

Abstract.—Nine lactating northern fur seals *Callorhinus ursinus* from St. Paul Island, Alaska, were instrumented with time-depth recorders and head-mounted radio transmitters in July and August 1985. Seven females were subsequently located at least once while at sea. Diving patterns obtained from females' time-depth recorders were then associated with their foraging locations. Generally two diving patterns were found; shallow-diving and deep-diving. The deep-diving pattern appears to be associated with feeding throughout the day over the continental shelf in water less than 200 m deep. The shallow-diving pattern is generally restricted to nighttime hours and probably occurs mostly over deep water. An analysis of the occurrence of food in stomachs of lactating fur seals collected in the eastern Bering Sea from 1958 to 1974 also suggests that seals collected over the continental shelf were more likely to be feeding during the day. We examine differences in the way shallow- and deep-diving females forage and discuss possible prey associated with the two diving patterns.

Diving Patterns and Foraging Locations of Female Northern Fur Seals

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The sexually dimorphic northern fur seal *Callorhinus ursinus* is a polygynous colonial breeder. Arrival of adult females and pupping are highly synchronous; most pupping occurs between 21 June and 31 July. Females give birth to a single pup within 1–2 days after arrival at the same site each year. Copulation occurs approximately 5 days after parturition, and females remain on shore 1–2 days more before going to sea to feed (Gentry and Holt 1986). The first feeding trip is the shortest, and subsequent trips gradually become longer (Gentry and Holt 1986). Periods of feeding at sea alternate with visits ashore to suckle their pups. The period from birth to weaning is approximately 125 days.

Compared with the land phase of the fur seal's life history, little is known of their life and behavior at sea. Kooyman et al. (1976) first reported on depth and duration of dives for a lactating northern fur seal. General patterns of diving behavior for breeding females were described by Gentry et al. (1986c). They found that individual females exhibit two discrete types of diving patterns: shallow and deep. Some females, exhibiting both patterns, showed the deep-diving pattern on the first and last days of a trip and the shallow pattern on other days. Fur seals ex-

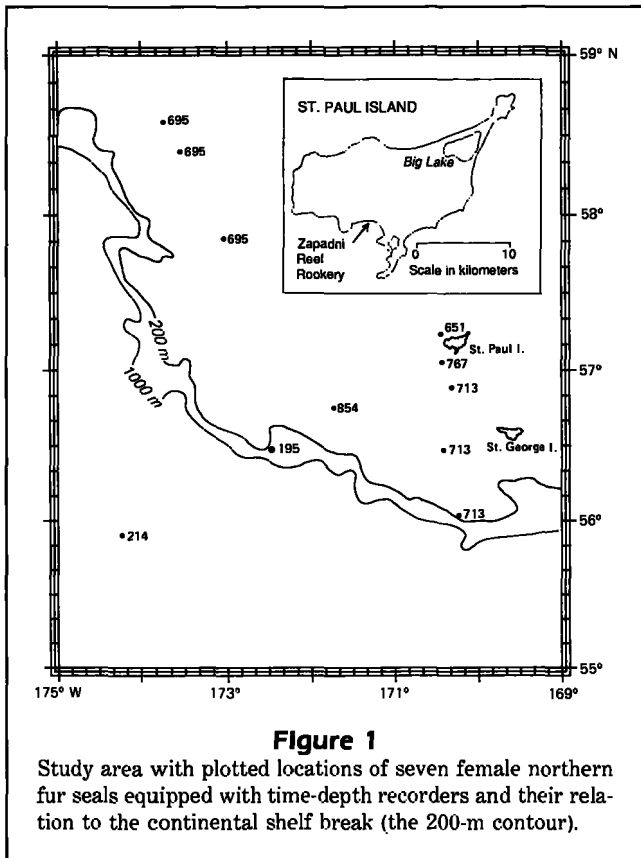
hibiting the deep-diving pattern typically dive to depths greater than 75 m without changing depth during a diving bout and dive at all hours of the day (Gentry et al. 1986c).

Feeding locations of individuals exhibiting different diving patterns, however, were unknown. Loughlin et al. (1987) initiated studies to determine what foraging areas in the Bering Sea were critical for lactating females. In 1984 using a ship, they located 11 females equipped with radio transmitters and tracked 4 of them to foraging locations. In 1985, they located 20 females with radio transmitters at sea from aircraft.

