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Diving Behavior of Female Northern Elephant Seals, *Mirounga angustirostris*

by

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, California 95064

Corresponding Author: B. J. Le Boeuf (408) 429-2845, 429-4026

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Le BOEUF, B.J., D.P. Costa, A.C. Huntley, and S.D. FELDKAMP. Dive Pattern of Female Northern Elephant Seals, Mirounga angustirostris.

The free-ranging dive pattern of seven adult female northern elephant seals 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 per hour 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 rein, resulting in only 14.4% of the recorded time at sea being spent on the surface. Surface intervals did not vary with the duration of preceding 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, long, nearly continuous dive pattern of female elephant seals differs from the dive pattern of other pinnipeds and may serve to facilitate foraging, energy conservation, and predator avoidance. The data suggest that most dives are aerobic and that metabolism varies in accordance with anticipated activity.

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 attached to free-diving pinnipeds that record diving performance and reflect foraging behavior (Kooyman 1975, 1981; Kooyman, Gentry and Urquhart 1976; Kooyman, Billups and FarWell 1983) . During the last decade, depth recorders have been used to obtain free-ranging dive records from four phocids (Kooyman et al. 1983; 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 with increasingly more sophisticated instruments. A glimpse of the marine habits of pinnipeds is beginning to emerge.

Data from time-depth recorders (TDRs) yield information on depth and duration of individual dives, diving schedules, time spent swimming, diving, or at the surface, duration of dive bouts , dive bouts per trip to sea, and day and night diving. These data describe the normal diving pattern and provide indirect evidence of foraging strategies employed. Dive data also provide information on physiological adaptations for diving. Free ranging dive patterns provide a perspective for evaluating studies of diving capacity in captive seals (e.g., Scholander 1940; Andersen 1966; Elsner 1969; Kooyman, Castellini and Davis 1981; Elsner and Gooden 1983). 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. Lactic acid build-up 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; Kooyman et al. 1983; Gentry and Kooyman 1986). Thus, TDRs shed light on the extent to which diving potential is reflected in diving performance.

This paper reports a study of free-diving and foraging 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 four 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 one month (Le Boeuf, Whiting and Gantt 1972; Reiter, Panken and Le Boeuf 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 behavior, and their predictable habits aid in determining the optimal time and place to attach and recover instruments.

A preliminary study of one adult female (Le Boeuf et al. 1986) revealed continuous diving for the first 11 days at sea, a mean dive duration of 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 of time differs from the dive pattern of other pinnipeds and raises a number of questions concerning oxygen utilization 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 which 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 ranging in age from 3 to 10 years old (Table 1) . One female carried instruments in both years, making the total number of females monitored seven. All subjects were marked individually (Le Boeuf and Peterson 1969) and their behavior and that of their pups was monitored daily throughout their stay on land. Each female gave birth, nursed her pup daily for about four weeks, and weaned her pup within two days after instrument attachment.

Subjects were immobilized with 4-6 mg/kg of ketamine

hydrochloride (Ketaset, Bristol Laboratories, Syracuse, N.Y.) (Briggs, Hendrickson and Le Boeuf 1975) a day before they were expected to go to sea. Departure was predicted from parturition date and age (Reiter, Panken and Le Boeuf 1981). Two darts containing a total of approximately 25-30 ml of ketamine (loo mg/ml) and 1-3 ml of 5 mg/ml diazapam (Valium, Roche Laboratories, Nutley, N.J.) were fired into the hind quarters with a CO_2 pistol (Cap-Chur Darts and Pistol, Palmer Chemical co.) as the subject rested on the periphery of the harem. Subsequent injections of 1-10 ml of ketamine and 1-3 ml of diazapam were administered with a syringe intramuscularly or intravenously when necessary.

Within 15 min after drug administration, the female was approached, measured, rolled onto a nylon stretcher and weighed with a 1000 $\pm$ 2.5 kg dynamometer (Chatillon WT-1000) that hung from an aluminum tripod (Costa et al. 1986). Her pup was weighed, measured, sexed, marked and tagged in the hindflippers (Le Boeuf and Peterson 1969).

The TDRs were photomechanical (J. Billups, Meer Instruments, Del Mar, California), identical to the type used in the preliminary study on elephant seals (Le Boeuf et al. 1986) (Figure 1). A full description of the 5 X 20 cm, 700 gm instrument, manufactured by J. Billups (Meer Instruments, Del Mar, California), is given by Kooyman (1981) and Kooyman, Billups and Farwell (1983). The TDR produces a photographic record of dive duration and dive depth in real time. Dives greater than 10 m in depth and 30 sec in duration can be resolved. Prior to

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 hrs before attachment to females.

The procedure for attaching the instruments was as follows. After cleaning the pelage with acetone, a PVC mold, 16 cm wide, was placed on the dorsal midline of each female above the shoulders (Figure 1). The mold was filled with marine epoxy (Evercoat Ten-set, Fibre-Evercoat Co., Cincinatti, Ohio) and the adhesive was worked under the hair. An 18 gauge, 3 X 14 cm aluminum plate, to which a TDR and a 9 X 3 cm radiotransmitter (148-150 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 hrs after the last drug administration; two females in 1986 (Rp and Sn1) departed 24-48 hours after the last drug injection.

Based on data collected in previous years (B. Le Boeuf and J. Reiter, unpublished) , we expected females to return to the rookery to molt in 68 $\pm$ 5 days. We began searching Año Nuevo Island and the nearby mainland point for returning subjects 65 days after each one left the rookery. In addition, a radio receiver (Telonics, Mesa, Arizona) attached to a strip chart recorder indicated the exact time of arrival of each female in the area to the nearest hour. All instrumented females returned to the Ano Nuevo rookery. Within a day after a female returned, she was immobilized, weighed and the depth recorder and transmitter were retrieved. The hose clamps protruding from the

epoxy mount were cut off. The epoxy mount fell off within two 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.

All dives of three females, from day 3 until the end of the record, were classified into six dive types based on their configuration, the latter being 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. The first two days were omitted to allow the animals to reach deep water off-shore. For each female, twelve dives of the type having a well-marked dive-bottom were selected randomly for measurement of ascent-descent speed and other rate measurements. We calculated the curvilinear arc of the recording pen of each record, checked it against the calibration marks, and drew this arc on a sheet of clear plastic. Using this template, we measured temporal deviation from the calculated arc of the pen, i.e., time from the surface to the bottom of a dive or vice versa for ascent and descent duration, respectively. Rates were derived by dividing depth by duration.

The timing circuit failed on one instrument half way 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.

Results

Time at Sea and Mass Gain

Females spent a mean of 72.6 ± 5.0 days at sea, gained a mean of 1.05 ± .18 kg per day over the entire period, and increased their mass over their departing weight by a mean of 24.1 ± 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, as reflected by lengthening the interval at sea or by causing a reduction in weight gain.

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. Each seal dived 2.7 ± 0.2 times per hour 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 three minutes on the surface. Mean dive depths for each female exceeded 345 m. Excerpts from the dive record of one female, Sn1 in 1985, illustrate the general diving pattern (Figure 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 816 m limit of the 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 (Figure 3).

An analysis of the distribution of dive depths by day for each female shows the following:

1. Dives were shallow on the first day at sea and became progressively deeper with time until a modal or preferred depth pattern was established by day 4 to 6. This pattern remained relatively constant for the remainder of each record. This pattern is illustrated in Figures 4, 5, and 6 for the females recorded in 1985. The modal or preferred dive depth of all females, once they had reached deep water, was in the range, 350 to 650 m. The interval preferred by Rp, Ca, Ali, Gi and Sn1 (1985) was 400-450 m, with the others preferring the intervals: 350-400 m (Dot), 500-550 m (Sn1 in 1986), and 600-650 m (Td).

2. All females went directly out 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 first day or the beginning of the second day. The mean interval between the time of departure and the first dive to 200 m or more was 18.9 ± 15.1 hrs (Range = 3.3-46 hrs).

3. After the first few days, the daily dive depths of some females assumed a bimodal distribution (Figure 4). This resulted from a diel pattern of diving that will be discussed later.

4. After six days at sea, dives less than 100 m in depth were extremely rare (.06%) and only 1.34% of the dives were shallower than 200 m. Thus, most of the shallow dives in Figure 3 occurred during the first few days at sea.

5. 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 (Figure 2). The dive rate decreased with the age and mass of females and 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). 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 hrs per day on the surface (Table 2).

The degree of continuous diving is indicated by analysis of the surface intervals between dives. A frequency distribution of

the surface intervals shows that the majority of all dives in each record was followed by a surface interval of less than five minutes (Table 3). The mean surface interval for each animal ranged from 2.2 to 4.2 ruin.

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 lasting longer than 10 min, averaged less than one per day for each female, with the exception of female Sn1 in 1986 (Table 4). The maximum ESI per record was variable, from less than an hour to slightly over 5 hrs. Similarly, total time per record spent in ESIS ranged from 1.5-22 hrs. The duration of continuous diving without an ESI averaged 754 dives, or approximately 11 days. The four-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 Sn1) as it was among females within the same year.

The temporal patterning and duration of ESIS provides no obvious clues to their function: (1) ESI's occurred during the beginning, middle and end of records. When each record was divided into 10 equal parts and the frequency of ESIS in each part was summed across females, the distribution was random. The record of female Sn1 in 1986, stood out from the rest. Eighty percent of her ESI's occurred on days 2-4; most of these were brief ($\bar{X}$ = 21.4 $\pm$ 18 rein). (2) ESIS occurred at almost all hours of the day. Summing the records across hours of the day

yielded 1-5 ESIS at all hours except 0000-0100, 0600-0800, 1600-1700, and 2100-2200. (3) Eleven of 15 ESI's greater than 60 min occurred between 0900 and 1400 hrs. However, this effect was due to the performance of Ali, Dot and Snl; Ca and Td had their longest ESI's during the night. (4) EsI's did not follow or precede long or deep dives, suggesting that recovery or anticipation of effort was not involved. The mean dive durations before and after the 15 longest ESI's were 18.6 ± 5.2 and 17.5 ± 3.7, respectively, shorter than the overall mean dive duration of all females (19.2 ± 4.3), and not significantly different from each other (Wilcoxon Signed Ranks, T = 21, df = 15, $p < .05$). Conversely, the mean surface interval before and after the 15 longest dives of all females was nearly identical (2.71 ± .44 and 2.78 ± .71, respectively) and not significantly different from the overall mean surface interval of all dives of all females (excluding ESI's), 2.76 ± .48. (5) The depth of preceding and succeeding dives suggests that each ESI occurred at sea in deep water and did not represent resting on land.

