Diving patterns of California sea lions, *Zalophus californianus*

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The diving patterns of 10 adult female California sea lions (*Zalophus californianus*) were examined during the summer breeding season on San Miguel Island, California, in 1982 and 1983 using time–depth recorders. During 17 feeding trips, representing 40.6 days at sea, animals made over 8900 dives, the deepest of which was estimated at 274 m, while the longest was 9.9 min. The majority of dives, however, were less than 3 min in duration and 80 m in depth. From estimates of body oxygen stores, we predict that dives up to 5.8 min can be supported aerobically. Therefore, cost–benefit considerations based on prey availability and encounter rate may be more important than physiological limits in shaping the foraging patterns of *Zalophus*. Sea lions were active virtually throughout their time at sea, resting on the surface for only 3% of the average trip. Peak diving frequency occurred during the twilight hours near sunrise and sunset. Dives were frequent, however, during all hours of the day and were typically clustered into bouts that lasted a mean (±SD) of 3.3 ± 1.5 h. We suggest that these bouts represent active feeding on discrete prey patches. During short bouts (<3 h), dive depth was less variable than for dives occurring between bouts. During longer bouts, dive depth changed in a manner consistent with pursuit of vertically migrating prey. During the 1983 El Niño, sea lions compensated for a reduction in food availability by lengthening dive bouts. These seasonal and diel variations in diving patterns suggest that the rate of prey encounter strongly influences the depth and duration of individual dives.

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La plongée a été étudiée par des enregistrements temps-profondeur chez 10 femelles adultes du Lion de mer de Californie (*Zalophus californianus*) au cours de la saison de reproduction d'été sur l'île San Miguel, en Californie, en 1982 et 1983. Les animaux ont fait plus de 8900 plongées au cours de 17 excursions de recherche de nourriture représentant 40,6 jours en mer; la plongée la plus profonde enregistrée a été de 274 m et la plongée la plus longue a duré 9,9 min. La majorité des plongées, cependant, duraient moins de 3 min et atteignaient moins de 80 m de profondeur. D'après l'estimation des réserves d'oxygène dans le corps, il est possible de prédire que les plongées de 5,8 min ou moins peuvent être aérobiques. Il faut conclure que des considérations coût–bénéfice basées sur la disponibilité des proies et la fréquence des rencontres ont probablement plus d'importance que les restrictions physiologiques dans la détermination des séquences de plongée chez *Zalophus*. Les lions de mer étaient actifs à peu près tout le temps lors de leur séjour en mer et ne se reposaient en surface que 3% du temps au cours d'une excursion. C'est au cours des heures de pénombre, à la tombée du jour et à l'aurore, que la fréquence des plongées était maximale. Les plongées étaient tout de même fréquentes à toute heure du jour et se produisaient ordinairement en séries qui duraient en moyenne 3,3 ± 1,5 h. Nous croyons que ces séries représentent des épisodes d'alimentation dans des bancs de proies à répartition contagieuse. Durant les épisodes de plongée courtes (<3 h), la profondeur des plongées était moins variable que dans le cas des plongées survenues dans les intervalles entre les séries. Au cours des épisodes de plongée plus longs, la profondeur des plongées variait et cette variation pourrait s'expliquer par la poursuite des proies à migrations verticales. En réaction au courant El Niño, en 1983, les lions de mer ont compensé la diminution des proies en prolongeant les périodes de plongée. Ces variations saisonnières et journalières des plongées semblent indiquer que la fréquence des rencontres avec des proies influence fortement la profondeur et la durée de chacune des plongées.

[Traduit par la revue]

Introduction

Unlike terrestrial predators, the foraging activities of aquatic mammals take place during breath hold. Feeding depths and time available for search, pursuit, and prey capture are limited by oxygen stores available upon submergence. These constraints undoubtedly influence the decision rules used by aquatic predators in locating and pursuing prey. However, physiological limits to breath hold may not be the most important factor shaping the diving patterns of foraging marine mammals. Instead, energetic cost–benefit considerations based on prey availability and encounter rates may have a more pronounced effect. Recent data indicate that many fur seal species rarely approach the calculated limits of dive depth

and duration (Gentry et al. 1986*a*). Their dives are normally shallow and of short duration. Consistent, diel variations in dive patterns also suggest that prey availability and location strongly influence the depth and duration of individual dives. Within absolute physiological limits, there may be considerable flexibility in the ways that marine mammals find and pursue prey.