This paper reports our efforts to link fur seal diving behavior and foraging locations by instrumenting females with both radio transmitters (to determine location) and dive recorders (measuring depth of dive). We examine differences among females in diving behavior and their patterns of foraging, and discuss how diving behavior correlates with possible prey species.

Study area and methods

This study was conducted at Zapadni Reef rookery on St. Paul Island, Pribilof Islands, Alaska, from 19 July to 16 August 1985 (Fig. 1). Nine female northern fur seals with pups were



captured with a noose pole, removed from the rookery, and placed on a restraint board (Gentry and Holt 1982). Each female was tagged on the fore-flippers (Allflex sheep ear tag) and equipped with a radio transmitter (164 Mhz, Advanced Telemetry Systems, Isanti, MN) and a photomechanical time-depth recorder (TDR) (Meer Instruments, Solana Beach, CA). Radio transmitters were attached to the top of each seal's head with quick-setting epoxy resin (Devcon EK-40) (Loughlin et al. 1987) and TDRs were attached to seals by harness (Gentry and Kooyman 1986). After the epoxy resin had hardened (20–25 minutes), each female was returned to her capture site and released. Females were recaptured with a hoop net on their next visit ashore and the TDR was removed by cutting the harness. When possible, the mass for each female was determined at each capture.

Females were located at sea using a twin-engine airplane equipped with a two-element Yagi antenna mounted on each side of the fuselage (Loughlin et al. 1987). A total of 60 hours was flown on predetermined transects within 300km of St. Paul Island at speeds of 100–120 knots and at 1200m altitude.

Film from recovered TDRs was developed in either Agfa Rodinol or Kodak D-19. Each record was repro-

duced on paper with a 7× enlargement using copy flow xerography. At least three points of each dive were digitized on an electronic digitizing pad: the start, the end, and the maximum depth. These points allowed computation of dive duration, depth, and interdive surface interval. Each record was analyzed for bouts of diving using the same criteria used by Gentry et al. (1986c) for *Callorhinus*: five or more dives with less than a 40-minute surface interval between each dive.

The duration of diving bouts, number of dives per bout, percent time below the surface, and number of dives per hour were calculated as indices of the patterns of foraging.

The percent time spent below the surface was calculated separately for all dive bouts that occurred at mean depths of less than 75 m and for bouts greater than or equal to 75 m. An ANOVA on percent time below the surface was made after an arcsine transformation of the data. All comparisons for significant differences in depth were made using ANOVA with significance accepted at $\alpha \leq 0.05$.

