

Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*

BURNEY J. LE BOEUF, DANIEL P. COSTA, ANTHONY C. HUNTLEY, AND STEVEN D. FELDKAMP

Department of Biology and Institute for Marine Sciences, University of California, Santa Cruz, CA, U.S.A. 95064

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The free-ranging dive pattern of seven adult female northern elephant seals (*Mirounga angustirostris*) was obtained with time–depth recorders during the first 14–27 days at sea following lactation. The instruments were recovered and mass gain at sea determined when the animals returned to the rookery at Año Nuevo, California, to molt. The seals gained a mean of 76.5 ± 13.9 kg during a mean of 72.6 ± 5.0 days at sea. The mean dive rate was 2.7 ± 0.2 dives/h and diving was virtually continuous during the entire period at sea. Mean dive duration was 19.2 ± 4.3 min with the longest submersion lasting 48 min. Mean surface interval between dives was 2.8 ± 0.5 min, so that only 14.4% of the recorded time at sea was spent on the surface. Surface intervals did not vary with the duration of preceding or succeeding dives. Modal dive depth for each female was between 350 and 650 m. The maximum dive depth was estimated at 894 m, a depth record for pinnipeds. The deep, nearly continuous dive pattern of female northern elephant seals differs from the dive pattern of other pinnipeds and appears to serve in foraging, energy conservation, and predator avoidance.

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Des enregistreurs de plongée ont permis de suivre l'activité de plongée en nature chez sept femelles adultes de l'Éléphant de mer du Nord (*Mirounga angustirostris*), durant les 14–27 jours en mer après la fin de la période d'allaitement. Au retour des animaux à la rookerie d'Año Nuevo en Californie pour la mue, les appareils ont été retirés et le gain de masse des animaux pendant leur séjour en mer, déterminé. Les animaux ont augmenté leur masse d'une moyenne de $76,5 \pm 13,9$ kg durant un séjour moyen de $72,6 \pm 5,0$ jours en mer. Le taux moyen des plongées était de $2,7 \pm 0,2$ plongées/h et les plongées se sont succédées pratiquement pendant toute la durée du séjour en mer. La durée moyenne d'une plongée était de $19,2 \pm 4,3$ min et la durée maximale, de 48 min. L'intervalle en surface entre les plongées durait en moyenne $2,8 \pm 0,5$ min; seulement 14,4% du temps en mer est donc passé en surface. La durée de l'intervalle entre les plongées était indépendant de la durée des plongées précédente ou subséquente. Le mode des profondeurs atteintes par chaque femelle se situait entre 350 et 650 m. La profondeur maximale enregistrée a été de 894 m, ce qui constitue un record chez les Pinnipèdes. Le comportement de plongée profonde et presque continue des Éléphants de mer femelles diffère de celui des autres Pinnipèdes et semble favoriser la quête de nourriture, la conservation de l'énergie et la fuite des prédateurs.

[Traduit par la revue]

Seals and sea lions reproduce on land or ice and feed at sea. Much is known about their onshore activities but only recently has their aquatic behavior come under investigation. This has been made possible by the development of depth recorders, instruments that can be attached to free-diving pinnipeds to record diving performance and thereby reflect foraging behavior (Kooyman 1975, 1981; Kooyman et al. 1976, 1983a; Hill 1986). During the last decade, depth recorders have been used to obtain free-ranging dive records from four phocids (Kooyman et al. 1983a; Schlexer 1984; Le Boeuf et al. 1986), two species of sea lions (Feldkamp 1985; Kooyman and Trillmich 1986a; Gentry 1987), and five species of fur seals (see Gentry and Kooyman 1986). Additional species are being investigated and increasingly more sophisticated instruments are being developed (Hill 1986; Guppy et al. 1986). A glimpse of the marine habits of pinnipeds is beginning to emerge.

Time–depth recorders (TDRs) provide information on depth and duration of individual dives, time spent diving and at the surface, and diving schedules. The normal diving pattern provides indirect evidence of foraging strategies and a perspective for evaluating studies of diving adaptations and diving capacity in captive seals. Interpretation of laboratory data without knowledge of the animal's natural behavior can be misleading (Snyder 1983). For example, in some of the pioneering research in the laboratory (Scholander 1940), animals were submerged for the maximum durations observed in nature. Lactate buildup following these dives led to the conclusion that anaerobic metabolism is important in natural diving. Recent evidence from free-diving seals carrying TDRs shows

that most dives are brief and aerobic (Kooyman et al. 1980, 1983b; Gentry and Kooyman 1986), like the brief dives of resting, restrained seals (Scholander and Irving 1942). Thus, TDRs shed light on the extent to which diving potential is reflected in diving performance.

This paper reports a study of free-diving behavior of female northern elephant seals, *Mirounga angustirostris*. Northern elephant seals breed in winter along the west coast of Baja California, Mexico, and California. After giving birth, a female nurses her pup daily for 4 weeks while fasting from food and water. At the end of this period, she copulates, weans her pup, and returns to sea to feed. After 10 weeks at sea, she returns to the rookery to molt, a process that takes about 1 month (Le Boeuf et al. 1972; Reiter et al. 1981). Female elephant seals are good subjects for diving studies because they are large (250–650 kg) and can carry TDRs without significant impediment to their swimming and diving behaviour (Le Boeuf et al. 1986), and their predictable habits aid in determining the optimal time and place to attach and recover instruments.

In a preliminary study (Le Boeuf et al. 1986), one adult female dived continuously for the first 11 days at sea. Mean dive duration was 21 min with a mean surface interval of 3 min between dives, resulting in only 11% of the recorded time at sea being spent on the surface. The mean dive depth was 333 ± 42.7 m and the deepest dive was 630 m. The continuous, deep, and long diving of elephant seals over such an extended period differs from the dive pattern of other pinnipeds and raises a number of questions concerning oxygen utili-

TABLE 1. Mass gain at sea of seven adult female northern elephant seals bearing time—depth recorders

Subject	Age (years)	Mass (kg)			Days at sea	Mass gain (kg/day)	% mass increase at sea
		Departure	Return	Gain			
Rp (1986)	3	247	305	58	74	0.78	23.5
Dot (1986)	4	253	326	73	75	0.97	28.8
Ca (1986)	5	307	402	95	75	1.26	30.9
Ali (1986)	6	325	384	59	62	0.95	18.2
Gi (1985)	7	300	380	80	71	1.13	26.7
Td (1985)	7	348	431	83	78	1.06	23.8
Snl							
1985	9	401	494	93	70	1.33	23.2
1986	10	399	470	71	76	0.93	17.8
Mean		322.5	399.0	76.5	72.6	1.05	24.1
SD		58.5	65.3	13.9	5.0	0.18	4.6

zation during diving, foraging strategy, sleep pattern, and predator avoidance.

We report a more extensive study of the diving behavior of female northern elephant seals. Our aim was to determine the dive pattern of known-age females during the first 2–4 weeks at sea following lactation. We present data on mass gain at sea, dive depth, dive duration, and surface interval duration between dives, information that is important for understanding diving adaptations and foraging economics.

Methods

Eight depth recorders were deployed at Año Nuevo Point, California, between 9 February and 8 March, three in 1985 and five in 1986. Subjects were lactating adult female northern elephant seals, tagged at weaning (Le Boeuf and Peterson 1969), ranging in age from 3 to 10 years (Table 1). One female carried instruments in both years, i.e., a total of seven females were monitored. All subjects were marked individually and monitored daily throughout their stay on land. Each female gave birth, nursed her pup daily for about 4 weeks, and weaned her pup within 2 days of the instrument being attached.

Subjects were immobilized with 4–6 mg/kg of ketamine hydrochloride (Ketaset, Bristol Laboratories, Syracuse, New York; see Briggs et al. 1975) 1 day before they were expected to go to sea. Departure was predicted from parturition date and age (Reiter et al. 1981). Two darts containing a total of approximately 25–30 mL of ketamine (100 mg/mL) and 1–3 mL of 5 mg/mL Diazepam (Valium, Roche Laboratories, Nutley, New Jersey) were fired with a carbon dioxide pistol (Cap-Chur Darts and Pistol, Palmer Chemical Co., Douglasville, Georgia) into the hind quarters of each subject as she rested on the periphery of the harem. Subsequent injections of 1–10 mL of ketamine and 1–3 mL of Diazepam were administered by syringe intramuscularly or intravenously when necessary.