Theoretical treatments of foraging by terrestrial predators have described a number of alternative strategies that animals in different habitats should use to maximize their net rate of energy intake (Schoener 1971; Pyke et al. 1977; Krebs 1978; Orians and Pearson 1979). For aquatic mammals, however, only Dunstone and O'Connor (1979*a*, 1979*b*) have addressed the question of foraging optimization. They investigated the trade-off between the benefits of continued search and the cost

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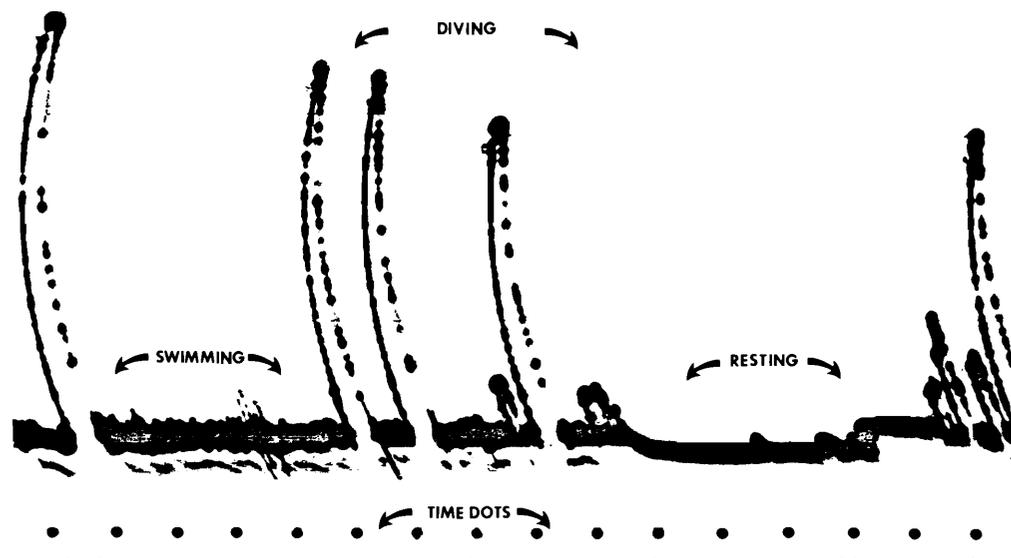
FIG. 1. Portion of a TDR record illustrating the traces produced from various activities. Dives appear as pointed traces. Their height is proportional to depth. During swimming, the recording arm oscillates, producing a wide baseline, while resting results in a flat image. Dive duration can be calculated from the width of the dive trace and the 12-min timing marks at the film edge.

of losing the prey because of oxygen depletion during pursuit by the mink (*Mustela vison*). The results of these studies demonstrated that search and pursuit times were negatively correlated, but that oxygen limits accounted for considerably less of the variation in hunting patterns than did optimal foraging considerations based on prey encounter rates.

Empirical evidence of the interactions between marine mammals and their prey, which might be used to test predictions of optimal breath-hold foraging, is lacking. Recent advances in recording instruments, however, now permit the collection of data on the behavior of foraging animals. As a result, information on several marine mammal and bird species is now available and provides a basis with which to compare their diving and feeding patterns (Kooyman 1981; Kooyman et al. 1982; Nagy et al. 1984; Croxall et al. 1985; Gentry et al. 1986a; Le Boeuf et al. 1988). Constraints imposed by an animal's physiology, morphology, and habitat and the energetic decision rules common to aquatic predators can be clarified by these comparisons.

The California sea lion (*Zalophus californianus*) is an ideal subject for studies of diving behavior. Its large size provides an interesting comparison to previous studies of smaller fur seals (Gentry et al. 1986a). Like other otariid pinnipeds, sea lions make repeated trips to sea during the breeding season, returning each time to suckle their pups. This enables the deployment and retrieval of dive recorders. Because they must return with sufficient energy to nourish their pups during their brief onshore fast, there is no doubt that feeding occurs during these offshore periods (Costa 1986).