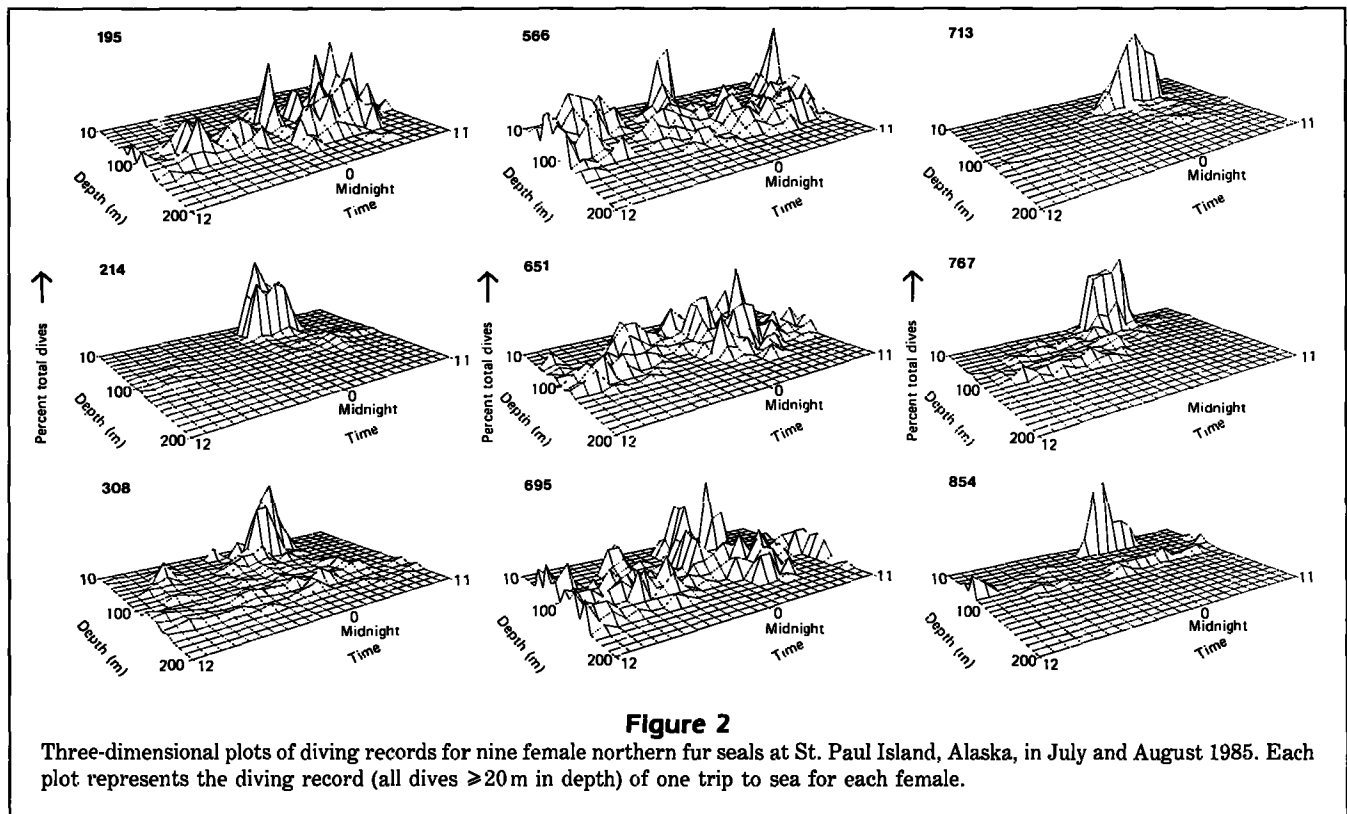
The number of dives per hour was calculated for daytime (0700–2259) and nighttime (2300–0659) hours and for the entire record for each female. Percent of total dives for day and night hours was also calculated.

To further test the relationship between foraging locations and dive patterns, we used data from the National Marine Mammal Laboratory's pelagic fur seal database, which provided a large sample of lactating females that had been collected from July to September, 1958–74, from the eastern Bering Sea. We compared the proportion of stomachs with food to empty stomachs of lactating females collected over the continental shelf (<200 m depth) and for those collected off the continental shelf (>200 m depth; chi-square analysis). For the comparison, we used specimens obtained between the hours of 0600–1000 and 1400–1900 (we chose 0600 and 1900 because they were the start and the termination of sampling, and we arbitrarily selected 1000 and 1400).

Results

Four of the nine females (nos. 195, 566, 651, 695) instrumented with TDRs and radio transmitters were deep divers, diving at all hours of the day; the other five (nos. 214, 308, 713, 767, 854) were shallow divers and dived primarily at night (Fig. 2).

Seven of these females, three deep divers and four shallow divers, were located at sea at least once. Female 195 was located on the third day of a 12-day trip at the continental shelf break. At this location the bathymetry changes rapidly, and because aerial locations are only approximate this female could have been



in water 140m to 1400m deep. On the day she was located, as well as on most days of her trip, she exhibited the deep-diving pattern. For a 24-hour period from 1200 on 4 August until 1200 on 5 August she made 70 dives (50% during the day) with a mean depth of 94.2m (SD 18.5).

Two females (651 and 767) were located only once, on their return to St. Paul from a foraging trip (Fig. 1, Table 1). Female 651 was located 2.5 hours before she returned ashore and after she had completed 99% of her foraging trip. Her last dive was 6.9 hours before being located. Female 767 was located 8.2 hours before she returned ashore and 2.5 hours after her last dive.

Female 695 was located on three separate days, each time she was 110–160km northwest of St. Paul Island, diving to depths greater than 100m over the continental shelf in water 110–140m deep. This female exhibited the deep-diving pattern every day of her 10-day trip, but also made seven dive bouts which had mean dive depths of less than 75m, five of which occurred during the night.

Female 214 was located on the fifth day of a 12-day feeding trip in approximately 3500m of water. On that day, as well as most other days, she exhibited the shallow diving pattern and dived primarily at night (Fig. 3).