Within 15 min of drug administration, the female was approached, measured, rolled onto a nylon stretcher, and weighed with a 1000 ± 2.5 kg dynamometer (Chatillon WT-1000) which hung from an aluminum tripod (Costa et al. 1986).

The TDRs were identical with the type used in a preliminary study on northern elephant seals (Le Boeuf et al. 1986) (Fig. 1). A full description of the 5 × 20 cm, 700-g instrument is given by Kooyman (1981) and Kooyman et al. (1983a). The TDR produces a photographic record of dive duration and dive depth in real time. Only dives greater than 10 m in depth and 30 s in duration can be resolved. Before deployment and immediately after recovery, all TDRs were calibrated to a maximum depth of 816 m using a pressure station. TDRs were switched on approximately 2 h before they were attached to subjects.

The procedure for attaching the instruments was as follows. After

the pelage was cleaned with acetone, a PVC mold, 16 cm wide, was placed on the dorsal midline of each female above the shoulders (Fig. 1). The mold was filled with marine epoxy (Evercoat Ten-set, Fibre-Evercoat Co., Cincinnati, Ohio) and the adhesive was worked under the hair. An 18-g, 3 × 14 cm aluminum plate, to which a TDR and a 9 × 3 cm radiotransmitter (148–180 MHz frequency) (Advanced Telemetry Systems, Bethel, Minnesota) was attached with hose clamps, was imbedded in the epoxy. The attachment was firm within 30 min. Most females departed the rookery and went to sea within 1.5–3 h of the last drug administration; in 1986, two females (Rp and Snl) departed 24–48 h after the last drug injection.

Based on data collected in previous years (B. Le Boeuf and J. Reiter, unpublished data), we expected females to return to the rookery to molt in 68 ± 5 days. A radio receiver (Telonics, Mesa, Arizona) attached to a strip chart recorder indicated to the nearest hour the time of arrival in the area of each female. Within a day of a female returning, she was immobilized and weighed and the depth recorder and transmitter retrieved. The epoxy mount fell off within 2 weeks when the animal molted. The TDR film record was developed, enlarged seven times, and digitized. Dive measurements were calculated, stored on floppy discs, and summarized by computer.

After inspection of the records, the dives of three females, from day 3 (when the animals were in deep water) until the end of each record, were classified into six dive types. The criteria for differentiating dives were based on dive configuration, as determined by duration, depth, ascent and descent rates, amount of time spent at the bottom of the dive, and activity (rate and direction of movement) during the dive. Dives within a type were similar in appearance and dissimilar from dives in other categories (see Results).

For each female, 12 dives of the type having a well-marked dive bottom were selected randomly for measurement of ascent and descent speeds and other rate measurements. To calculate ascent and descent rates, we determined the arc that the recording light-emitting diode of each TDR made when it was instantaneously decompressed from 1200 psi (1 psi = 6.895 kPa), enlarged it, and drew it on a sheet of clear plastic. We then measured the temporal deviation of the dive trace from the instantaneous arc on descent and ascent, i.e., time from the surface to the bottom of a dive and *vice versa*. Rates were derived by dividing depth by the time difference.

The timing circuit failed on one instrument halfway through the record (female Rp); dive durations for the remainder of the record were extrapolated. These data are excluded in calculations of overall means and standard deviations of dive duration and in all other summary statistics involving dive duration.

The depth of 18 dives that exceeded the upper calibration mark of 816 m was extrapolated by assuming a sharp, spiked bottom (a characteristic of all measurable dives deeper than 700 m) and a continuous linear relationship between pressure (dive depth) and the distance traveled by the indicating arm across the film.

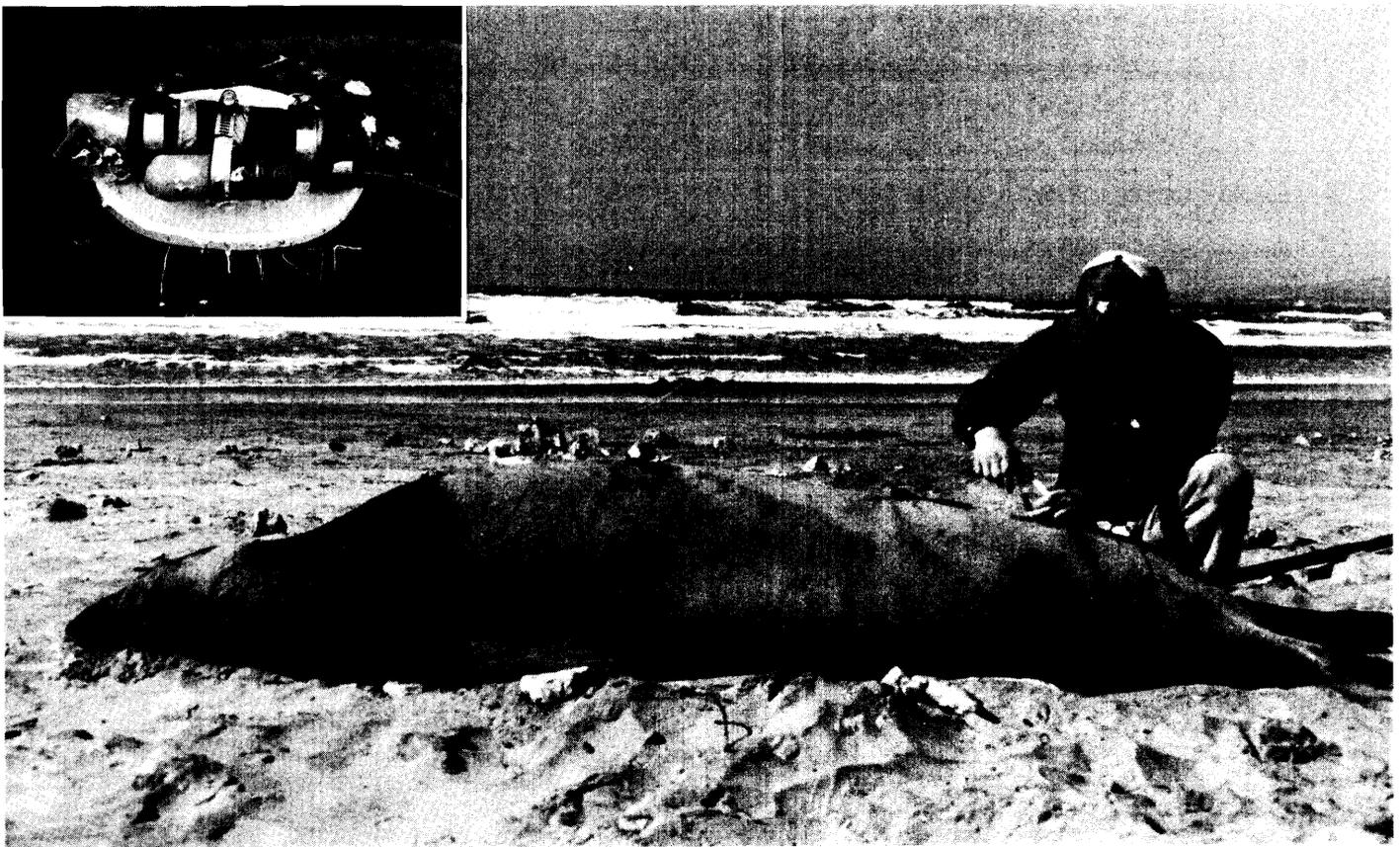


FIG. 1. D. P. Costa takes a blood sample from a sedated adult female elephant seal with attached time—depth recorder and radiotransmitter. A close-up of the instruments imbedded in an epoxy mount glued to a female's pelage is shown in the inset.