Dive Duration

Mean dive duration varied from 16.4 to 22 min among the six females recorded (Table 2). Mean dive duration appears to increase with 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. However, the sample size is too small to be confident of this relationship.

Mean dive durations per day for each female were shortest on

the first day at sea, increased significantly up to day 4, and then remained fairly constant until the end of the record. For example, the mean daily dive duration 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 for days 1-10, respectively. Figure 7 illustrates these changes for the longest diver, Snl in 1985. On day 1, 85% of her dives were less than 16 rein; by day 4, only .9% of her dives were this brief. By day 5, her most frequent dives were in the intervals 18-20 and 24-26 min.

A frequency distribution of the dive durations of all females shows that the majority of dives (81.5%) were in the interval 12-24 min (Figure 8). Dives shorter than 10 min and longer than 30 min were rare.

Surface intervals did not vary systematically with the duration of preceding dives (Figure 9). This is further illustrated by the most extreme ease, the surface intervals following the longest submersion and the series of long dives that followed (Figure 10). On March 14, 1985, beginning at 0221 hrs, a dive by female Snl lasting 47.7 min was followed by five dives lasting over 30 min each. The mean surface interval following these dives was 2.17 $\pm$ .25, below her mean surface interval for all dives. During this period, 3.9 hrs, the female spent only 13 min 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 (Figure 11) . The same relationship is

apparent in the diving performance of each female. For each individual, the period of relatively shallow dives at night was labile in its onset and variable in length.

Additional comparisons of diving behavior at midday (looo-1400 hrs) and at midnight (2200-0200 hrs) reveal that: (1) dives were 27% more frequent during night hours (1,576 vs 1,245), (2) mean depth of day dives exceeded night dives by almost 100 m (466 Vs 370 m), and (3) mean duration of day dives exceeded night dives by more than 4 min (21.5 vs 17.3 rein). All of these differences are statistically significant (t tests, $p < .05$).

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 (Figure 12). This relationship 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 to 15 rein, the magnitude of change correlating positively with the age and mass of the females. This dual function, illustrated for two females in Figure 12, is characteristic of the diving records of all 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 below 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

We were able to distinguish six dive types, after an animal was at sea for two days (Table 5). The majority of the dives of each female recorded in 1985 were type D, deep dives with a 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 (Figure 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 series at all times of day and night but less frequently around midnight and the early morning hours.

Ascent-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 break-point at the end of descent and at the beginning of ascent. The table shows that: (1) Ascent-descent rates in the range, .4 to 2.7 m/see 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, pers. comm.). (2)

Both ascent and descent rates varied with dive type. (3) 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 slower than for type D dives (t's = 3 or greater, df = 11, p c .05). (4) Within the same dive type, individual differences as great as twofold, occurred between individuals in both ascent and descent rates. (5) The rate of ascent was more rapid than descent in two females and the reverse held for the third female. (6) 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

Results of diving under natural conditions show that female northern elephant seals have extraordinary capacities for breath holding, and withstanding changes in high pressures to permit deep diving. The normative data presented put the results of physiological studies of diving under laboratory conditions in perspective and help us to understand the relevance of laboratory studies of this species to normal activities in the animal's life. We argue below that the present study yields insights into foraging behavior and the nature of the niche exploited by 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, is almost 50% greater than the previous depth record held by a pinniped, the Weddell seal, Leptonychotes weddelli (Kooyman 1968). At these depths, the pressure bearing on the animal is 90 atmospheres (atm). More remarkable than tolerating this enormous pressure is the rate of compression experienced by the animal (Dossett and Hempleman 1972; Miller 1972). The record setting 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 rein, averaging 8.18 atm/min or 1.35 m/see. This is far greater than the compression rate of 1.25 atm/min that is standard in some laboratories investigating the effect 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 to 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, Kooyman and Goebel 1986; Kooyman, Davis and Croxall 1986; Kooyman and Gentry 1986; Trillmich, Kooyman, Majluf and Sanchez-Grinan 1986; Kooyman and Trillmich 1986b). Sea lions (Zalophus californianus, Z. c. wollebaeki, and Phocarctos 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, Leptonychotes weddelli, is in the range 30-280 m, varying greatly with season and location (Kooyman 1975; 1981; Kooyman et al. 1980; Kooyman et al. 1983). Most dives of monk seals, Monachus schauinslandi, are between 10 and 40 m (Kooyman, Billups and Farwell 1983; Schlexer 1984). Among cetacea, few species dive as deep as elephant seals. The exceptions may include sperm whales, Physeter catodon, who have been ensnared in deep-sea cables and tracked with echo-ranging equipment, suggesting dives to at least 1,100 m (Heezen 1957; Yablokov 1962; Gaskin 1964; Lockyer 1977), and white whales, Delphinapterus leucas, that have been trained to dive to depths of 647 m (Ridgway et al. 1984). Circumstantial evidence indicates that most baleen whales, dolphins and the sea otter, Enhydra lutris, are relatively shallow divers that feed in the top 100 m (e.g., Slijper 1958; Leatherwood et al. 1982; Wursig et al. 1984; Jacobsen 1985; Wells 1986; Wursig, Wells and Croll 1986; Newby 1975; Estes, Jameson and Johnson 1981).

The data on diving depths are in accord with records of elephant seals being caught in fishing gear and at-sea observations that suggest 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 $\pm$ 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 Conception to the Oregon border from February 1980 to January 1983 (each transect running east to west from the coastline over the continental shelf (0-199 m), the

continental slope (200-1999 m), and offshore beyond the continental slope (greater than 2000 m) to 140 km from shore), only 165 northern elephant seals were sighted, 4.3% of the total number of pinnipeds observed (Bonnell, Pierson and Farrens 1983). Eighty one percent of the elephant seals were seen over the continental slope or further offshore; 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 that they encounter little competition for prey at the depths where they feed along the west coast of Mexico, the United States, and Canada (Condit and Le Boeuf 1984) . It is clear from dive depth profiles that they would not be competing with fur seals, California sea lions, harbor seals, Phoca vitulina, sea otters or diving birds. Their range does not overlap with white whales and sperm whales are not abundant in the northern elephant seal's range. Most commercial fishing in this region occurs in the top 100 m zone. Perhaps low competition for food at these depths is a major reason why northern elephant seals have made such a rapid recovery from near-extinction in the last century (Bartholomew and Hubbs 1960; Bonnell et al., 1978; Le Boeuf, 1981; Cooper and Stewart, 1983).

The depths attained by female elephant seals, and our mass gain data, suggest that they are actively feeding in the deep scattering layer in the mesopelagic zone between 100 - 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 (Figures 4 and 11), 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 by the habits of its prey and that foraging is continuous throughout the day and night. Although foraging effort may be greater during the day than at night because the seals are diving deeper, and as a result, less long, 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 localize 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 and they have a higher energy content than fishes that remain in bathypelagic waters (Childress and Nygaard, 1973). 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). Perhaps the prey pursued is specific to ambient light conditions but this

is unknown.

Continuous Diving

The continuous diving schedule of female northern elephant seals contrasts with that of other pinnipeds studied. All of the latter exhibit bouts of diving and it is assumed that diving bouts represent foraging. Fur seals and sea lions engage in bouts lasting 2-4 hrs; 1.5 to 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 hrs (Kooyman 1975; Kooyman et al. 1979; Kooyman et al. 1980). During dive bouts, diving is continuous with most dives being brief and 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 diving in elephant seals brings up several questions: How long does uninterrupted diving continue? Is this pattern characteristic of the other period that females spend at sea, after the molt when they are gestating? Is this pattern typical of both sexes? The present data do not speak to these questions and answers will require further research. We are also at a loss to explain the function of the rare exceptions to continuous diving, the ESI's. The longest ESIS tend to occur at midday, when dive depths and dive durations are greatest. However, one cannot conclude that they signify rest since these periods are brief and infrequent and they do not necessarily follow or precede a set of long, deep dives, indicating effort expended or to be expended. ESI's might reflect satiety but this is unlikely since many of them occur early in the period at sea.

What is the function of this high rate of diving? We speculate on three possibilities: feeding, sleep or energy conservation and predator avoidance.

Feeding. The association between diving and successful foraging is supported by several lines of evidence: 1) Females gained weight at the mean rate of 1 kg per 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 per day at sea. 2) 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 and 2.7 m/sec, respectively. This suggests that the animals were traveling quickly to a certain depth, remaining there, and then traveling quickly back to the surface. 3) 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 1600 to just past midnight, female sn1 dived 26 times to a mean depth of 419.8 ± 15 m; the entire range was 53 m, from 391 to 444 m. 4) The diel pattern of diving, as discussed earlier, suggests feeding

on vertically migrating animals throughout the day.

Energy conservation. Elephant seals may expend less energy diving than resting or swimming at the surface, which would make it expedient to continue diving even when not feeding. This is suggested by three lines of indirect evidence. First, diving is associated with a decrease in temperature and metabolic rate in seals forced to dive (Scholander 1940; Scholander, Irving and Grinnell 1942), trained to dive (Elsner 1965) and diving naturally (Kooyman et al. 1980; Qvist et al. 1986). Metabolic depression is brought about mainly by cardiovascular changes that redistribute blood to vital structures while restricting blood flow to other organs, i.e., the "diving response" (Elsner and Gooden 1983).