Female 713 was also located on three consecutive days. She exhibited a foraging pattern of deep diving, day and night, on the first and last days of a foraging trip and shallow diving at night on other days. She was located on 25 July, the fifth day of a 7-day trip, 80km south of St. Paul Island at the continental shelf break in approximately 200m of water. On that day she dived exclusively at night with a mean depth of dive of 46.7m (SD 17.1, n 171). This was the night following her location at the shelf break. On the sixth day and on the last day of her trip she was located over the shelf and dived both during the day and night to much greater depths (mean depth of dive 101.3m, SD 26.9, n 67 for the sixth day, and 103.5m, SD 11.0, n 11 for the last day).

Female 854 was located on the first day of a 4-day trip over the continental shelf but within 18km of the 200-m depth contour. From the time she left shore (2208) until she was located 20.8 hours later she had made 22 dives—all but three were greater than 75m (\bar{x} 75.6, SD 7.6). Of these dives, 77% were made before dawn. Her second night at sea was spent actively diving to depths of less than 35m (n 70, \bar{x} 22.8, SD 19.6). She began diving at 2353 and dived continuously until 0340. This female was in transit across the continental shelf during the night, making occasional dives

Table 2

Record lengths, times to first and from last diving bouts, and mass of nine female northern fur seals instrumented with time-depth recorders in July and August 1985, St. Paul Island, Alaska.

Female ID	Start		Total hours	Time to first dive bout ¹	Time from last dive bout ²	Mass (kg) ³		
	Date	Time				1	2	Gain
Deep divers								
195	8/01	2308	290.22	4.72	12.25	34.0	37.6	3.6
566	8/06	1425	225.25	34.08	22.67	41.3	45.4	4.1
651	7/20	1442	196.33	14.72	12.75	31.3	33.6	2.3
695	7/23	1204	253.17	20.52	18.18	48.5	49.9	1.4
Shallow divers								
214	7/30	1820	295.42	11.87	14.63	31.3	33.1	1.8
308	7/24	2042	242.50	2.98	15.13	—	39.5	?
713	7/20	1342	178.28	23.03	8.12	—	34.0	?
767	7/22	0041	114.75	18.98	18.73	39.5	—	?
854	8/02	2208	91.01	4.65	3.00	40.1	40.4	0.3

¹Time to first dive bout is the time from departure from shore until the first dive bout measured in hours. A dive bout is defined as any series of dives greater than five dives with surface intervals of less than 40 minutes (Gentry et al. 1986c).

²Time from the last dive bout (in hours) until the female returns to shore.

³Mass 1 is the mass taken upon deployment (the first capture), and mass 2 is the mass taken upon recapture (the second capture).

to depths greater than 75m and then once near the shelf break, she began diving to shallow depths.

Female mass and depth of dive

Seven of the nine females were weighed at instrument deployment, and eight were weighed when the instrument was recovered (Table 2). All females weighed twice showed a mass gain (range 0.3–4.1 kg). Time at sea ranged from 91 to 295 hours. Length of time at sea was not correlated with diving patterns or mass of the female (r^2 0.0). No correlation was found between mass of individuals and their diving patterns (r^2 0.0).

The mean maximum depth of dive for each deep diver was greater than 75 m whether considering day dives or night dives (Table 3). The mean maximum depth of dive for the shallow-diving females was less than 75 m (Table 3). When considering only night dives, shallow-diving females showed mean maximum depths of less than 50 m.

Two of the deep divers (195 and 651) showed no difference in depth of dives between day and night. The other seven females showed a significant difference in depth of dives between day and night. Six females dived deeper during the day than at night. The seventh (566) had significantly deeper dives at night than during the day (Table 3).

Time from shore to the first dive bout and return

The time between departure from shore and the first dive bout was highly variable, as was the time between the last dive bout and the return to shore (Table 2). These times ranged from about 3 to 34 hours. Mean time to first dive bout was 15.06 hours (SD 10.26) and the mean time from last dive bout to shore was 13.94 hours (SD 5.88). There was no significant difference between the time to first dive bout and the time from the last dive bout (Mann-Whitney $P = 0.86$).