In this study, we examined the diving patterns of female sea lions during these foraging trips. Although no information was obtained on prey availability, inferences based on optimal foraging predictions were made as to the factors that might influence the observed behavior. Average dive durations were compared with predicted values to assess the effects of oxygen limitations on feeding patterns. Comparisons with other species, for which similar data are available, give insights into the foraging constraints imposed by the environment and those that reflect functional limits.

Methods

This study was conducted at San Miguel Island, California (34°N; 120°25'W). Time–depth recorders (TDRs) were deployed on nine lactating, adult California sea lions between mid-July and mid-August 1982, and on five animals during mid-July 1983.

The TDR is a 500-g mechanical device that records, in real time, the depth and duration of every dive an animal makes over a 2-week period. A complete description of this 5 × 20 cm instrument is given by Kooyman et al. (1983) and Gentry and Kooyman (1986). Dives, along with time marks are recorded on photographic film by a light-emitting diode (LED) mounted on a movable, pressure sensitive bourdon tube. Only dives greater than 10 m in depth and 30 s in duration can be resolved. Before deployment and after recovery, all TDRs were calibrated to a maximum depth of 207 m using a portable pressure station.

The appearance of the LED trace can also provide an indirect measure of activity (Gentry and Kooyman 1986). Along with dives that appear as pointed traces on the film, the baseline (recorded when the animal is on the surface) may be either broad and wavy, or narrow and flat (Fig. 1). A broad baseline is caused by movement or chatter of the bourdon tube arm, and we interpret this trace to indicate surface swimming. Similarly, we interpret a flat baseline as representing inactivity of the animal or its resting on the surface. From these images a time budget of the animal's activities at sea can be constructed (Fig. 1).

Sea lions that were observed nursing a pup were captured with hoop nets and physically immobilized using a large restraint board with a detachable neck brace (Gentry and Holt 1982). TDRs were fastened to each animal with a harness constructed from straps of 2.5 cm wide tubular nylon webbing (Gentry and Kooyman 1986). A very high frequency (VHF) radio transmitter (5 cm length × 2 cm diameter; Advanced Telemetry Systems) was also attached to the harness to facilitate locating the animal on shore. When animals returned from sea they were recaptured, the TDR removed, and the animal released.

Analysis

Upon recovery, the film was developed and enlarged. Dive traces and timing marks were digitized and printouts obtained of the time each dive occurred, its depth, duration, and length of the following surface interval (Gentry and Kooyman 1986). During analysis, it became clear that dives occurred in clusters, separated by compara-

tively long surface intervals. To analyze these dive bouts, we established their ending points in time using a bout-ending criterion (BEC) that was determined by constructing surface interval − survivorship curves (Gentry and Kooyman 1986). For each animal, the number of post-dive surface intervals with a duration greater than a given time t was plotted logarithmically against t on the ordinate (Fig. 2). This formed a decreasing function with a slope proportional to the probability of a surface interval of given duration occurring at any time after the last surface interval recorded (Fagen and Young 1978). A break in the slope, therefore, signifies a change in the probability of surface interval occurrence.

For each animal two inflection points were observed: one at 2 to 3 min and the other between 7 and 11 min (Fig. 2). Following the procedures outlined in Gentry and Kooyman (1986), the second point was chosen to represent the BEC. To further define a bout, the minimum number of dives was arbitrarily set at 10. A dive bout, therefore, consisted of 10 or more dives not separated by a surface period exceeding the BEC.

Dive bouts were analyzed separately for mean dive depth, duration, and surface interval length. Interbout intervals were calculated as time from the last dive in a bout until the first dive of the next. Transit times to and from the feeding grounds were established by calculating the time from shore departure to the first dive bout and that spent in returning to land from the last dive bout.