Second, depression of metabolism 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 temperatures of 11.9 °C to temperatures averaging 5 °C at 500 m at this time of year (M. Silver, pers. comm.). On land, 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. In Weddell seals, core body temperature drops about 3 °C during long dives to - 2° C (Kooyman et al. 1980; Qvist et al. 1986). A similar decline is likely in elephant seals since they are spending most of their time in deep cold water.

Third, we argue that the female elephant seals are sleeping

during all or part of certain dives. Reduction in energy consumption is one of the functions of sleep (Brebbia and Altschuler 1965; Snapp and Heller 1981; Berger 1984). We discount two other possibilities. It is unlikely that the seals did not sleep at all in light of the universal presence of sleep in other animals (Zepelin and Rechtschaffen 1974) . One expects that the seals slept some portion of every day at sea. This would also be predicted from their behavior on land; individuals of both sexes and all age categories sleep daily. Sleeping on the surface of the water is unlikely given what we know about sleep when these animals are on land. Elephant seals breath irregularly on land (Bartholomew 1954; Kenny 1979). During behavioral sleep (i.e., supine, inactive, with eyes closed, and increased arousal threshold) , 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 show that all apneas greater than 1 min occur during sleep, and that less than 10 % of the total sleep time is associated with eupnea (Huntley 1984). Thus , if sleep on land is associated with breath holding, it is likely to be associated with breath holding at sea. Sleeping at the surface while breathing is unlikely because this would necessitate a complete change in sleeping pattern. Breath hold sleep at the surface is also unlikely because the animal must replenish oxygen stores and expel excess CO_2 following a dive. Moreover, from the regression equation for total sleep time in mammals based on body mass (Zepelin and Rechtschaffen 1974), one would expect a 333 kg seal to sleep 27 % of the time or 6.5 hrs per day. Elephant seal

females spent a mean percentage of only 14.4 % of the time at the surface, 3.46 hrs per day. Even if all of this time was spent sleeping, it would be less than the predicted amount of sleep.

Elephant seals probably sleep underwater while at sea, but it is not clear when it occurs, how long it lasts, or whether it resembles the sleep state in terrestrial mammals. Weaned pups and juveniles in captivity have been observed sleeping at the bottom of a pool. However, it is unlikely that the free-diving females were sleeping and inactive during descent or ascent because the depths reached would require rapid drift rates in the range of .7 to 2.7 m/see. Most likely, the seals slept while swimming on ascent and descent or they slept at the bottom of some dives. The latter would provide the most secure sleeping arrangement against near surface predators (see below]. Some dives were characterized by long inactive periods at the bottom of the dive (dive type E). However, these dives were rare in two of the three individuals measured. Preliminary data from microprocessors with attached swim velocity meters indicate zero swim velocity rates in some dives during the first few days at sea but it is not clear whether this represents sleep or waiting for prey (G. Kooyman, P. Ponganis, pers. comma) .

This logic suggests an efficient strategy of recovery from a large reproductive effort during which females lose 42.2 $\pm$ 4.9 % of their mass (Costa et al. 1986) . Females minimize energy output while realimenting.

Predator avoidance. Continuous, deep diving might also play a role in predator avoidance. The principal predator of northern

elephant seals is the white shark, Carcharodon carcharias. These animals appear to be shallow water predators, making most of their attacks on seals near rookeries (Ainley et al 1981; Le Boeuf, Riedman and Keyes 1982). Most white sharks sightings are in pelagic waters nearshore (Klimley 1985). We know of no reports of white sharks being observed 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 (Figure 2). The result is minimizing the amount of time spent near the surface.

Aerobic diving

One of the most interesting aspects of this study is the apparent lack of a relationship between dive duration and the following surface interval (Figures 9 and 10). If anaerobic metabolism was used to sustain the longest dives, we would expect a concomitant long recovery period on the surface. Kooyman et al. (1980) found a positive correlation between dive duration and surface recovery time following Weddell seal free-ranging dives that exceeded the aerobic dive limit. The aerobic dive limit (ADL) is defined as the maximum breath hold that is possible without any increase in blood lactic acid concentration (LA) during or after the dive (Kooyman et al. 1980). This limit is

set by available 0_2 stores, diving metabolic rate, degree of peripheral vasoconstriction, and the rate of LA production and removal (Kooyman 1985). The absence of extended surface recovery periods following long dives in elephant seals suggest that these animals were either able to reduce metabolic rates to aerobic levels, or they metabolized accumulated LA by utilizing body 0_2 stores during subsequent shorter dives.

Following the procedure of Kooyman et al. (1983), we calculated the theoretical ADL of northern elephant seal females using measurements of body oxygen stores and an assumed metabolic rate. In an average sized departing female weighing 333 kg, we estimate a total available 0_2 store of 24.2 1 (Lenfant et al 1970; Kooyman 1973; Kooyman et al. 1980; Castellini and Somero 1981; Kooyman et al. 1983; P. Thorson, unpublished data). If metabolism during diving is estimated to be equal to that predicted by the Kleiber (1975) equation for a resting, post-absorptive, adult animal that is thermoneutral (2.44 ml 0_2 "rein^{-1}·kg^{-1}) (see Lavigne et al. 1986), then sufficient oxygen would be available to sustain a dive for 30 min. Ninety eight percent of the recorded dives were shorter than this estimated limit, a result similar to that found in other seals and fur seals (Kooyman et al. 1980; Kooyman et al. 1983; Kooyman and Gentry 1986). However, during many dives, the animals were neither resting nor fasting, but swimming, diving, hunting and feeding throughout the period recorded, and we assume, throughout most of the period at sea. If we assume a higher metabolic rate during diving of 1.5 times that predicted by Kleiber (Kooyman 1985), then the estimated ADL reduces to 20 min. Of all recorded

dives, only 62.8 % were less than 20 min in duration. We conclude that on long duration dives exceeding 20 rein, metabolism is reduced to near resting levels.

Of further interest are the 2% of the dives that exceeded the predicted ADL of 30 min. All females had dive durations exceeding this limit and in no case did ensuing surface intervals deviate significantly from the overall mean surface interval. This suggests that these dives were also aerobic. Using the estimated 0_2 stores presented above, a diving metabolic rate of 0.67 times resting must be postulated for a 45 min dive to be sustained aerobically. We do not know if metabolism is normally reduced to this degree. Captive studies suggest that elephant seals have this capacity. In a female forced to dive, Van Citters et al. (1965) recorded a change in heart rate from 60 beats/rein during resting to 4 beats/rein near the end of a 40 min submersion. Work on Weddell seals has shown that average diving metabolism is lower than metabolism while resting at the surface (Kooyman et al. 1973) and Kooyman et al. (1980) conclude that this is due to lowered metabolism during dives. During the free ranging dives of elephant seals that exceed the 30 min ADL, activity may be reduced by reducing blood flow to certain organs. This suggests a lowering of swimrates (Kooyman 1985) or sleep.

Variable swimrates may explain the difference in dive duration above and below a certain depth (Figure 12). In northern fur seals (Gentry, Kooyman and Goebel 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 this 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. In order to maximize bottom time, the females may increase their swimrate and shorten travel time to depth at the expense of reducing the overall time submerged. This suggests that the diver adjusts its swimrate to the depth of the anticipated dive. This conjecture is consistent with the hypothesis that during most natural dives the diver is not so much defending itself against asphyxia (Elsner et al. 1966), but instead is utilizing 0_2 at a rate commensurate with a planned dive (Kooyman 1985).

In conclusion, the dive pattern of female elephant seals differs fundamentally from that of other pinnipeds. Our understanding of the physiological processes governing free ranging dives has come from examination of diving bouts of coastal species during brief trips to sea. This may require modification to explain continuous diving in the pelagic elephant seal. Data presented here provide additional support for the statement that the dive pattern that best serves foraging consists of aerobic dives, where only blood and muscle oxygen stores need to be replenished (Kooyman et al. 1980). Lastly, the results suggest that metabolism is labile and varies with activity and the duration of the dive.

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

Subject (year)	Age (yrs)	Mass (kg) Departure	Recovery	Gain	Days at sea	Mass gain per day	% Mass increase at sea
Rp (1986)	3	247	305	58	74	.78	23.5
Dot (1986)	4	253	326	73	75	.97	28.8
Ca (1986)	5	307	402	95	75	1.26	30.9
Al i (1986)	6	325	384	59	62	.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
Snl (1986)	10	399	470	71	76	.93	17.8
Means		322.5	399.0	76.5	72.6	1.05	24.1
Stan. Dev.		58.5	65.3	13.9	5.0	.18	4.6

Table 2. Summary statistics from the diving records of seven adult female northern elephant seals obtained in 1985 and 1986 from time-depth recorders. The first 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 calculating the overall maximum and mean dive duration, number of dives per hour, and percent time on the surface.

Subject	Record Duration Hrs	Record Duration Total Dives	Number of Dives (hr)	Record Duration Spent on Surface (%)	Max. Depth (m)	Mean Depth (m)	Max. Dur. (rein)	Mean Dur. (rein)
Rp	421	1539	3.7	21.4	668	389 +135	23.3	12.9 ±3.1
Dot	598	1822	3.0	16.6	894	370 ±158	30.6	16.4 ±3.1
Ca	458	1175	2.6	12.3	886	413 ±165	35.9	20.5 ±4.5
Al i	318	819	2.6	16.8	822	363 ±162	35.8	19.4 +4.9
Gi	468	1370	2.9	16.0	854	480 +145	35.2	17.2 ±3.3
Td	320	942	2.9	11.0	868	420 ±178	32.4	18.1 ±3.9
Snl (1985)	363	883	2.4	11.0	760	345 ±142	47.7	22.0 ±5.0
Snl (1986)	619	1486	2.4	16.9	828	419 ±166	44.5	20.8 ±5.2
Totals	3,565	10,036						
Means			2.7	14.4	822	400	37*4	19.2
Standard Deviations			.2	2.8	76	156	6.3	4.3

Table 3. Mean surface interval (± 1 S. D.) and frequency distribution of surface interval duration following all dives of six female elephant seals.