TABLE 2. Summary statistics from the diving records of seven adult female northern elephant seals obtained in 1985 and 1986 from time—depth recorders

Subject	Record duration		No. of dives/h	Record duration spent on surface (%)	Max. depth (m)	Mean depth \pm SD (m)	Max. duration (min)	Mean duration \pm SD (min)
	Hours	Total dives						
Rp	421	1 539	3.7	21.4	668	389 \pm 135	23.3	12.9 \pm 3.1
Dot	598	1 822	3.0	16.6	894	370 \pm 158	30.6	16.4 \pm 3.1
Ca	458	1 175	2.6	12.3	886	413 \pm 165	35.9	20.5 \pm 4.5
Ali	318	819	2.6	16.8	822	363 \pm 162	35.8	19.4 \pm 4.9
Gi	468	1 370	2.9	16.0	854	480 \pm 145	35.2	17.2 \pm 3.3
Td	320	942	2.9	11.0	868	420 \pm 178	32.4	18.1 \pm 3.9
Sn1								
1985	363	883	2.4	11.0	760	345 \pm 142	47.7	22.0 \pm 5.0
1986	619	1 486	2.4	16.9	828	419 \pm 166	44.5	20.8 \pm 5.2
Total	3565	10 036						
Mean			2.7	14.4	822	400	37.4	19.2
SD			0.2	2.8	76	156	6.3	4.3

NOTE: The 1st day of each record was excluded in calculating means and standard deviations of dive depth and duration. Dive duration statistics for female Rp are extrapolations; these are excluded in calculations of the overall maximum and mean dive duration, number of dives per hour, and percent time on the surface.

Results

All instrumented females returned to the Año Nuevo rookery and all recorders were recovered.

Time at sea and mass gain

Females spent a mean of 72.6 ± 5.0 days at sea, gained a mean of 1.06 ± 0.18 kg/day over the entire period, and

increased their mass by a mean of $24.1 \pm 4.6\%$ (Table 1). These results do not differ significantly from those obtained from three uninstrumented females monitored in 1982 (Le Boeuf et al. 1986). Therefore, we assume that the instruments did not impede movement or feeding significantly, which would have been reflected by a longer interval at sea or by a reduction in weight gain, respectively.

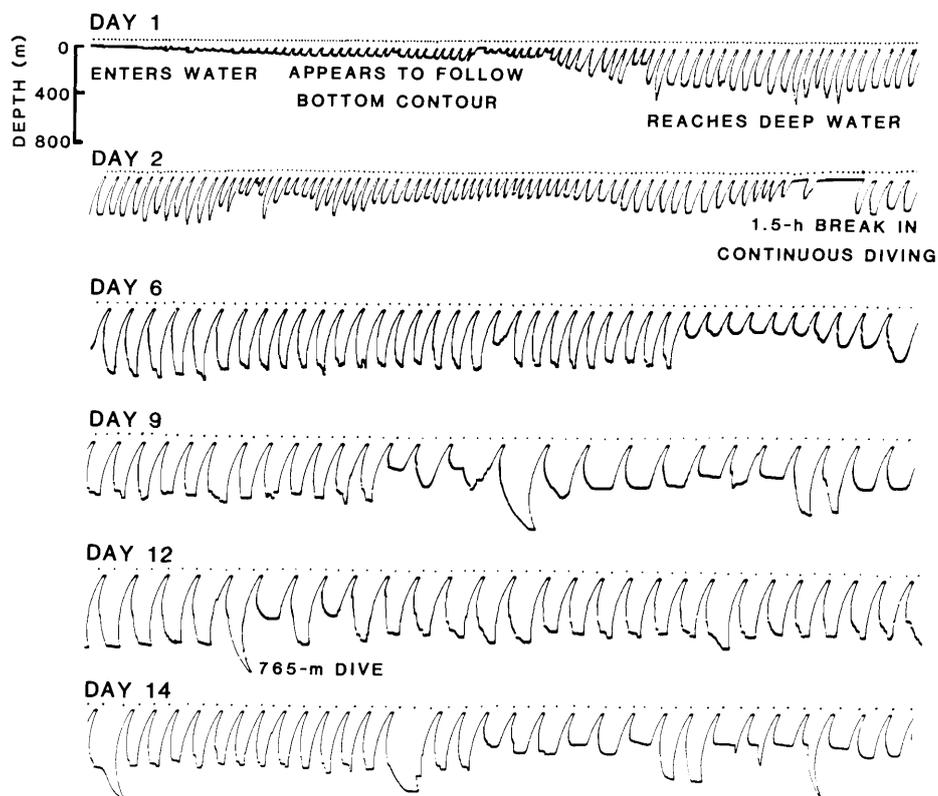


FIG. 2. Excerpts from the dive record of Snl in 1985. The timing dots at the top of each daily record are 12 min apart.

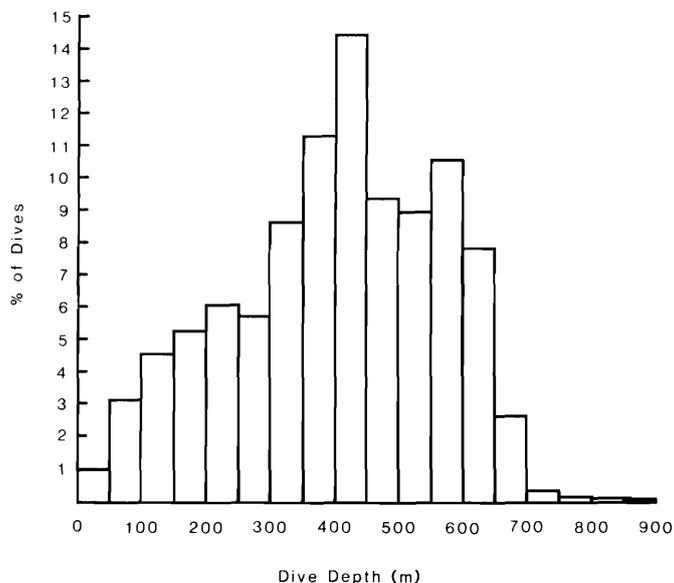


FIG. 3. A frequency distribution of dive depths of all females.

Diving pattern summary

Summary statistics for all females are shown in Table 2. Over 10 000 dives were recorded in 157 days at sea. The general pattern of diving was as follows. On average, each seal dived 2.7 ± 0.2 times/h throughout the entire length of the dive record, which varied from 14 to 27 days. Dive durations averaged 19.2 ± 4.3 min followed by about 3 min on the surface. Mean dive depths for each female exceeded 345 m. Excerpts from the dive record of one female, Snl in 1985, illustrate the general diving pattern (Fig. 2).

Three findings stand out. Females dived deep, they dived

virtually continuously, spending most of the time at sea underwater, and surface intervals were brief regardless of the duration of preceding dives. We describe each result in turn and address additional aspects of the diving pattern.

Dive depth

The mean depth of all dives for each female was between 345 and 480 m (Table 2). The maximum dive depth of all females except Rp, the youngest, smallest female, exceeded the limit of the recording instrument. The deepest dive was estimated at 894 m. However, dives deeper than 700 m were infrequent, as revealed by a frequency distribution of dive depths for all females combined (Fig. 3).

