoliths (Scheffer, 1955). We found squid beaks but never otoliths in the stomachs of seals who had not fed for 35 days. This may be a result of differential digestion rates. In addition, there are limitations to each technique for evaluating diet (see Table 1). For example, it is not likely that a seal would be observed at the surface eating a squid, although sharks were seen being captured in this way. Moreover, sample sizes were small.

Other pinnipeds in the northern Pacific feed on squids and fishes. However, no other species feeds on the variety of squids that elephant seals do. For example, Fiscus and Kajimura (1965, 1967) collected 486 fur seal, *Callorhinus ursinus*, stomachs along the west coast of North America and found only seven cephalopod species, compared to 15 species known from elephant seal stomachs. Harbor seals, *Phoca vitulina*, and California and Steller's sea lions, *Zalophus californianus* and *Eumetopias jubata*, also feed on few squids (Scheffer and Sperry, 1931; Antonelis and Fiscus, 1980). Sharks have rarely been identified as prey of fur seals (Shultz and Rafn, 1936; May, 1937; Fiscus and Kajimura, 1965, 1967; Anonymous, 1970) and Steller's sea lions (Pike, 1958; Mathisen et al., 1962; Spalding, 1964; Fiscus and Baines, 1966), despite the fact that many studies involved sacrificing animals and taking fresh stomach contents in which shark remains should be identifiable. In contrast, the Pacific hake, which we found on several occasions as elephant seal prey, repeatedly turns up as an important component in the diet of many pinnipeds (Fiscus, 1979; Antonelis and Fiscus, 1980).

The most frequent prey species observed were the squids (*Octopoteuthis deletron, Onychoteuthis borealjaponicus*, gonatids, and cranchids) and a fish, the Pacific hake. These are pelagic animals that live far offshore in deep water over the continental slope. They migrate vertically each day, being found in extremely deep water during daylight and in the top 200–400 m at night (Nelson and Larkins, 1970; Roper and Young, 1973). Pacific hake are a schooling fish, one of the most abundant in California (Ahlstrom, 1965; Grinols and Tillman, 1970). Pelagic cephalopods probably live in schools as well. *Onychoteuthis* and gonatid squid are among the most abundant cephalopods in central California (Anderson, 1978). The habits and distribution of these animals suggest that elephant seals are pelagic, offshore predators who feed principally at night and whose favored prey are abundant schooling cephalopods and fishes. Corroboration for part of this hypothesis comes from aerial surveys during which elephant seals were observed far offshore over deep water (M. L. Bonnell and M. O. Pierson, pers. comm.).

Our results do not suggest how deeply elephant seals dive to capture their prey. Pacific hake and the pelagic cephalopods all occur within 200 m of the surface at night (Nelson and Larkins, 1970; Roper and Young, 1973). The seals captured by fishermen at around 200 m below the surface substantiate an earlier report by Scheffer (1964) and suggest a minimum diving depth. However, 200 m is not unusually deep for a pinniped (Kenyon and Scheffer, 1955; Sergeant, 1973). Weddell seals (*Leptonychotes weddelli*) dive to three times this depth (Kooyman, 1966). The widely held opinion that elephant seals dive extremely deeply (Anthony, 1924; Harrison and Kooyman, 1968) is neither supported nor refuted by the data on feeding habits. However, studies we have just begun using depth recorders confirm predictions of deep diving abilities.

Tag returns suggest that feeding grounds of elephant seals are north of their rookeries, extending from southern California (32°N) to northern Vancouver Island (52°N). Seals are segregated on the feeding grounds according to birthplace, with seals from northern rookeries feeding further north.

Seasonal migrations are also indicated by these results. Juvenile seals move northward from their rookeries during the summer by an average distance of 900 to 1,000 km. They return to haul out in the fall (Le Boeuf et al., 1974) with many seals hauling out at a rookery north of their birthplace (Reiter et al., 1981, Le Boeuf, 1981). During the winter, while adults are breeding, juveniles again go to sea, moving northward by a shorter distance than during the summer.

Curiously, juvenile seals from different rookeries do not move to the same location to feed. Rather, seals from each rookery migrate about the same distance northward, leaving seals segregated by birth site on the feeding grounds. Perhaps prey abundance increases in a steady gradient northward, but a seal is limited to a certain distance of travel because of the energetic cost of swimming or because it must return to haul out on schedule.

Adult males migrate northward during the spring and fall, hauling out in July and August to molt and from December to March to breed. Adult females are at sea for 10 weeks during the spring and again for about seven months during the summer and fall. They haul out in April and May to molt and January and February to breed. The available data show no northward movement by females but more are needed.

The northward movement during the summer is probably associated with food supply. Some indirect evidence can be found in the life cycle of one prey, the Pacific hake. Hake move inshore and northward during the summer to an area from central California to Washington (Nelson and Larkins, 1970). Elephant seal and California sea lion movements parallel those of the Pacific hake (Mate, 1975; Ainley et al., 1982).

Feeding habits and feeding sites of elephant seals remain poorly known compared to other northern Pacific pinnipeds such as the northern fur seal and Steller's sea lion. However, patterns emerge in the data we collected. Elephant seals feed well offshore on deep water species to a greater extent than other pinnipeds and they follow a pattern common among all animals by moving northward to feed during the summer.

Acknowledgments

The late Dr. C. L. Hubbs and the second author began collecting data on food habits of elephant seals in 1974. Some of the information on prey species we report here came from specimens examined by Hubbs or reported to him by A. Kelly, R. Gilmore, J. H. Wormuth, N. F. Marshall, J. Antrim, and D. Powell, and several workers from the San Diego Zoo. We also received reports of elephant seal food habits from R. J. Stroud, R. Jones, M. R. Graybill, S. Jeffries, and J. Stern.

J. Reiter and A. Huntley collected several of the stomachs we examined at Año Nuevo, and R. Gantt collected specimens at San Miguel Island. The Scripps Institution of Oceanography provided the research vessel "Ellen B. Scripps" for our work around Vancouver Island. The Center for Coastal Marine Studies at the University of California, Santa Cruz, provided logistical support for work on Año Nuevo Island.

We sought the assistance of several scientists in identifying prey remains. Squid beaks were identified by C. H. Fiscus, M. Clarke, J. R. Raymond Ally, and E. Chu. Otoliths were identified by J. E. Fitch and E. Chu. G. A. Antonelis provided useful information on his work on elephant seal food habits. C. W. Condit, S. Mesnick, M. Allaback, C. L. Ortiz, E. Keith, and A. Huntley read drafts of the manuscript and offered many useful suggestions.

This research was presented in partial fulfillment of the Ph.D. in biology at the University of California, Santa Cruz, by R. Condit. It was supported in part by National Science Foundation grant BSR 8117024-01 to B. J. Le Boeuf and a National Science Foundation predoctoral fellowship to R. Condit.

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Submitted 20 July 1983. Accepted 5 November 1983.