Activity budgets were constructed from records with clear swimming and resting traces. Time spent swimming was determined as all surface activity excluding resting and time spent on the surface between dives occurring within bouts. During a dive bout, surface intervals between dives were generally brief and likely did not indicate travel, but instead were associated with replenishing O_2 stores. Time spent diving was calculated as the total time that the animal was submerged. Sea lions were considered resting when the dive trace appeared flat (Fig. 1).

To calculate distance travelled from the amount of time spent swimming, estimates were made of both swim speed and the instrument's hydrodynamic impact (Appendix). These calculations indicate that adult sea lions should travel at an average velocity of 2.5 m/s (9 km/h) when carrying the TDR package. Empirical data collected on other otariid species of differing body size, however, suggest that this value may be slightly high owing to the assumption of similar relative transport costs between juveniles and adults (P. J. Ponganis, personal communication). The average velocity of 9 km/h should therefore be viewed as approximate and the calculated foraging ranges regarded as maximum estimates.

Results

In 1982, all nine animals returned to shore with the instrument package. One TDR failed, so that eight diving records were obtained (ZC-5 through ZC-12). In 1983, only two of the five animals returned to the study site (ZC-17 and ZC-20). A total of 10 dive records was therefore obtained from individual animals. Because several of the animals made more than one trip to sea prior to recapture, a total of 17 feeding trips was recorded (Table 1). On 6 of these, film in the TDR ran out while the animal was still at sea. On 11 of the trips, the return to shore was recorded.

Since all animals carried radio tags, it was possible to tell when they returned to San Miguel Island. However, records clearly showed that two animals (ZC-10 and ZC-17) were on land for periods ranging from 12 to 33 h although they did not return to the study site. Nevertheless, because offshore rocks and other islands occur near San Miguel, these onshore periods are taken to represent the end of a trip to sea.

Performance

Over 8900 dives were logged in 40.6 recorded days at sea. The trace of the deepest dive, although completely recorded on
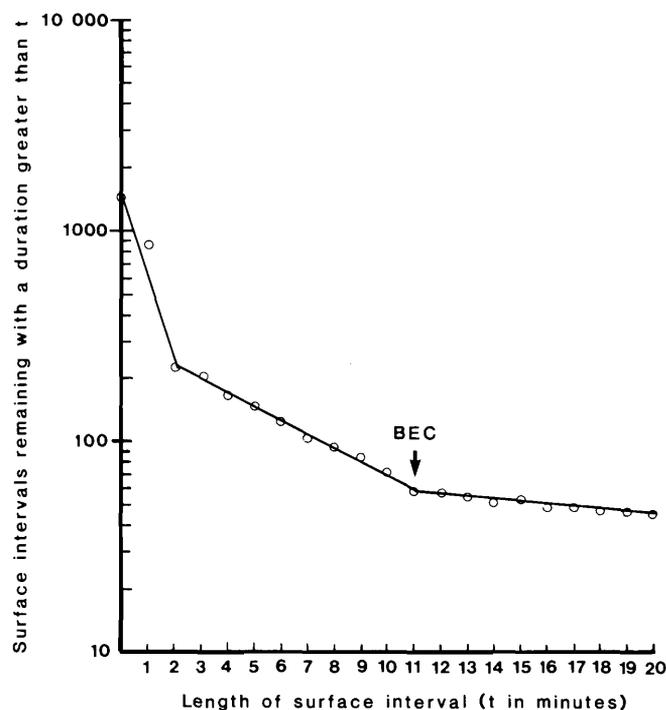
FIG. 2. A log survivor plot demonstrating the method used to determine bout-ending criteria (BEC). Surface intervals with a duration greater than a given time (t) are plotted against time on the abscissa. This produces a decreasing function whose slope is proportional to the probability of surface interval occurrence. Breaks signify a change in probability. For this animal (ZC-12), the second inflection point at 11 min was chosen as the BEC.

the film, exceeded the calibration of the instrument and was estimated at 274 m (ZC-9; Table 1) by assuming a linear correlation between pressure and the distance travelled by the recording arm. The maximum dive duration was 9.9 min (ZC-11; Table 1).

Despite these maxima, sea lions were relatively shallow and short duration divers. For individual animals, dive times averaged 1.5 to 2.8 min and mean depths ranged between 31 and 98 m (Table 1). The majority of all dives were 1.0 to 1.9 min in length (Fig. 3) and between 20 and 50 m in depth (Fig. 4).