Female	Mean (rein)	Percent of Surface Intervals		
		Less than 5 min	5-9.9 min	10 min or greater
Dot	3.3 ± 7.7	97.4	2.1	.5
Ca	2.9 ± 8.8	98.9	.6	.5
Al i	3.7 ± 13.4	96.2	1.7	2.1
Gi	3.3 ± 1.1	98.2	1.4	.4
Td	2.2 ± 5.0	99.5	.2	.3
Snl (1985)	2.7 ± 3.0	99.2	.5	.3
Snl (1986)	4.2 ± 8.4	83.1	13.9	3.0

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

Female	Longest Bout of Continuous Diving		Extended Surface Intervals			
	Number of dives	Duration (days)	Number	Mean Duration (hrs)	Maximum Duration (hrs)	Total Duration (hrs)
Dot	1337	18.2	9	1.2 ± 1.5	4.6	10.7
Ca	643	11.1	6	1.6 ± 1.4	3.4	9.8
Ali	410	5	17	.9 ± 1.4	5.1	15.2
Gi	788	12.2	6	.2 + 0.1	.4	1.5
Td	692	10.9	3	1.1 ± 1.2	2.5	3.4
Snl (85)	738	13.1	3	.7 ± 0.6	1.4	2.1
Snl (86)	641	11	44	.5 ± 0.7	4.2	22.2

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.

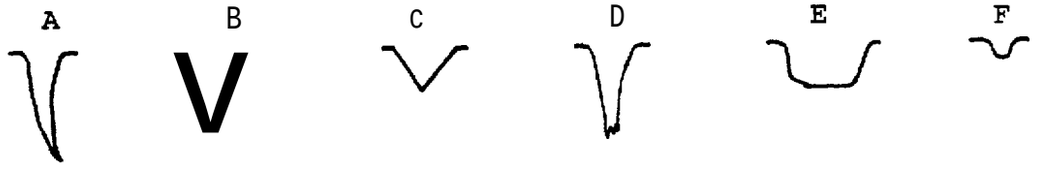
	Dive Types					
	A	B	C	D	E	F
Depth (m) 0 400 800						
Gi	17.44	3.84	8.58	70.14		
Td	3.03	15.16	7*39	65.45	1.82	7.03
Snl (1985)	.82	.33	2.79	77.14	18.26	.49

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.

Female	Dive Type	Rate (m/see)		Duration (rein)		Depth (m)
		Descent	Ascent	Total	Bottom	
Gi	D	1.96 .43	1.10 .16	17.34 2.77	4.02 1.34	547 97
	A	1.86 .46	1.02 .13	17.77 2.61		687 93
	B	.55 .05	.88 .17	22.22 3.94		449 70
Td	D	1.40 .24	2.11 .44	19.82 1.82	8.28 2.00	569 92
	A	.99 .23	2.07 .45	18.04 2.84		718 127
	B	.41 .07	1.22 .39	24.94 4.65		436 64
Snl (1985)	D	.65 .13	2.73 .88	23.10 3.04	7.05 1.59	491 73
	E	.40 .12	2.32 .99	30.00 2.85	14.74 3.20	284 37

Legends to Figures

Figure 1. D. 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.

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

Figure 3. A frequency distribution of dive depths of all dives of all females.

Figure 4. Percentage distribution of daily dives according to depth for female Gi.

Figure 5. Percentage distribution of daily dives according to depth for female Td.

Figure 6. Percentage distribution of daily dives according to depth for female Snl in 1985.

Figure 7. Percentage distribution of daily dives according to dive duration for female Snl in 1985.

Figure 8. A frequency distribution of all dive durations of six females (Rp excluded).

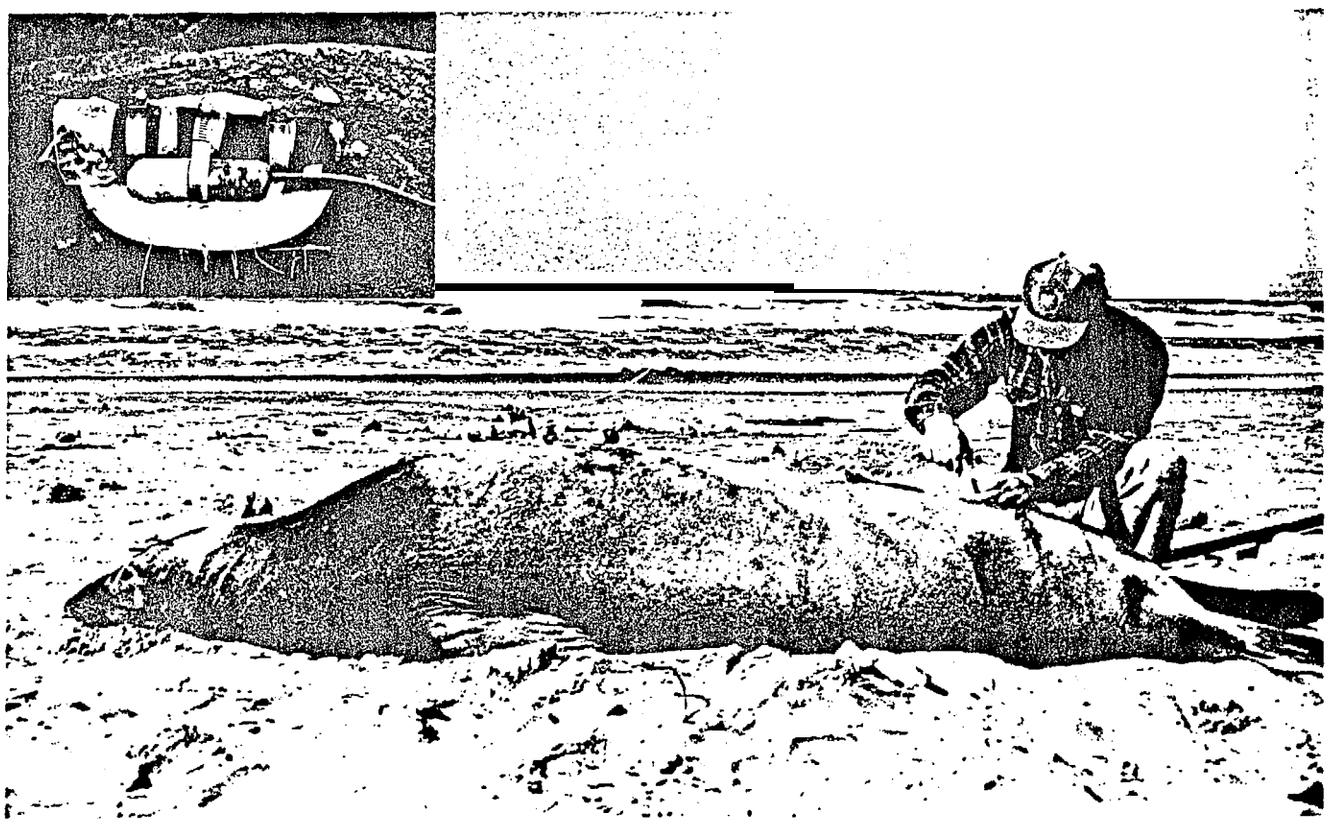
Figure 9. Scatter plots of surface interval as a function of the preceding dive duration for three females. The asterisks denote surface intervals that exceeded 35 min.

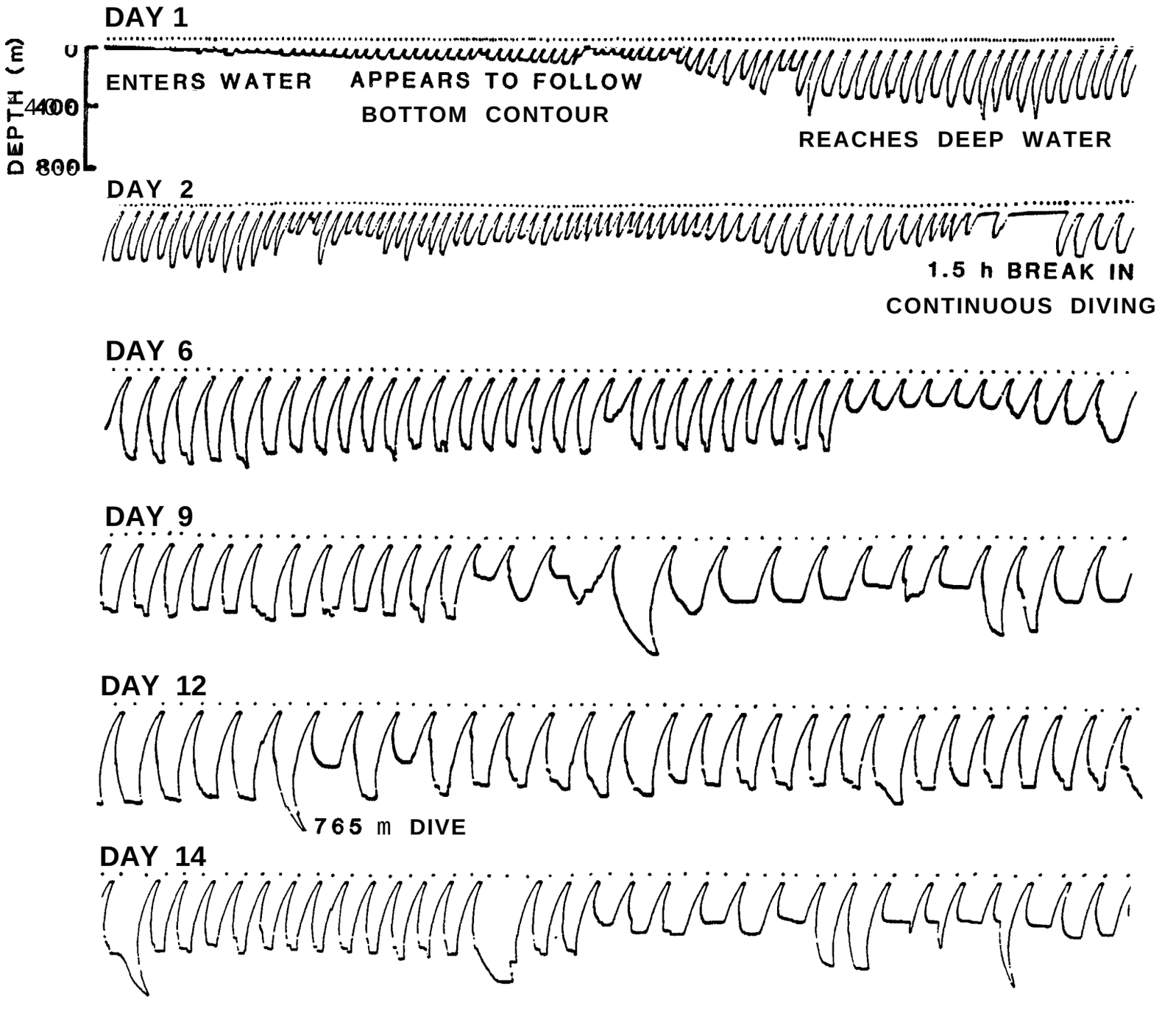
Figure 10. An excerpt from day 9 of the dive record of Snl in 1985 showing the surface intervals following the longest dive recorded and a series of long dives.