An analysis of the distribution of dive depths by day for each female shows the following. (i) Dives were shallow on the 1st day at sea and became progressively deeper with time until a modal or preferred depth pattern was established by day 4–6 (Fig. 4). This pattern was maintained for the remainder of each record. The modal or preferred dive depth of all females, once they had reached deep water, was in the range of 350–650 m. The interval preferred by Rp, Ca, Ali, Gi, and Snl (1985) was 400–450 m, with the others preferring the intervals 350–400 m (Dot), 500–550 m (Snl in 1986), and 600–650 m (Td). (ii) All females went directly from shore to deep water. Figure 2 shows the typical pattern. Each female was diving deeper than 200 m, the depth of the continental shelf, by the end of the 1st day or the beginning of the 2nd day. The mean interval between the time of departure and the first dive to 200 m or more was 18.9 ± 15.1 h (range = 3.3–46 h). The initial dive pattern was similar in all animals and did not vary with time since the animal was drugged. (iii) After the first few days, the daily dive depths of some females assumed a bimodal distribution. This resulted from a diel pattern of diving that will be discussed later. (iv) After 6 days at sea, dives less than

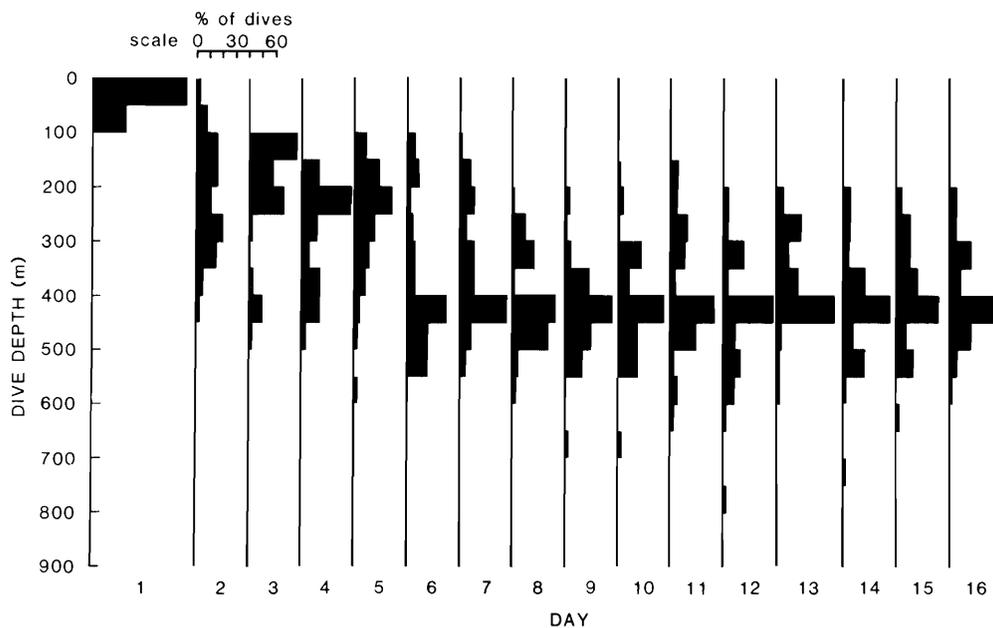


FIG. 4. Percentage distribution of daily dives according to depth for female Snl in 1985.

100 m in depth were extremely rare (0.06%) and only 1.34% of the dives were shallower than 200 m. Thus, most of the shallow dives shown in Fig. 3 occurred during the first few days at sea. (v) Mean and maximum dive depths did not vary systematically with age or mass (Table 2).

Continuous diving

All seals began diving as soon as they entered the water and dived virtually continuously throughout the recording period, which was determined by battery life or length of the recording film (Fig. 2). Because of steady diving and brief intervals on the surface between dives, the subjects averaged 85.4% of the time at sea underwater. In other words, they spent on average only 3.5 h/day on the surface (Table 2). Dive rate decreased with increasing age and mass of females. Dive rate was remarkably similar in the individual measured in two consecutive years, despite year-to-year differences in mean depth of dives, mean dive duration (Table 2), and mean surface interval between dives (Table 3).

The degree of continuous diving is indicated by analysis of the surface intervals between dives. A frequency distribution of the surface intervals shows that most dives in each record were followed by a surface interval of less than 5 min (Table 3). The mean surface interval for each animal ranged from 2.2 to 4.2 min.

Additional information on the frequency and duration of continuous diving is gained from analysis of deviations from the basic pattern. Extended surface intervals (ESIs), defined as surface intervals longer than 10 min, averaged less than one per day for each female, with the exception of female Snl in 1986 (Table 4). The maximum ESI per record was variable, from less than 1 h to slightly over 5 h. Similarly, total time per record spent in ESIs ranged from 1.5 to 22 h. The longest sequence of continuous diving without an ESI averaged 754 dives, or approximately 11 days. The 4-year-old female, Dot, dived continuously for over 18 days. The frequency of ESIs and their total duration was as variable in the same female from one year to the next (female Snl) as it was among females within the same year.

ESIs occurred at all hours of the day and appeared to be dis-

tributed randomly throughout the length of each record. They did not follow or precede long or deep dives. The mean dive durations before and after the 15 longest ESIs were 18.6 ± 5.2 and 17.5 ± 3.7 min, respectively, both shorter than the overall mean dive duration for all females (19.2 ± 4.3 min), and not significantly different from each other (Wilcoxon signed rank test, $T = 21$, $df = 15$, $p > 0.05$). Dives preceding and following ESIs were deep (200 m or more) indicating that ESIs occurred at sea in deep water and did not represent resting on land.

Dive duration

A frequency distribution of the dive durations of all females shows that most dives (81.5%) were in the interval 12–24 min (Fig. 5). Dives shorter than 10 min and longer than 30 min were rare.

Mean dive duration varied from 16.4 to 22.0 min among the six females for which complete records were available (Table 2). Mean dive duration appears to increase with increasing mass and age; the youngest, smallest female, Dot, had the lowest mean and maximum dive duration and the oldest, largest female, Snl, had the highest mean dive duration and exhibited the longest dive, 47.7 min.

Mean dive durations on a daily basis for each female were shortest on the 1st day at sea, increased significantly up to day 4, and then remained essentially unchanged until the end of the record. For example, the mean daily dive durations of all females combined (except female Rp) were 12.0, 15.6, 17.9, 20.2, 20.8, 20.6, 20.8, 21.1, 20.5, and 20.8 min for days 1–10, respectively.

Surface intervals did not vary systematically with the duration of preceding dives (Fig. 6). The mean surface interval before and after the 15 longest dives of all females was nearly identical (2.71 ± 0.44 and 2.78 ± 0.71 min, respectively) and not significantly different from the overall mean surface interval of all dives of all females (excluding ESIs), 2.76 ± 0.48 min. This point is further illustrated by the surface interval durations following the longest submersion recorded and a series of long dives that followed (Fig. 7). On March 14, 1985, beginning at 02:21, a dive by female Snl lasting 47.7 min was

TABLE 3. Mean surface interval (\pm SD) and frequency distribution of surface interval duration following all dives of six female elephant seals

Subject	Mean surface interval (min)	Percentage of surface intervals		
		<5 min	5–9.9 min	\geq 10 min
Dot	3.3 \pm 7.7	97.4	2.1	0.5
Ca	2.9 \pm 8.8	98.9	0.6	0.5
Ali	3.7 \pm 13.4	96.2	1.7	2.1
Gi	3.3 \pm 1.1	98.2	1.4	0.4
Td	2.2 \pm 5.0	99.5	0.2	0.3
Snl				
1985	2.7 \pm 3.0	99.2	0.5	0.3
1986	4.2 \pm 8.4	83.1	13.9	3.0

TABLE 4. The duration of continuous diving and the frequency of extended surface intervals (ESIs) lasting 10 min or longer, obtained from six female northern elephant seals

Subject	Longest bout of continuous diving		Extended surface intervals			
	No. of dives	Duration (days)	No.	Mean duration (h)	Max. duration (h)	Total duration (h)
Dot	1337	18.2	9	1.2 \pm 1.5	4.6	10.7
Ca	643	11.1	6	1.6 \pm 1.4	3.4	9.8
Ali	410	5	17	0.9 \pm 1.4	5.1	15.2
Gi	788	12.2	6	0.2 \pm 0.1	0.4	1.5
Td	692	10.9	3	1.1 \pm 1.2	2.5	3.4
Snl						
1985	738	13.1	3	0.7 \pm 0.6	1.4	2.1
1986	641	11	44	0.5 \pm 0.7	4.2	22.2

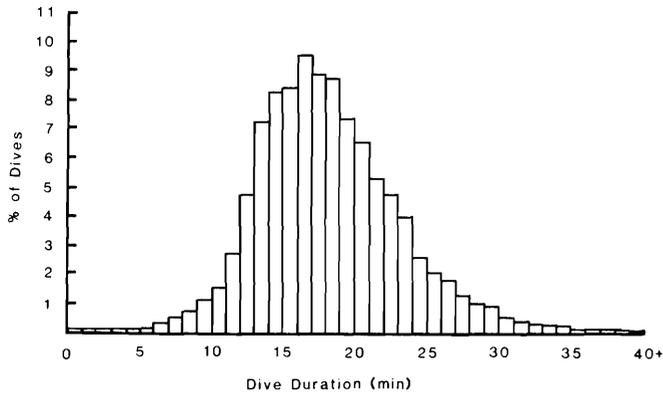


FIG. 5. A frequency distribution of all dive durations of six females (Rp excluded).

followed by five dives lasting over 30 min each. The mean surface interval following these dives was 2.17 ± 0.25 min, below the mean surface interval for all dives by Snl. During this period, 3.9 h, the female spent only 13 min in total at the surface.