Feeding trips ranged from 0.7 to 6.5 days in duration, with a mean ($\pm$SD) of 2.5 $\pm$ 1.4 days. During this time, sea lions averaged 202 $\pm$ 56 dives per day. The activity budgets of seven animals were determined by analyzing 14 feeding trips from the clearest records. During an average trip of 52.8 $\pm$ 24.5 h, they averaged 32.7 $\pm$ 12.6% of their time diving, 41.4 $\pm$ 18.0% swimming between dive bouts, and only 3.1 $\pm$ 3.1% resting on the surface (Table 2). Time on the surface between dives within bouts accounted for the remaining 22.8%. Because of the brief nature of surface intervals between these dives, it was not possible to distinguish between resting and swimming behaviors.

Based on the time spent swimming and a mean estimated velocity of 9 km/h (Appendix), sea lions travelled an average of 199 $\pm$ 125 km while at sea (Table 2). The time spent in travel to the first dive bout (mean = 3.4 $\pm$ 3.4 h; N = 15) was not significantly different from the time spent in returning from the last dive bout (mean = 4.7 $\pm$ 4.9 h; N = 11) (t-test; $p > 0.05$), corresponding to distances of 30.6 and 42.3 km, respectively. During the 11 completely recorded feeding trips,

TABLE 1. *Zalophus californianus* dive characteristics (means ± SD are given where appropriate)

Animal	No. of trips to sea	Total no. of dives	Mean dive depth (m)	Maximum dive depth (m)	Mean dive duration (min)	Maximum dive duration (min)	Mean surface interval within dive bouts (min)
ZC-5	1	287	56.8±43.8	207	1.7±1.3	6.0	1.4±1.3
ZC-6	1	489	56.4±53.0	207	1.5±1.5	6.2	3.1±2.0
ZC-7	1 or 2	838	98.2±43.3	196	2.8±1.3	6.2	2.1±1.4
ZC-8	1	931	31.1±35.1	207	1.5±1.2	7.5	0.8±1.5
ZC-9	1	720	58.0±49.3	274	2.4±1.4	7.6	0.7±1.4
ZC-10	3	543	38.9±18.8	207	1.9±0.8	7.1	0.8±1.1
ZC-11	1	1005	76.3±49.5	234	1.7±1.6	9.9	1.4±1.3
ZC-12	2	1478	70.7±41.3	235	2.0±1.3	9.1	1.0±1.6
ZC-17	5	2132	77.2±60.6	241	2.8±0.8	9.3	1.7±1.7
ZC-20	1	508	54.0±46.6	233	2.4±1.5	8.2	1.1±1.8
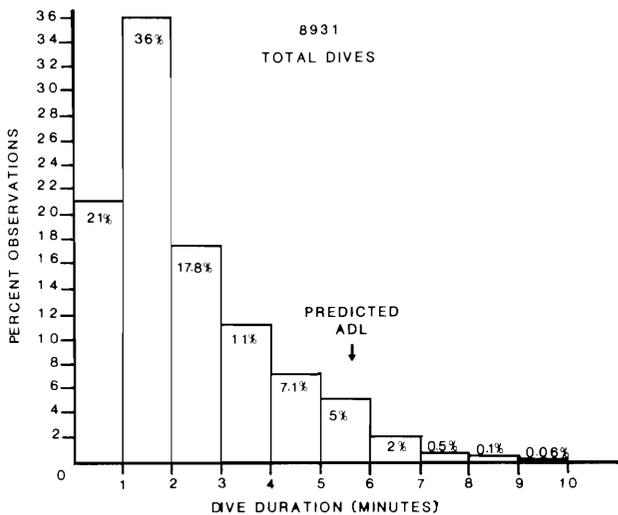
FIG. 3. Percent observations of all recorded dive durations. The predicted ADL of 5.8 min is illustrated by the arrow. Only 4% of the dives exceeded this estimated limit.