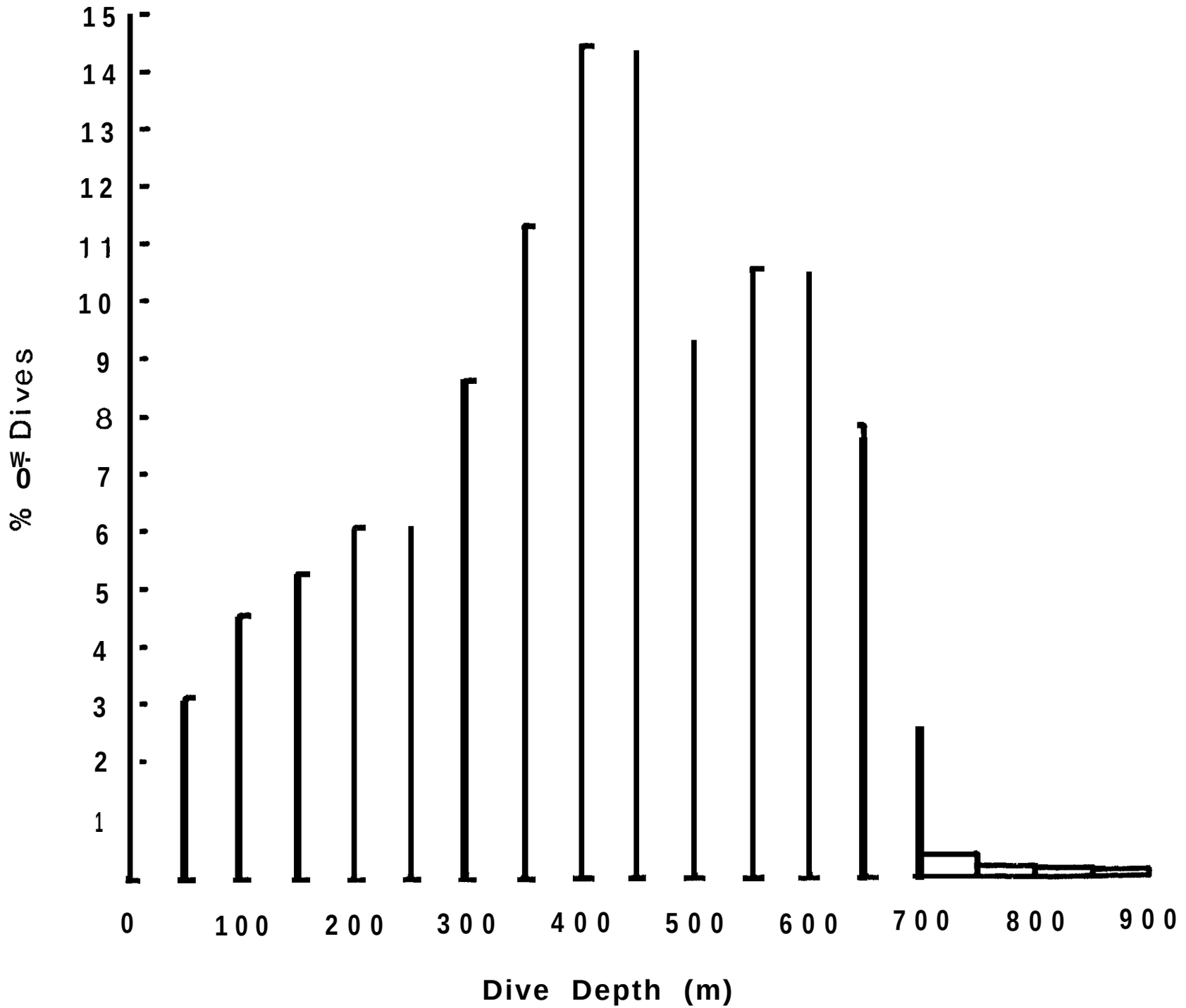
Figure 11. Frequency distributions of dive duration, dive

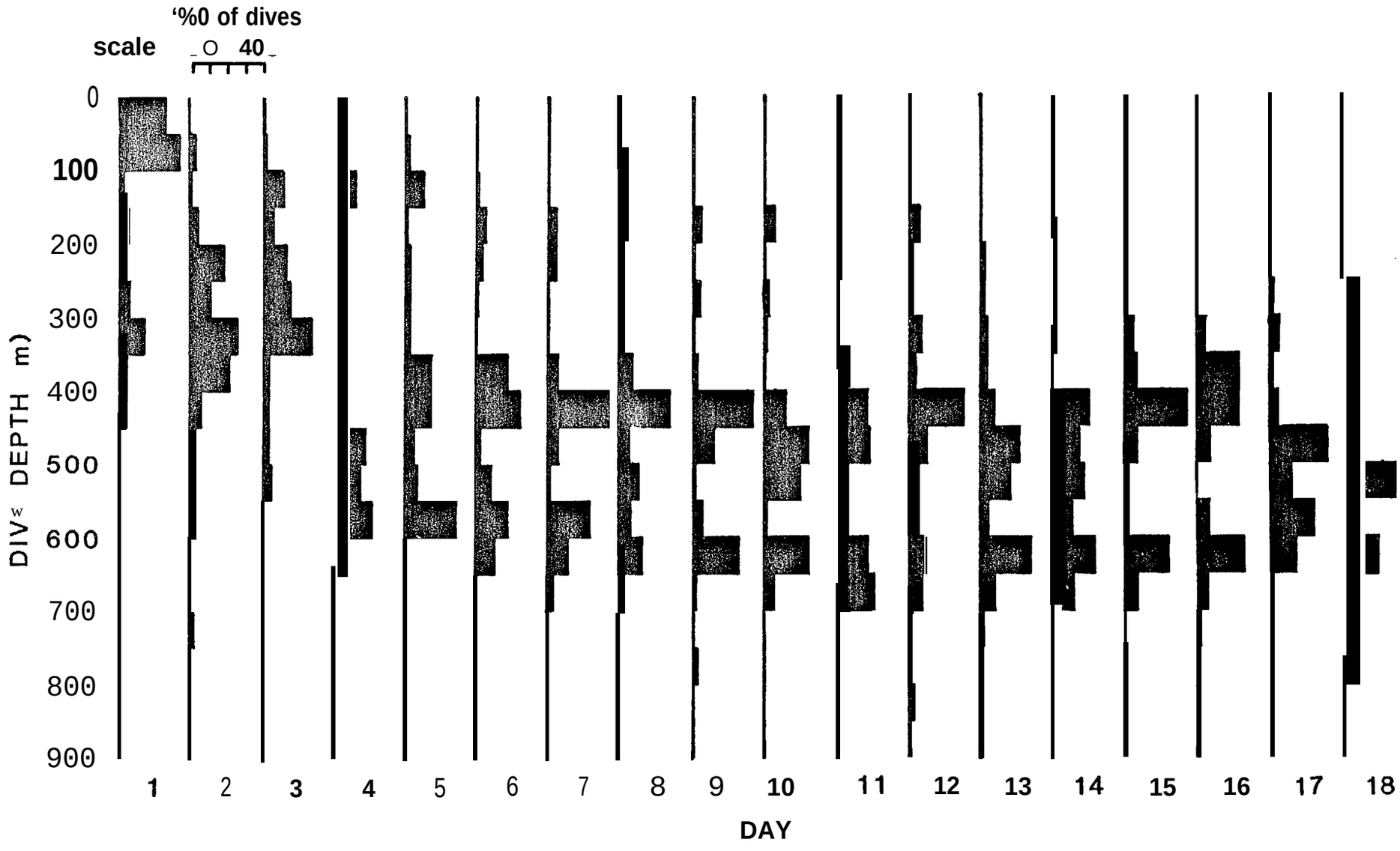
depth and dive number by hour of day. The shaded area denotes dark. The distributions are based on all dives of six adult females.