Daily changes in dive pattern

Night dives were more numerous, shallower, and of shorter duration than day dives, as revealed by a record of all dives of all females by hour of day (Fig. 8). The same relationship is apparent in the diving performance of each female. For each individual, the period of relatively shallow dives at night was

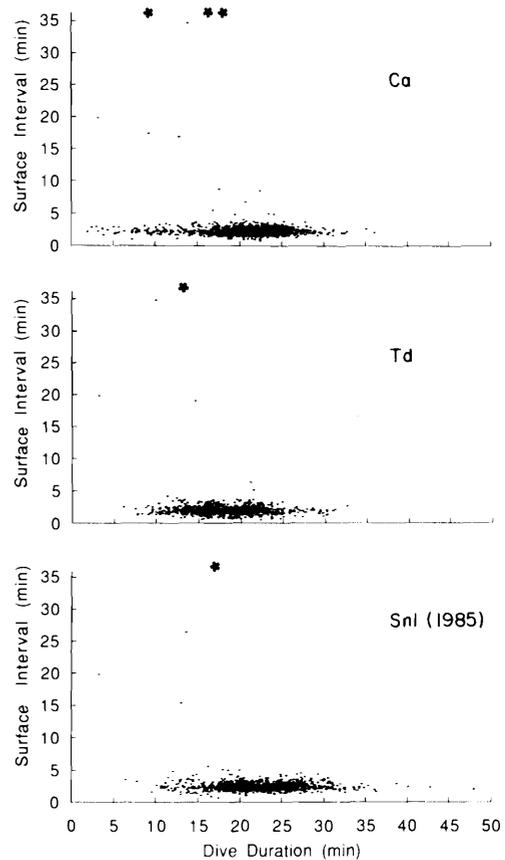


FIG. 6. Scatter plots of surface interval as a function of the preceding dive duration for three females. The asterisks denote surface intervals that exceeded 35 min.

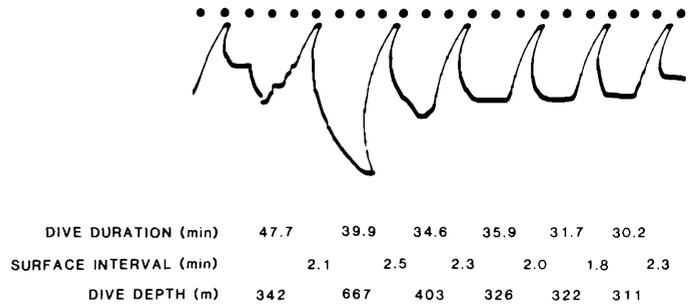


FIG. 7. An excerpt from day 9 of the dive record of Snl in 1985 showing the surface intervals following the longest dive recorded and a series of long dives. The timing dots at the top of each daily record are 12 min apart.

labile in its onset and variable in length.

Additional comparisons of diving behavior at midday (10:00–14:00) and at midnight (22:00–02:00) reveal that (i) dives were 27% more frequent during night hours (1576 vs. 1245), (ii) mean depth of day dives exceeded that of night dives by almost 100 m (466 vs. 370 m), and (iii) mean duration of day dives exceeded that of night dives by more than 4 min (21.5 vs. 17.3 min). All of these differences are statistically significant (*t*-tests, *p* < 0.05).

Relationship between dive duration and dive depth

Dive duration increased with increasing dive depth up to a certain depth, decreased abruptly, then began to climb again with further increases in depth (Fig. 9). This relationship

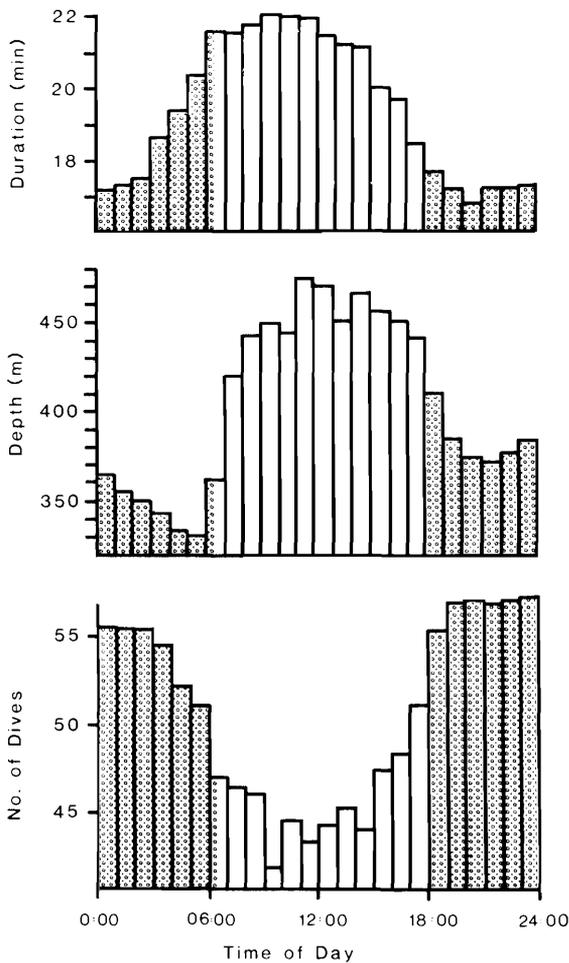


FIG. 8. Mean dive duration, mean dive depth, and mean dive number by hour of day. The shaded areas denotes darkness. The distributions are based on all dives of six adult females.

between dive duration and dive depth, and the two functions per record, are characteristic of the diving records of all females. The breakpoint, or apparent change from one function to another, was near 400 m for all females except the youngest, Dot, whose breakpoint was 300 m. At this point, dive duration decreased by approximately 6–15 min, the magnitude of change correlating positively with the age and mass of the females. The slope of the regression lines of each function (for relatively shallow dives before the breakpoint and for deeper dives after the breakpoint) is positive for all animals. With the exception of the dives of less than 200 m, most of which occurred on the first few days at sea, the relationship between dive duration and dive depth is not a time-based progression.