There were no differences in either the time to the first dive bout or the time from the last dive bout when comparing shallow divers with deep divers. The mean time to the first dive bout was 12.30 hours (SD 8.74) for shallow divers and 18.51 hours (SD 12.26) for deep divers (Mann-Whitney $P = 0.46$). The mean time from the last dive bout to shore for shallow divers was 11.92 hours (SD 6.29) and for deep divers was 16.46 hours (SD 4.93; Mann-Whitney $P = 0.54$).

Foraging patterns

Deep divers showed a much lower percentage of dives at night than the shallow divers (Table 4). Females 566 and 695 made less than 50% of their dives at night. In general, shallow divers made greater than 70% of their dives at night (females 214 and 713 >90%) and deep divers less than 70%.

Table 3

Mean depth of dive for each dive record and for each record by day and night of nine female northern fur seals from St. Paul Island, Alaska, during July and August 1985.

Female ID	Record total			Day hours			Night hours			P-value ¹
	Mean depth	SD	N	Mean depth	SD	N	Mean depth	SD	N	
Deep divers										
195	101.5	22.0	440	102.1	18.3	205	101.0	24.8	235	0.590
566	75.3	31.2	439	72.4	28.0	285	80.8	35.9	154	0.007
651	76.0	27.3	496	75.3	27.0	193	76.5	27.4	303	0.632
695	85.1	34.1	504	93.0	30.8	259	76.7	35.3	245	0.001
Shallow divers										
214	38.7	23.1	1369	87.1	15.9	134	33.5	16.9	1235	0.001
308	60.6	42.1	832	94.8	41.6	230	47.5	34.3	602	0.001
713	45.4	21.7	900	85.1	25.4	55	42.8	18.7	845	0.001
767	33.3	27.7	431	72.9	22.6	90	22.8	17.6	341	0.001
854	40.6	28.2	312	63.6	15.2	80	32.6	27.3	232	0.001

¹P-values are derived from a one-way ANOVA for differences in mean depth of dive between day and night hours.

Table 4

Total dives and dives/hour for day and night dives of nine female northern fur seals from St. Paul Island, Alaska, during July and August 1985.

Female ID	N dives	% total dives		Dives/hour		
		Day	Night	Total	Day	Night
Deep divers						
195	440	46.6	53.4	1.8	1.1	3.5
566	439	65.1	34.9	1.9	1.7	2.8
651	496	38.9	61.1	2.5	1.3	6.3
695	504	51.4	48.6	2.0	1.3	4.0
Shallow divers						
214	1369	9.8	90.2	4.7	0.6	16.8
308	832	27.6	72.4	3.4	1.3	10.0
713	900	6.1	93.9	5.0	0.4	20.1
767	431	20.9	79.1	3.8	1.0	14.6
854	312	25.6	74.4	3.4	1.2	9.7

The number of dives/hour for the entire trip was greater for shallow divers than for deep divers (Mann-Whitney, $P = 0.02$). The maximum number of dives/hour for deep divers was 2.5 (\bar{x} 2.0, SD 0.31), whereas the minimum number of dives/hour for shallow divers was 3.4 (\bar{x} 4.1, SD 0.75). Although deep divers tended to execute more dives per hour at night than during the day, the difference was not significant (Mann-Whitney, $P = 0.11$). Shallow divers did, however, make more dives per hour at night than during the day (Mann-Whitney, $P = 0.02$). Regardless of which diving pattern females exhibited, they always made more dives per hour at night than during the day.

Diving bouts

No differences in the total number of dive bouts per trip were detected between shallow and deep divers (Table 5). Although the number of dives that did not meet the dive-bout criteria tended to be greater for the deep divers, this difference was not significant (Mann-Whitney, $P = 0.07$). Differences in bout durations, number of dives per bout, and number of dives per hour within bouts were all greater for shallow divers (ANOVA, $P = 0.01$ for duration, $P = 0.01$ for dive number, $P = 0.02$ for dives/hour).

When all bouts were divided into those less than 75 m and those greater than or equal to 75 m, the percent of time spent below the surface was significantly different for shallow- and deep-diving bouts (ANOVA, $P = 0.01$). A greater percent of

time was spent below the surface for shallow bouts (<75 m, \bar{x} 0.35 hour, SD 0.11, n 59) than for deep bouts (\geq 75 m, \bar{x} 0.29 hour, SD 0.12, n 102).

Pelagic fur seal studies

During the hours 0600–1000, the stomachs of 740 postpartum females were sampled, 504 over the shelf and 236 off the shelf (Table 6). From 1400 to 1900 hours, 750 postpartum females were sampled, 513 over the shelf and 237 off the shelf.