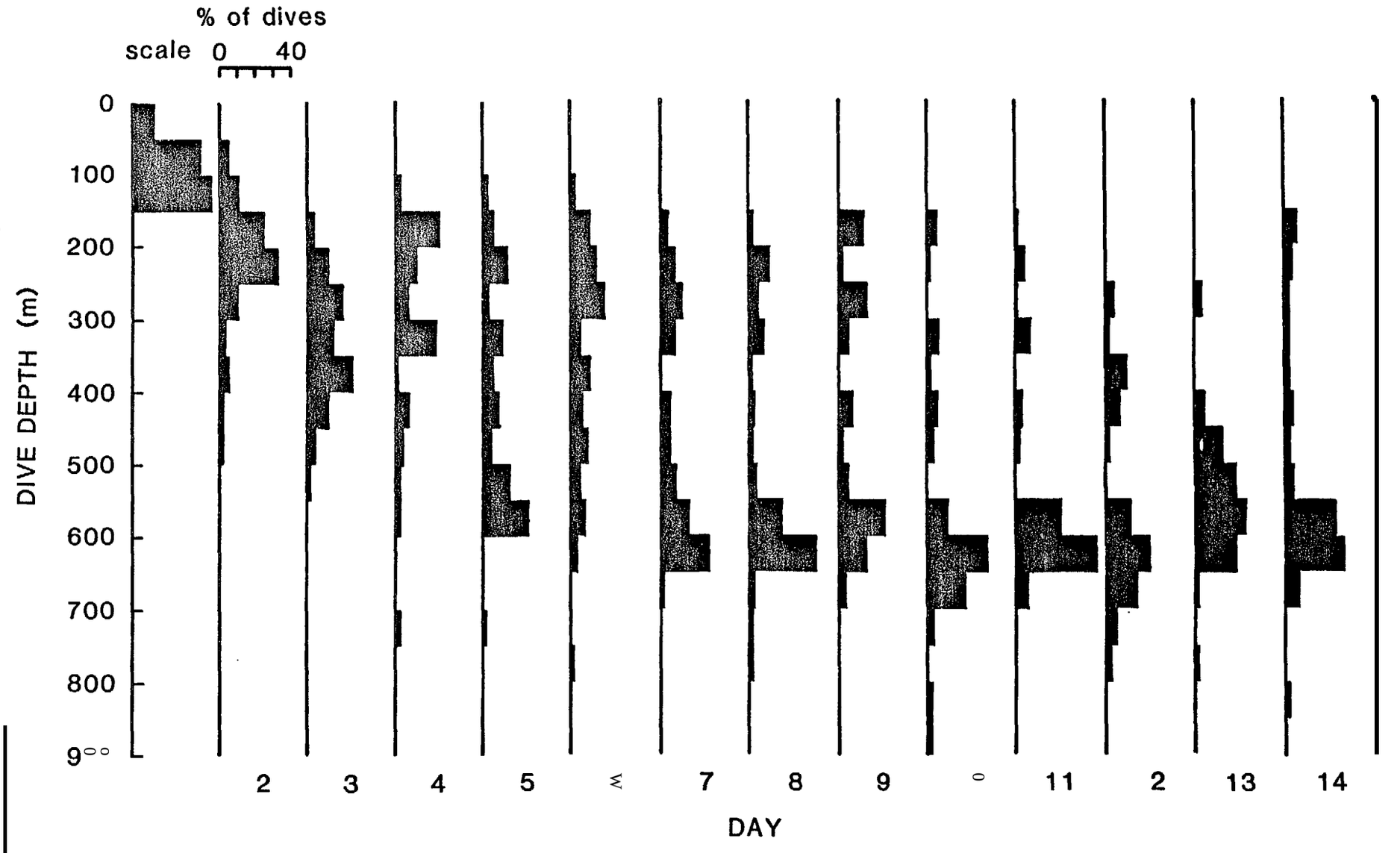
Figure 12. Dive duration in relation to dive depth for female Td and female Snl in 1985 and 1986. The distributions are based on all dives for each female.

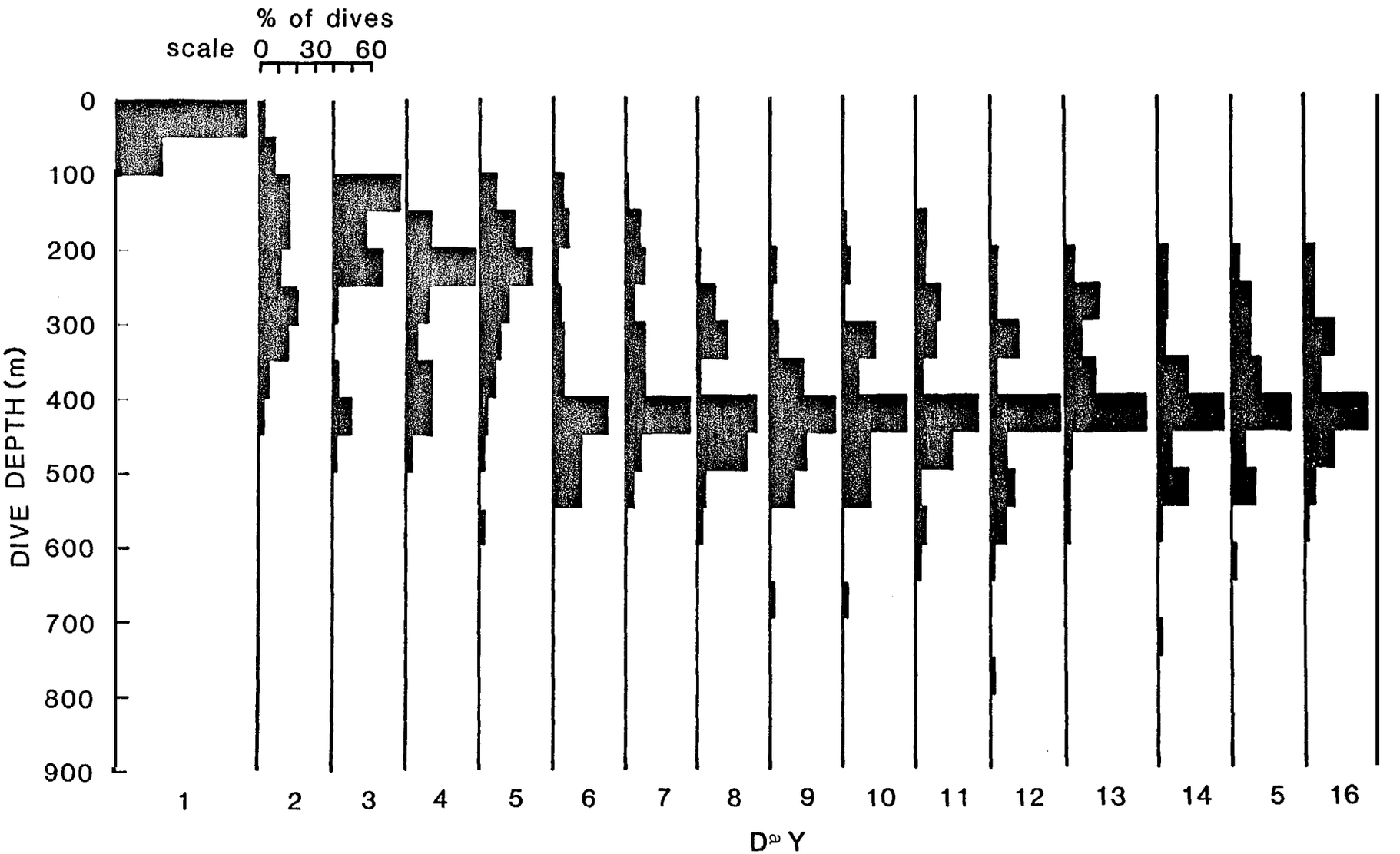


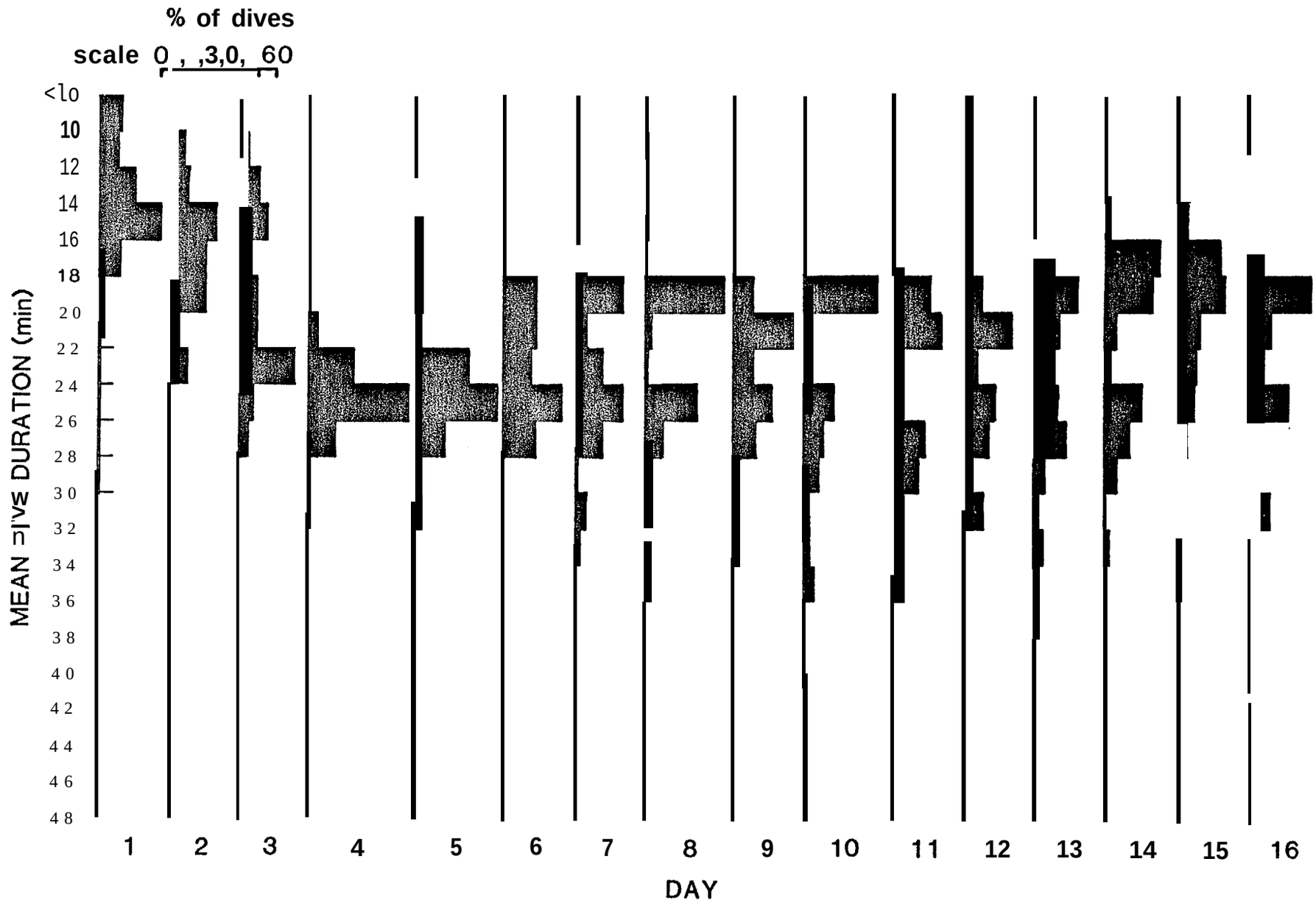

DAY 1
DEPTH (m)
0
400
800
ENTERS WATER
APPEARS TO FOLLOW
BOTTOM CONTOUR
REACHES DEEP WATER
DAY 2
1.5 h BREAK IN
CONTINUOUS DIVING
DAY 6
DAY 9
DAY 12
765 m DIVE
DAY 14