Dive types

A frequency distribution of dive types for each of three females is shown in Table 5. Most dives by each female were type D, deep dives with steady descent to a certain depth (the dive bottom) where the animal remained for a mean range of 23–42% of the total dive duration (Table 6) before ascending abruptly and steadily to the surface. Type D dives had either a relatively flat bottom with few small changes in depth in either direction or a “jagged” bottom with frequent small changes in depth (Fig. 2). The frequency distribution of other dive types varied greatly across individuals with some dive types being rare or absent in some records. Type D dives occurred in long

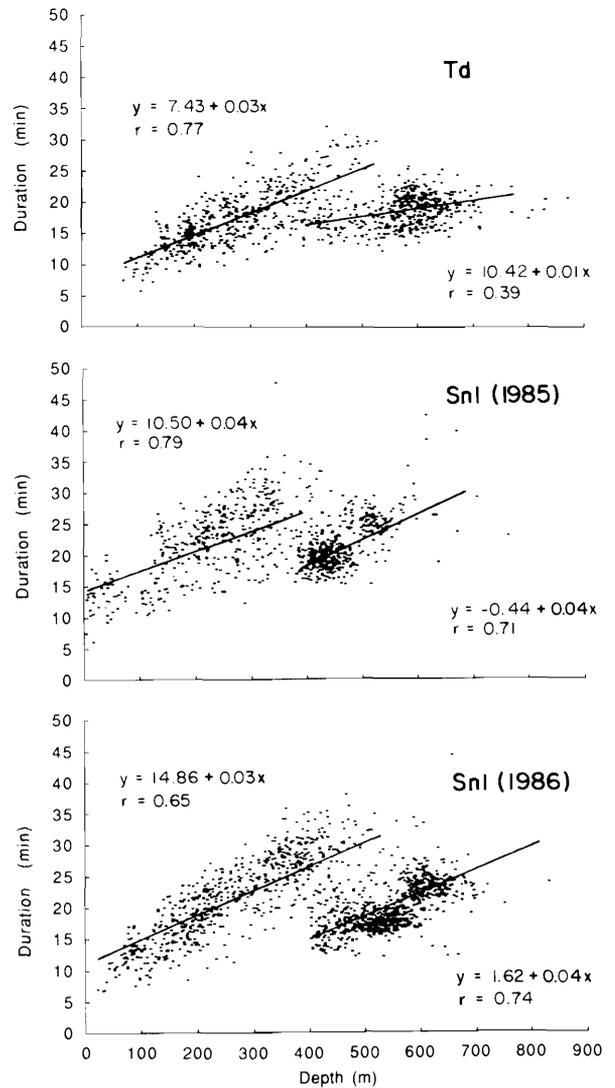


FIG. 9. Dive duration in relation to dive depth for female Td and female Snl in 1985 and 1986. The distributions are based on all dives for each female.

TABLE 5. Percentage distribution of total dives for three females broken down into six dive types (the period covered is from day 3 to the end of each record)

	Dive types					
	A	B	C	D	E	F
Gi	17.44	3.84	8.58	70.14	—	—
Td	3.03	15.16	7.39	65.45	1.82	7.03
Snl (1985)	0.82	0.33	2.79	77.14	18.26	0.49

series at all times of day and night but less frequently around midnight and the early morning hours.

Ascent and descent rates and bottom time

We calculated the ascent rate, descent rate, and time at the bottom of dives for dive types D, A, E, and B for the three females recorded in 1985 (Table 6). These rates could be calculated for these dives because of the sharp breakpoints at the

TABLE 6. Means and standard deviations of dive rates, dive segments, and dive depths for selected dive types of three adult females ($N = 12$ for each dive type)

Dive	Subject	Rate (m/s)		Duration (min)		Depth (m)
		Descent	Ascent	Total	Bottom	
Type D	Gi	1.96±0.43	1.10±0.16	17.34±2.77	4.02±1.34	547±97
	Td	1.40±0.24	2.11±0.44	19.82±1.82	8.28±2.00	569±92
	Snl (1985)	0.65±0.13	2.73±0.88	23.10±3.04	7.05±1.59	491±73
Type A	Gi	1.86±0.46	1.02±0.13	17.77±2.61		687±93
	Td	0.99±0.23	2.07±0.45	18.04±2.84		718±127
Type B	Gi	0.55±0.05	0.88±0.17	22.22±3.94		449±70
	Td	0.41±0.07	1.22±0.39	24.94±4.65		436±64
Type E	Snl (1985)	0.40±0.12	2.32±0.99	30.00±2.85	14.74±3.20	284±37

end of descent and at the beginning of ascent. The table shows the following. (i) Ascent and descent rates in the range 0.4–2.7 m/s were recorded. This is in accord with preliminary data obtained from swim velocity meters attached to female northern elephant seals (G. L. Kooyman and P. Ponganis, personal communication). (ii) The fastest descent and ascent rates for all females occurred during type D dives. Descent and ascent rates for type B and type E dives were significantly lower than for type D dives ($t \geq 3$, $df = 11$, $p < 0.05$). (iii) Within the same dive type, individual differences as great as twofold occurred between individuals in both ascent and descent rates. (iv) The rate of ascent was more rapid than that of descent in two females and in type B dives of the third; the reverse was true for type D and A dives by the latter. (v) Time at the bottom of dives averaged about one third of the total dive duration of type D dives and almost half of the dive duration of type E dives. The great variability of ascent and descent rates across dive type and between individuals makes it difficult to generalize these rates to females or to the species, except within broad limits.

Discussion

Female northern elephant seals diving under natural conditions have extraordinary capacities for breath holding and for withstanding high hydrostatic pressures. We argue below that the present study yields insights into foraging behavior and the habitat of elephant seals, diving adaptations and metabolism during diving, and the role of continuous diving.

Deep diving

Northern elephant seals are among the deepest diving mammals. The maximum depth recorded, 816 m, and the maximum depth estimated, 894 m, are almost 50% greater than the previous depth record for a pinniped, the Weddell seal, *Leptonychotes weddelli* (Kooyman 1968). At 900 m, pressure bearing on the elephant seal is 90 atm (1 atm = 101.325 kPa). More remarkable than their toleration of this enormous pressure is their toleration of the rate of compression they experience (Dossett and Hempleman 1972; Miller 1972). The 894-m dive lasted 22.5 min and we assume that it had a spiked bottom (type A dive). The seal went from 0 to 90 atm in about 11 min, averaging 8.18 atm/min or 1.35 m/s. This is far greater than the compression rate of 1.25 atm/min that is standard in some laboratories investigating the effects of pressure on mammals (Miller 1972). At faster rates, thresholds for the appearance of tremors and convulsions are lowered (Miller 1972).

Most dives by females in this study were in the range 350–650 m, far below 200 m where most other marine mammals

and marine birds feed, and where most human fishing activities take place. Fur seals (*Callorhinus ursinus*, *Arctocephalus gazella*, *A. pusillus*, *A. australis*, and *A. galapagoensis*) feed at mean depths in the range 26–175 m (Gentry et al. 1986; Kooyman et al. 1986; Kooyman and Gentry 1986; Trillmich et al. 1986; Kooyman and Trillmich 1986b). Sea lions (*Zalophus californianus*, *Z. c. woolebaeki*, and *Phocarcos hookeri*) dive in the mean depth range of 37–180 m (Feldkamp 1985; Kooyman and Trillmich 1986a; Gentry 1987). The mean depth range of Weddell seals, *L. weddelli*, is in the range 30–280 m, varying greatly with season and location (Kooyman 1975, 1981; Kooyman et al. 1980, 1983b). Most dives of monk seals, *Monachus schauinslandi*, are between 10 and 40 m (Kooyman et al. 1983a; Schlexer 1984). Among cetacea, few species dive as deep as elephant seals. The exceptions may include sperm whales, *Physeter catodon*, ensnared in deep-sea cables and tracked with echo-ranging equipment, which have suggested dives to at least 1100 m (Heezen 1957; Yablokov 1962; Gaskin 1964; Lockyer 1977), and white whales, *Delphinapterus leucas* (Ridgway et al. 1984), and pilot whales, *Globicephala* (Bowers and Henderson 1972), trained to dive to depths of 647 and 610 m, respectively. Some dolphins can dive to depths in the 300–500 m range (reviewed in Ridgway 1986). Most baleen whales (e.g., Slijper 1958; Leatherwood et al. 1982; Würsig et al. 1984, 1986; Dolphin 1987), as well as the sea otter, *Enhydra lutris* (Newby 1975; Estes et al. 1981; Dolphin 1987), are relatively shallow divers that feed in the top 150 m.

The data on diving depths are in accord with records of elephant seals caught in fishing gear, and at-sea observations suggesting that elephant seals feed primarily off the continental shelf beyond the 200-m mark. Most seals entangled in fishing gear have been caught at depths of 200 ± 20 m (Scheffer 1964; Condit and Le Boeuf 1984). In monthly aerial transect surveys conducted over the open ocean along the coast of California from Point Concepcion to the Oregon border from February 1980 to January 1983 (each transect running east to west from the coastline to 140 km offshore), only 165 northern elephant seals were sighted, 4.3% of the total number of pinnipeds observed (Bonnell et al. 1983). Of the elephant seals observed, 81% were seen over the continental slope or further offshore, i.e., in waters deeper than 200 m. The mean distance of sighted animals from the mainland was 35.2 km with the maximum distance being 140 km. These results are consistent with our findings that females spend most of their time at sea underwater and that they feed in deep water beyond the continental shelf.