Females collected in the morning hours off the continental shelf were more likely to have food in their

Table 5

Dive bout¹ statistics and effort within dive bouts for nine female northern fur seals, from St. Paul Island, Alaska, in July and August 1985.

Female ID	Dive bouts	Dives excluded (%)	Bout duration (hours)			Dives per bout			Dives/hour in bout		
			\bar{x}	SD	Max.	\bar{x}	SD	Max.	\bar{x}	SD	Max.
Deep divers											
195	26	4.8	2.5	2.3	9.2	16	13	51	8.9	5.7	28.0
566	24	10.5	2.8	2.0	7.9	16	13	54	6.6	4.2	16.7
651	15	4.4	3.8	3.0	11.7	32	26	93	8.4	4.0	16.2
695	26	9.3	2.7	1.8	7.7	18	14	63	7.0	4.2	17.8
Shallow divers											
214	20	3.0	3.8	2.2	8.3	66	65	163	13.5	10.3	32.3
308	25	4.9	3.0	1.8	7.7	32	37	135	10.5	10.0	35.7
713	9	1.8	4.6	2.4	8.2	98	75	184	20.1	12.8	33.3
767	7	3.2	4.2	2.9	7.8	60	55	145	12.8	6.7	24.4
854	9	2.6	3.0	1.9	8.6	34	24	74	13.2	9.5	30.3

¹A dive bout is defined as any series of dives greater than five dives with surface intervals of less than 40 minutes (Gentry et al. 1986c).

Table 6

The percent of stomachs with food of lactating northern fur seals collected over the continental shelf (in water <200 m deep) and off the continental shelf (>200 m deep). Collections were made from July through September, 1958-74.

Time (hours)	Over the shelf	Off the shelf
0600-1000	80.0 (403/504)	95.3 (225/236)
1400-1900	54.0 (277/513)	39.7 (94/237)

stomachs than females collected over the shelf (chi-square, $P < 0.001$). Afternoon samples showed a reverse trend with a higher incidence of food in stomachs of seals collected on the shelf than off the shelf (chi-square, $P < 0.001$).

Discussion

Dive patterns and foraging locations

The results of this study show that northern fur seal females diving in deep water beyond the continental shelf primarily exhibit the shallow-diving pattern and dive predominantly at night. Females feeding at or near the shelf break may exhibit both diving patterns. Females located on the continental shelf (which had not already completed their feeding trip) were more likely to exhibit the deep-diving pattern and dived to depths of greater than 75 m throughout the day and night. However, females found over the continental shelf had, at times, shallow dive bouts (<30 m) at night.

The pelagic fur seal database provided insight into the relationship between diving patterns and feeding locations of fur seals in the Bering Sea. If the deep-diving pattern is associated with feeding on the continental shelf, and deep divers feed during the day, one can test the hypothesis that females found over the continental shelf during the day have a greater probability of having food in their stomachs than those females found off the shelf, which would be diving predominantly at night. The analyses of the northern fur seal pelagic database support our finding that the deep-diving pattern is associated with the continental shelf by showing that females collected over the continental shelf were more likely to be feeding during the day.

Dive patterns and probable prey

The feeding locations and dive patterns observed in this study are consistent with the known distribution of fur seal prey items. Kajimura (1984) summarized the variation in principal forage species for fur seals, depending on location. Fur seals feeding in the Bering Sea beyond the continental shelf over deep water fed on oceanic squid of the family Gonatidae (primarily *Gonatus* spp., *Berryteuthis magister*, and *Gonatopsis borealis*) or deep-sea smelts of the family Bathylagidae. These prey species, and fish with swim bladders, exhibit diel vertical migration and are at relatively shallow depths at night as they move vertically in synchrony with the deep scattering layer (Roper and Young 1975, Pearcy et al. 1977). It is during the night that they are fed upon by fur seals which rarely dive beyond 200 m (Gentry

et al. 1986b). Fur seals foraging over the shelf were likely to feed on walleye pollock *Theragra chalcogramma*, Pacific herring *Clupea harengus pallasi*, and capelin *Mallotus villosus* (Kajimura 1984). Each of these prey items is distributed throughout the water column over the shelf, depending on the sex and age of the individual and time of day; however, they are principally found near the bottom (Bakkala and Wakabayashi 1985). Even when prey are near the bottom over most of the shelf floor, they are shallower than the maximum diving depths observed for most fur seals and are accessible during all hours of the day.