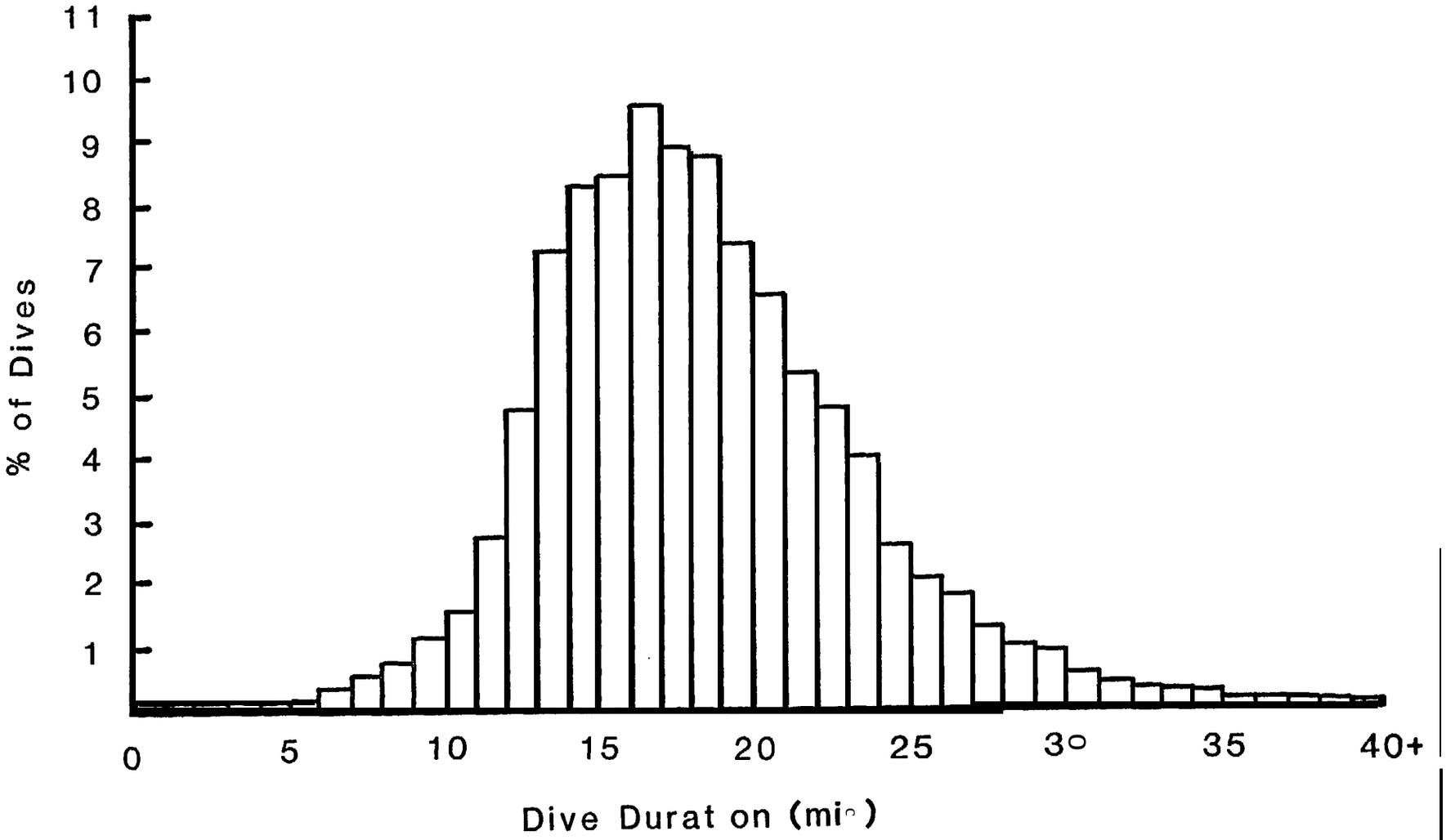

15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
% of Dives
0
100
200
300
400
500
600
700
800
900
Dive Depth (m)

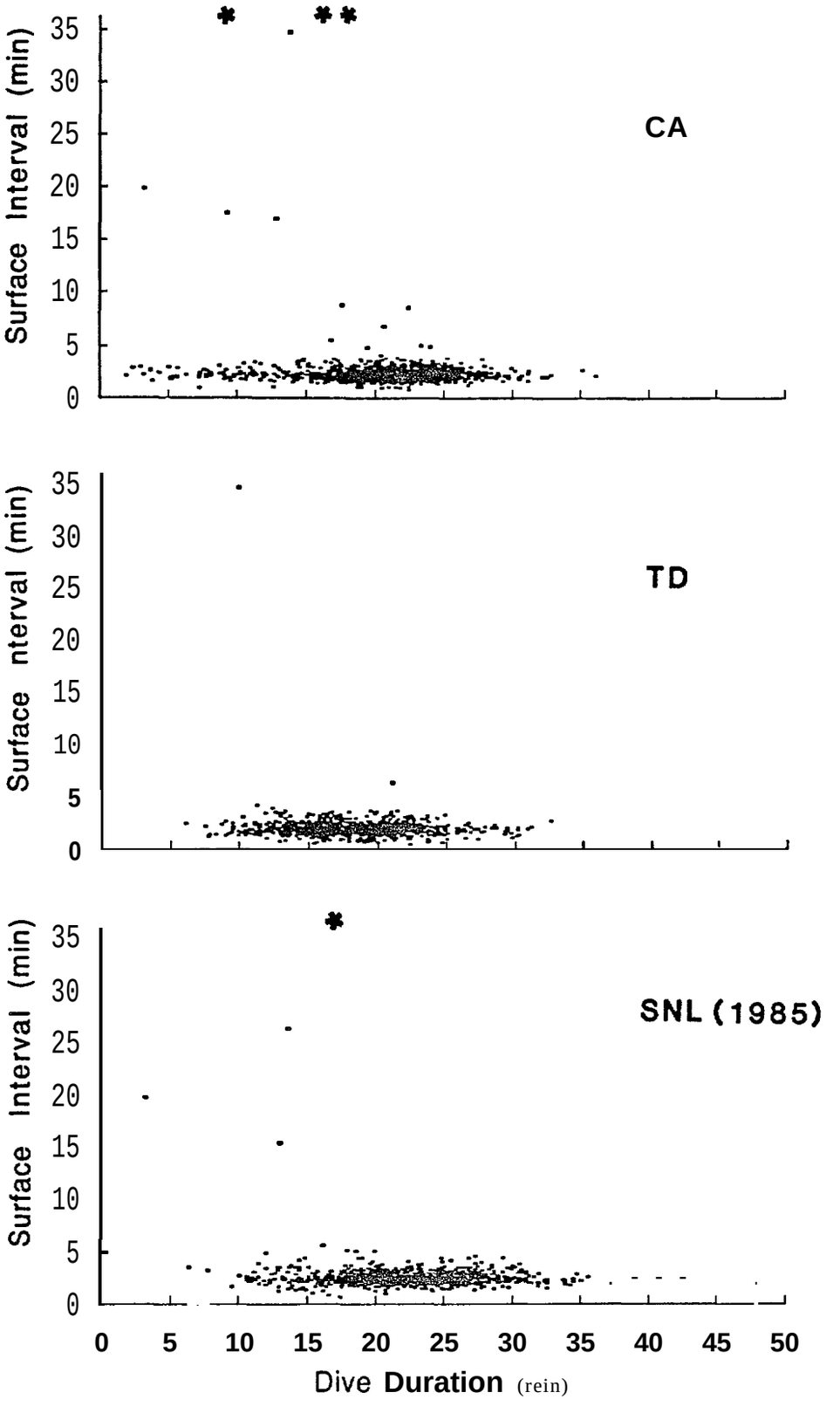

'%0 of dives
scale
0
40
0
100
200
300
400
500
600
700
800
900
DIV« DEPTH m)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
DAY

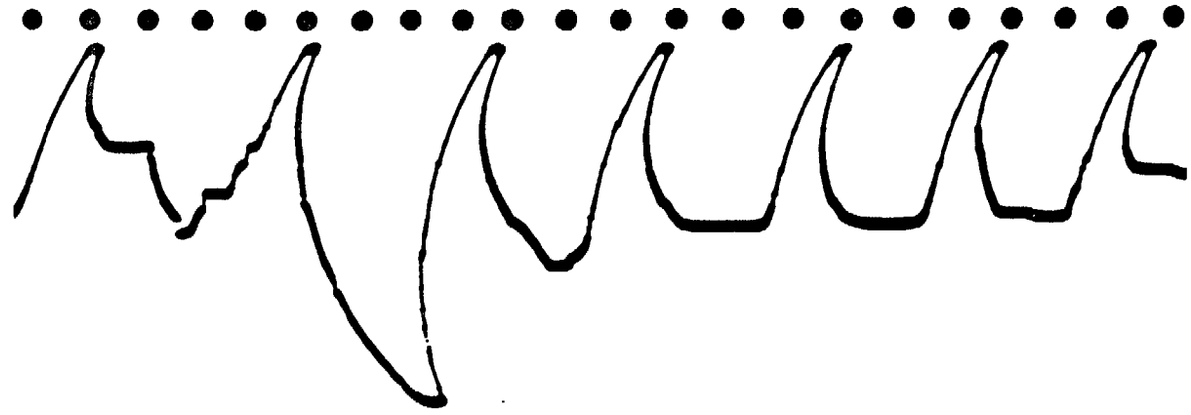

% of dives
scale 0 40
DIVE DEPTH (m)
0
100
200
300
400
500
600
700
800
900
2
3
4
5
7
8
9
11
2
13
14
DAY