The deep diving pattern of northern elephant seals suggests little overlap and competition for food with sympatric pinni-

peds, cetacea, and human fishing activities throughout their feeding range, the west coast of Mexico, the United States, and Canada (Condit and Le Boeuf 1984). Perhaps low competition for untapped resources in deep water was a major factor in their rapid recovery from near-extinction in the last century (Bartholomew and Hubbs 1960; Le Boeuf 1981; Cooper and Stewart 1983).

The depths attained by female elephant seals suggest that they feed actively in the deep scattering layer in the mesopelagic zone between 100 and 1000 m. A distinguishing characteristic of this zone is that many fishes make nightly vertical migrations from it up to the epipelagic zone (Marshall 1971, 1979). Known prey of elephant seals, such as squids and Pacific hake, *Merluccius productus* (Condit and Le Boeuf 1984), school in large numbers and migrate from deep water during the day up to 200–400 m at night (Nelson and Larkins 1970; Roper and Young 1973). The diel pattern of diving exhibited by females in this study (Fig. 8), with the shallowest dives occurring at night, corresponds with the daily schedule of these vertical migrators. This suggests strongly that the seal's dive pattern is set up by the habits of its prey and that foraging may be continuous throughout the day and night. Although foraging effort may be greater during the day than at night because the seals are diving deeper, this may be offset somewhat by the behavior of the prey. Active migrators are sluggish at depths during the day and are thought to be easy prey for predators (Barnham 1971).

If elephant seals are visual predators, how do they locate prey in this twilight zone of the ocean, where light gradually fades to extinction? Preying on bioluminescent animals is one possibility. Most of the fishes migrating towards the surface at night are bioluminescent (Childress and Nygaard 1973), and several species of squid, on which elephant seals prey (Condit and Le Boeuf 1984), have elaborate luminous organs (Marshall 1979). However, elephant seals also feed on nonbioluminescent animals (Condit and Le Boeuf 1984), which suggests that ambient light levels may dictate the prey species pursued.

Continuous diving

The continuous diving schedule of female northern elephant seals contrasts with that of other pinnipeds studied and more closely resembles the repeated dive pattern with short surface intervals observed in leatherback sea turtles, *Dermochelys coriacea* (Eckert et al. 1986). All other pinnipeds studied exhibit bouts of diving and it is assumed that such bouts represent foraging. Fur seals and sea lions usually engage in bouts lasting 2–4 h; 1.5–16 of these bouts occur during feeding trips lasting 1–7 days (Gentry and Kooyman 1986; Feldkamp 1985). Dive bouts in Weddell seals occur daily and last about 8–11 h (Kooyman 1975; Kooyman et al. 1979, 1980). During dive bouts, diving is continuous; most dives are brief, at a mean dive depth of about 200 m. Between dives, Weddell seals rest on the surface of the water or on ice.

The machine-like consistency of deep diving in elephant seals brings up the question of its utility. What is the function of this high rate of deep diving? We speculate on three possibilities: feeding, predator avoidance, and energy conservation.

Feeding

The association between diving and successful foraging is supported by several lines of evidence. (i) Females gained weight at the mean rate of 1 kg/day over the entire period at sea. From water influx data, we estimate that females consume 6.2% of their mass daily (unpublished data). Therefore, we

estimate that females in this study consumed approximately 20 kg of prey/day at sea. (ii) The majority of the dives of three females sampled had a form indicating activity at the bottom of the dive (type D dives). If this activity reflects foraging, then most dives served this function. Time spent at the bottom of these dives was a significant portion of the dive duration and varied little from dive to dive. The link between type D dives and feeding is further strengthened by the fact that descent and ascent rates were faster for these dive types than for any others, with means of 1.96 ± 0.43 and 2.73 ± 0.88 m/s, respectively. This suggests that the animals were travelling quickly to a certain depth, remaining there, and then travelling quickly back to the surface. Moreover, these rates are similar to those of feeding Weddell seals (Qvist et al. 1986) and humpback whales, *Megaptera novaeangliae* (Dolphin 1987). (iii) The uniformity of dive depth over a long series of dives suggests that the prey patches remain at the same depth over time and are dense enough for high encounter rates. It appears that seals often exploit a certain depth layer for several hours. For example, during a period from 16:00 to just past midnight, female Snl dived 26 times to a mean depth of 419.8 ± 15 m; the entire range of dive depths was 53 m, from 391 to 444 m. (iv) The diel pattern of diving, as discussed earlier, suggests that the seals were feeding on vertically migrating animals throughout the day.

While it is certain that part of the time at sea is spent feeding, it is not clear to what extent foraging accounts for the continuous nature of diving. Continuous diving could reflect a low catch rate, foraging on small prey that must be consumed in large numbers, or some other function.

Predator avoidance

Predator avoidance may be an added benefit to continuous, deep diving. The principal predator of northern elephant seals is the white shark, *Carcharodon carcharias* (Le Boeuf et al. 1982), a shallow-water predator that makes most of its attacks on seals near rookeries (Ainley et al. 1981). Most white shark sightings are in pelagic waters nearshore (Klimley 1985). We know of no observations of white sharks below 100 m. By remaining submerged at great depths for 85% of the time, elephant seals effectively reduce the probability of an encounter with a near-surface predator. The manner of swimming out to deep water from the rookery lends further support to this idea. Elephant seals do not swim at the surface or "porpoise" like sea lions. Instead, they dive repeatedly, with the dives getting progressively deeper, as if they are swimming to and from the bottom until deep water is reached (Fig. 2). The result is to minimize the time spent near the surface.

Energy conservation

Elephant seals may expend less energy diving than resting or swimming at the surface, making it expedient to continue diving even when they are not feeding. Reduction in overall metabolism may result from sleeping, the dive response, and reduced swim rates.

Reduced energy consumption is one of the correlates of sleep (Brebbia and Altschuler 1965; Snapp and Heller 1981; Berger 1984). In light of the universal presence of sleep in other animals (Zepelin and Rechtschaffen 1974), it could be expected that the seals slept for some portion of each day at sea. Elephant seals sleep daily in captivity (S. Ridgway, personal communication) and in nature when they are hauled out on land (Bartholomew 1954; Huntley 1984).

Elephant seals probably sleep underwater while at sea. Like

gray seals, *Halichoerus grypus*, they have been observed sleeping at the bottom of a pool in captivity (Ridgway et al. 1975). The irregular, terrestrial sleep pattern, with most sleep occurring during breath holding (Bartholomew 1954; Kenny 1979), suggests a likely sleep pattern in the diving elephant seal. Adult females alternate apneas of about 9 min with periods of eupnea lasting about 6 min (B. Le Boeuf, unpublished data). Electrophysiological studies of weaned pups on land show that sleep always occurs during apnea and only occurs 10% of the time during eupnea (Huntley 1984). A similar pattern may hold at sea, with most sleep occurring during diving rather than during breathing at the surface. If this is the case, all or part of some dives may result in energy conservation. Huntley (1984) showed that sleep apnea in weaned elephant seal pups results in a 23% reduction of basal metabolic rate (BMR). Moreover, sleeping near the bottom of dives would provide the most secure sleeping arrangement against near-surface predators.

Hypometabolism is also associated with the diving response, a collection of physiological events including apnea, bradycardia, and redistribution of cardiac output that brings about a significant reduction in perfusion and delivery of O₂ and substrates to most organs and tissues (e.g., liver, kidney, and non-working muscle) while sparing central organs and skeletal muscles used for swimming (Scholander 1940; Elsner and Gooden 1983; Hochachka and Guppy 1987). This response is associated with a decrease in temperature and metabolic rate in seals forced to dive (Scholander 1940; Scholander et al. 1942), trained to dive (Elsner 1965), and diving naturally (Kooyman et al. 1980; Guppy et al. 1986; Qvist et al. 1986). In free-ranging Weddell seals, Kooyman et al. (1973) observed a lower metabolic rate during diving than during resting at the surface.