The results of foraging effort for shallow and deep divers in this study are consistent with the results of Gentry et al. (1986c) in their study of diving of females from St. George Island. Costa and Gentry (1986) used isotopic turnover methods to measure food intake and metabolic rate in female fur seals instrumented with time-depth recorders. In that study of two deep-diving and two shallow-diving fur seals, the deep divers ate less food and expended less energy but gained similar body mass on a single trip to sea. Our results confirm their conclusion. In this study, using four measures—bout duration, dives per bout, dives per hour, and time spent below the surface—deep divers expended less effort on foraging than shallow divers. Deep divers apparently obtain greater energy per dive.

The difference in foraging effort of diving types may be explained by differences in energy content of prey, success rate for prey capture, and/or average size of prey captured. If success rate per dive and average size of prey were similar for both diving types, then energy content for the prey of deep divers would have to be greater. If prey were of similar size and energy content, then the prey of deep divers would have to be easier to capture. If success rate and energy content were similar, then the prey captured by deep divers would have to average a greater size per dive. Unfortunately, no data exist on success of individual dives.

Data on the energy content of prey items of northern fur seals suggest that *Gonatus* sp. and walleye pollock have similar energy content (M.A. Perez and T.R. Loughlin, NMFS Natl. Mar. Mammal Lab., Seattle, unpubl. data). No data exist for energy content of bathylagids. Perez and Bigg (1986) report on the size range of prey found in the stomachs of northern fur seals collected during 1958–74: walleye pollock, 4–40 cm (1721 prey from 71 stomachs); gonatid squid, 5–24 cm (>59 prey from 10 stomachs); deep-sea smelts, 8–12 cm (986 prey from six stomachs). The size range for Myctophiform fish prey and the mean size of prey were not reported.

Transit times

The most frequently used measure of transit time, derived from time-depth records, has been the time from shore to the first diving bout and from the last dive bout to shore (Gentry and Kooyman 1986). Data from the current study show that female fur seals frequently feed while traveling to very distant feeding locations and that the time from shore to the first diving bout is only a subset of the total time in transit.

There was no difference in the time from shore to the first dive bout for the two types of diving patterns observed in this study. Similarly, the times from the last dive bout to arrival ashore were not different. Furthermore, no correlation was found between these times and feeding trip duration. It has been suggested, however, that a correlation exists between feeding trip duration and distance to feeding area (Gentry et al. 1986a). Gentry et al. (1986a) found that regressing transit time of individuals upon their trip duration resulted in a poor fit (r^2 0.357). When they compared species averages using two tropical and two sub-polar otariid species, the correlation was much greater (r^2 0.761). They concluded that transit time may largely determine trip duration for the species, but its effect is partly obscured by the large variation in transit times and trip duration of some individual animals.

The results of Loughlin et al. (1987) and of this study show that females feed while in transit to primary foraging areas. A correlation may exist between trip duration and total time spent in transit; however, measuring the time from shore to the first diving bout and from the last diving bout to shore is only a subset of actual time spent in transit and therefore an inadequate measure of total transit time. Without knowledge of either the swim velocity or the location of females (either through radio-tracking or with some instrument carried by the animal to record location) it is not possible to discern from a record of a time-depth recorder the actual time spent in transit.

Classification of diving patterns

It is important to point out that any classification of diving patterns gives the impression that they are more discrete than they really are. It is more accurate to view any particular diving record as fitting into a continuum from strictly shallow diving at night to exclusively deep diving at all hours. The terminology used to categorize these diving patterns may overemphasize the importance of depth. It should be remembered that though deep- and shallow-divers are classified as such, the depth of dives may not be as important for identifying the pattern as the time of day in which diving occurs.

Before the advent of dive-recording instruments, one of the most important measurements used to assess changes in prey availability for pinnipeds and sea birds was the length of foraging trips. Foraging trips, however, may be useful only in documenting large-scale changes in prey availability (e.g., El Niño events). Dive-recorder instruments provide the opportunity to measure changes in the foraging environment on a finer scale. This work underscores the importance of quantifying dive patterns in elucidating differences in foraging strategies and in changes in the foraging environment.

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