% of dives
scale 0 30 60
DIVE DEPTH (m)
0
100
200
300
400
500
600
700
800
900
1
2
3
4
5
6
7
8
9
10
11
12
13
14
5
16
Day

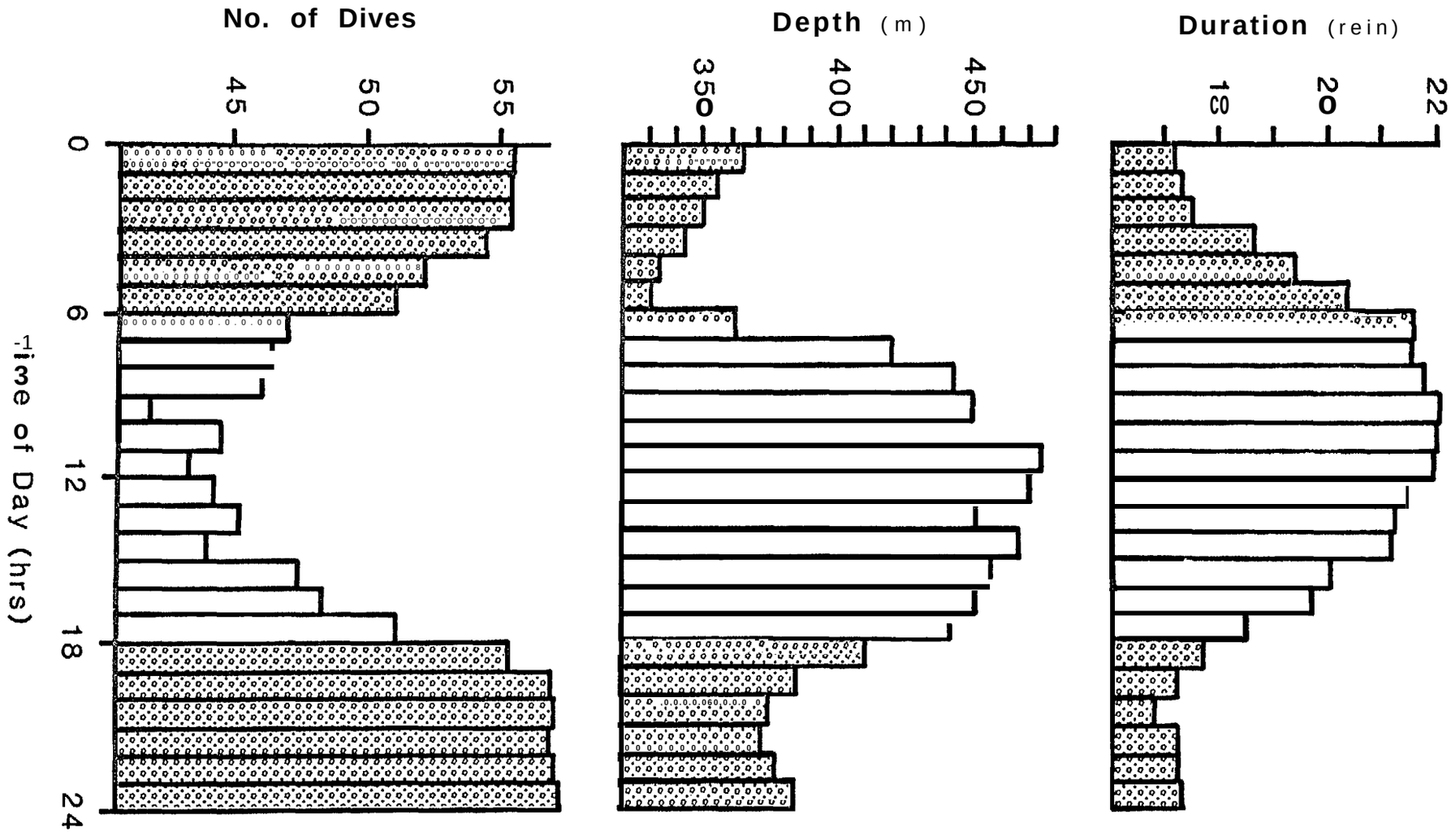

% of dives
scale 0 , ,3,0, 60
<lo
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
46
48
MEAN DIVE DURATION (min)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
DAY

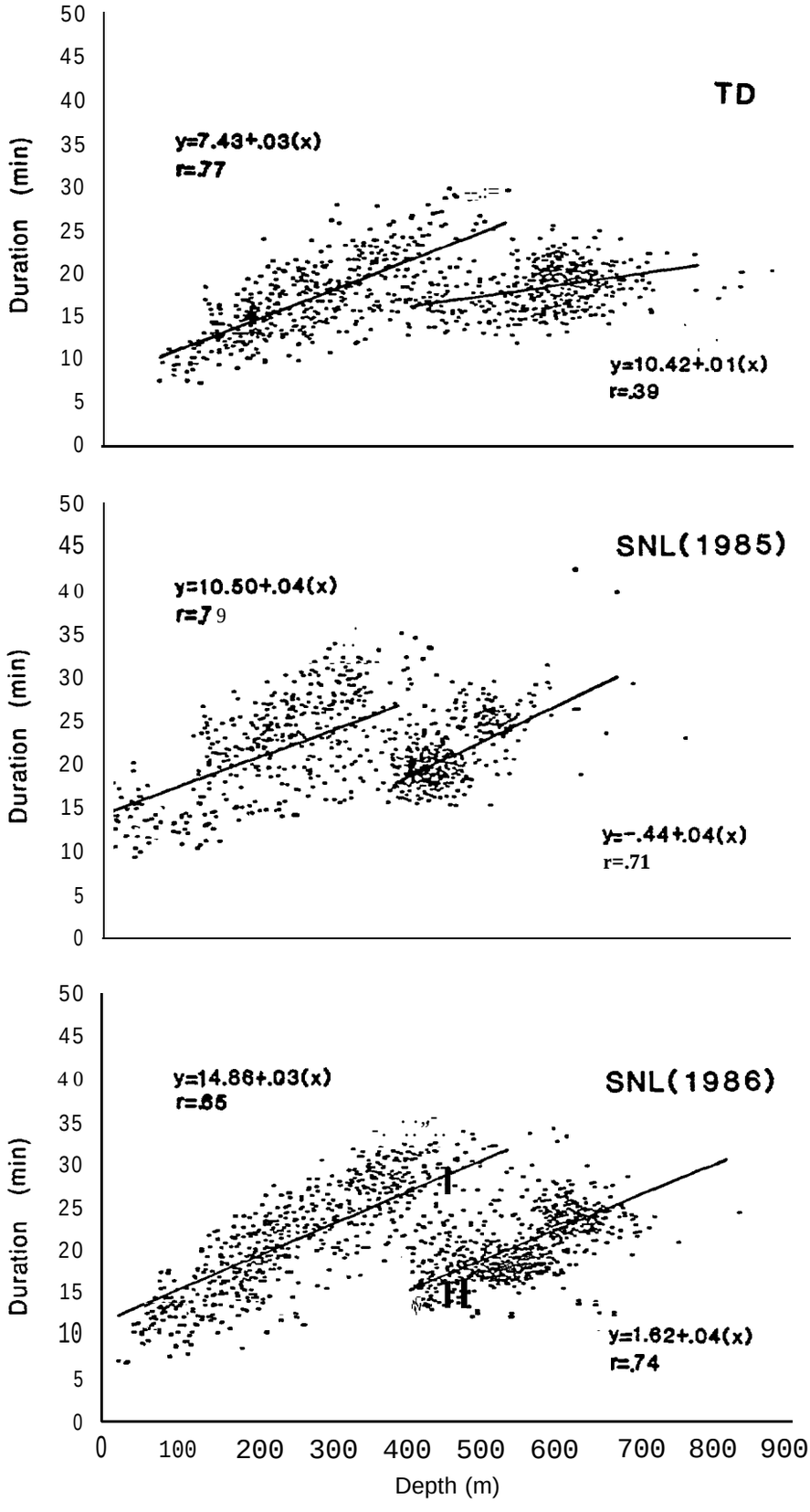

11
10
9
8
7
6
5
4
3
2
1
% of Dives
0
5
10
15
20
25
30
35
40+
Dive Durat on (mi)


Surface Interval (min)
35
30
25
20
15
10
5
0
CA
Surface nterval (min)
TD
SNL (1985)
0 5 10 15 20 25 30 35 40 45 50
Dive Duration (rein)



DIVE DURATION (rein)	**47.7**		**39.9**		**34.6**		**35.9**		**31.7**		**30.2**	
SURFACE INTERVAL (rein)		**2.1**		**2.5**		**2.3**		**2.0**		**1.8**		**2.3**
DIVE DEPTH (m)	**342**		**667**		**403**		**326**		**322**		**311**	


No. of Dives
45
50
55
Depth (m)
350
400
450
Duration (rein)
13
20
22
0
6
12
18
24
Time of Day (hrs)


TD
y=7.43+.03(x)
r=.77
y=10.42+.01(x)
r=.39
SNL(1985)
y=10.50+.04(x)
r=.79
y=-.44+.04(x)
r=.71
SNL(1986)
y=14.86+.03(x)
r=.65
y=1.62+.04(x)
r=.74
Duration (min)
Depth (m)
0
5
10
15
20
25
30
35
40
45
50
100
200
300
400
500
600
700
800
900