Metabolic depression would appear to be facilitated by continuous exposure to cold waters and ingestion of cold prey. Our subjects were diving into the thermocline, going from surface water temperatures of 11.9°C to deep water temperatures averaging 5°C at 500 m at that time of year (M. Silver, personal communication). On land, body temperatures of adult elephant seals vary from 37 to 33°C, decreasing during periods of inactivity (McGinnis and Southworth 1971) and at night (Bartholomew 1954). This suggests that they have the capacity to lower their temperatures. During long dives to water with temperatures of -2°C, the core body temperature of Weddell seals drops about 3°C (Kooyman et al. 1980; Qvist et al. 1986). Hill et al. (1987) report decreases of about 2°C in aortic temperature of an adult male Weddell seal before sustained diving commences; they suggest that this reduction in temperature decreases the metabolic rate and O₂ consumption of central organs by 10–20%, thereby extending dive capacity. A similar decline may occur in elephant seals since they are diving continuously and spending most of their time in deep, cold water.

Depressed metabolism is one possible explanation for the absence of extended surface recovery periods following long dives in elephant seals. Surface intervals were as brief after a long dive as after a short one (Figs. 6 and 7). The exceptional ESIs did not necessarily follow or precede a long dive or a set of long dives, ruling out recovery from O₂ debt or anticipation of effort to be expended. A positive relationship between dive duration and the duration of the succeeding surface interval has been recorded in several diving mammals, e.g., sperm whales (Gaskin 1964), Weddell seals (Kooyman et al. 1980), and

humpback whales (Dolphin 1987). Recovery time at the surface is needed to repay the incurred O₂ debt and return blood pH to pre-dive levels. For example, in Weddell seals, peak blood lactate concentration increases exponentially with dives in excess of 20 min; the surface recovery period for return of lactate to pre-dive levels increases with longer dives (Kooyman et al. 1980).

The lack of a relationship between dive duration and succeeding surface intervals in elephant seals implies that whole body metabolism is aerobic during dives, with lactate production matched by lactate utilization. The production of anaerobic metabolites is contained, eliminating the necessity to metabolize lactate at the surface.

Calculation of the metabolic rate needed to sustain long dives aerobically indicates that such dives must be associated with hypometabolism. In a postlactation female weighing 333 kg, we estimated a total available O₂ store (blood, lung, and muscle) of 24 L (Lenfant et al. 1970; Kooyman 1973; Kooyman et al. 1980, 1983b; Castellini and Somero 1981; P. Thorson, unpublished data). To sustain a 45-min dive aerobically, the metabolic rate cannot exceed 0.67 times the BMR (Kleiber 1975; Lavigne et al. 1986). Although 45-min dives are infrequent, their occurrence without an extended surface interval is significant.

Hochachka and Guppy (1987) argue that hypometabolism during exceptionally long dives is associated with the diving response. Using radiolabeled isotopes administered during voluntary dives, Guppy et al. (1986) calculated that a 450-kg Weddell seal operates on only 45% of its resting metabolic rate during diving. They infer that switching down of metabolic rate is accomplished by a reversed Pasteur effect sustained in hypoperfused regions of the body whenever the diving response is employed.

Guppy et al. (1986) suggest that kidney perfusion must be decreased in Weddell seals to sustain dives. However, because elephant seals are submerged approximately 86% of the time that they are at sea (Table 2), the kidney and liver must be perfused for much of this time. The extreme reduction in kidney perfusion in Weddell seals of approximately 90% from pre-dive levels during short, forced dives (Zapol et al. 1979) and long, natural dives (Davis et al. 1983) is unlikely during most dives of elephant seals. Assuming renal perfusion values similar to those of Weddell seals before and during dives in a female northern elephant seal with 66 L of blood (P. Thorson, personal communication) that remains underwater 86% of the time over a series of dives, renal perfusion would be only 21% of the pre-dive resting level. This is unusually low given that the elephant seal is apparently feeding on many dives. The kidney perfusion rate of feeding harbor seals, *Phoca vitulina*, doubles after feeding (Hiatt and Hiatt 1942; Schmidt-Nielsen et al. 1959). We infer that substantial kidney perfusion must be maintained during most dives, a conclusion supported by the finding that kidneys are perfused in Weddell seals during aerobic dives of less than 20 min (Davis et al. 1983). Oxygen consumption by the kidney is proportional to glomerular filtration rate and, hence, kidney perfusion (Valtin 1973; Davis et al. 1983). Perfusion of the liver and kidney during a dive therefore elevates the animal's rate of oxygen consumption.

Cardiac output and the rate of oxygen consumption also depend on swimming speed (Hochachka and Guppy 1987). Since the amount of O₂ in the body is set at the beginning of the dive, the length of a dive supported aerobically is determined by the animal's metabolic rate, which is influenced by swim-

ming speed and organ perfusion rates. Our data suggest an association between metabolic rate and the depth and duration of dives, i.e., the seal must swim faster to dive deeper and, in doing so, expends more energy. If so, elephant seals may utilize the bulk of their available oxygen stores on most dives.

Kooyman et al. (1983b) calculated the aerobic dive limit (ADL) for Weddell seals based upon available oxygen stores and metabolic rate. The ADL is defined as the maximum breath hold possible without any increase in blood lactate (LA) concentration during or after the dive (Kooyman et al. 1980). This limit is set by available O₂ stores, diving metabolic rate, degree of peripheral vasoconstriction, and the rate of LA production and removal (Kooyman 1985). Dives that exceed the calculated ADL incur a buildup of anaerobic by-products and require an extended surface interval to process these metabolites and return pH to pre-dive levels. The lack of an association between dive duration and succeeding surface interval duration in elephant seals implies that their ADL was never exceeded. This aerobic dive pattern best serves foraging because it yields the greatest amount of time underwater (Kooyman et al. 1980). Furthermore, if the putative variable nature of the metabolic rate (owing to adjustments in organ perfusion and activity during diving) is correct, elephant seals may approach their ADL on most dives. That is, the ADL varies with the average metabolic rate during each dive.

The concept of a variable metabolic rate during diving is supported by indirect evidence that swim speed varies between dives. Variable swim rates may explain the differences in dive duration above and below a certain depth (Fig. 9). In northern fur seals (Gentry et al. 1986) and California sea lions (Feldkamp 1985), dive duration increases linearly with depth. Since these animals spend little time at depth, this suggests that average swim rate remains constant during dives regardless of depth. However, female elephant seals exhibit a complex relationship between dive duration and dive depth. Duration increases linearly with depth in dives of less than 400 m. At that depth, dive duration is markedly reduced and then a new function begins with dive duration increasing with depth. We interpret this discontinuity as a "shift of gears" in which the animal resets its oxygen utilization rate. To maximize bottom time, the females may increase their swim rate and shorten travel time to depth at the expense of reducing the overall time submerged. This suggests that the diver adjusts its swim rate to the depth of the anticipated dive. This conjecture is consistent with the hypothesis that during most natural dives the diver is using O₂ at a rate commensurate with a planned dive (Kooyman 1985).

To the extent that metabolic depression is characteristic of diving in female elephant seals, diving should serve purposes of rest and conservation of energy as well as feeding and predator avoidance. Continuous diving would be an efficient means of recovery from a costly reproductive effort during which females lose $42.2 \pm 4.9\%$ of their mass (Costa et al. 1986), viz., minimizing energy loss while attempting to maximize energy intake.

In conclusion, the dive pattern of female elephant seals differs fundamentally from that of other pinnipeds. Our current understanding of the physiological processes governing free-ranging dives derives from examination of diving bouts of coastal species during brief trips to sea. Modifications may be necessary to explain continuous diving in the pelagic elephant seal.

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