FIG. 4. Percent observations of all recorded dive depths. Less than 5% of all dives were greater than 200 m in depth.

animals averaged 8.5 ± 6.7 h (16.5 ± 12.7% of their total trip time) in transit (Table 3).

Diving bouts

Sea lions averaged 3.5 dive bouts per day with a mean duration of 3.3 ± 1.5 h each (Table 4). The longest recorded bout of continuous diving was 16.3 h (ZC-17). Intervals between dive bouts were highly variable (range, 0.2−19.9 h) with a mean of 2.9 ± 1.8 h. There was no relationship between dive bout length and length of either the preceding or following interbout intervals; nor was there any correlation between time of day and dive bout occurrence.

Sea lions spent an average of 50% of their total time at sea engaged in diving bouts (Table 5). Of all recorded dives, 86% occurred within these groupings. Moreover, during dive bouts sea lions spent 54% of their time underwater, diving at a mean rate of 16.4 ± 3.1 dives/h (Table 5).

Analysis of the interbout activities of seven sea lions representing 14 feeding trips to sea showed that these animals swam a mean of 2.2 ± 3.1 h (range, 0−16.6) between dive bouts, covering an estimated distance of 20.2 ± 28.2 km (range, 0−149.8). Resting occupied a mean of 0.4 ± 0.7 h. Four animals did not travel between one or more dive bouts (10 out of

92 interbout intervals analyzed), but instead rested 100% of the time. These resting intervals were invariably less than 1.2 h in length.

Analysis of dives within dive bouts revealed that dive duration was positively correlated with depth ($R^2 = 0.73$, $p < 0.05$; Fig. 5), indicating that deeper dives require more time and energy than shallower ones. This is further supported by plotting dive frequency against mean dive depth for individual bouts, which reveals an exponential decline in frequency with increasing depth (Fig. 6). No correlation was observed between dive time and length of the following surface interval.

Patterns of diving

While diving patterns were often obscured by individual variation, certain generalities were observed. Sea lions dived at all times, although some showed a preference for day or night diving. For example, ZC-7, ZC-9, and ZC-10 all exhibited daytime peaks of diving activity, while ZC-5, ZC-12, ZC-17, and ZC-20 made more dives during the night. Dives by the remaining animals (ZC-6, ZC-8, and ZC-11) occurred in roughly equal numbers throughout the day and night (Fig. 7). These patterns probably represent a continuous range of variation between individuals rather than discrete categories. In general, however, the majority of dives by diur-

TABLE 2. Activity patterns of Z. californianus at sea

	Mean	Range	SD	N
Trip length (days)	2.5	0.7–6.5	1.4	16
Dives per day	202	109–300	56.0	16
% time diving	32.7	15–56	12.6	14
% time swimming	41.4	9–69	18.0	14
% time resting	3.1	0–10	3.1	14
Estimated distance travelled (km)	199	17–435	125.1	14

TABLE 3. Transit times to and from feeding areas

	Mean	Range	SD	N
Time to first dive bout (h)	3.4	0.2–11.5	3.4	15
% time in transit to first dive bout	6.8	0.6–23.3	7.8	15
Estimated distance travelled to first dive bout (km)*	30.9	1.5–103.5	30.3	15
Time from last bout to shore (h)	4.7	0.4–15.1	4.9	11
% time in transit from last dive bout	9.4	0.5–29.7	8.8	11
Estimated distance travelled from last dive bout (km)*	42.0	3.6–139.5	44.1	11
Total time spent in transit (h)	8.5	0.9–20.5	6.7	11
% of total trip time spent in transit	16.5	2.2–39.5	12.7	11

*Based on estimated swimming speed of 9 km/h.

nal feeders were shallow (<100 m) (Fig. 7). Similarly, nocturnal divers also made shallow dives at night and during twilight hours, but often exceeded 150 m during the day. Animals with no clear preference for day or night diving exhibited various combinations of these two patterns.

Pooled data for all animals show that dives were most numerous during the twilight hours, with the smallest number occurring during midday (Fig. 8). Beginning at sunrise, dives became progressively deeper and longer in duration until about noon when these trends began to reverse. For all animals combined, dives between 12:00 and 13:00 averaged 100.7 ± 39.4 m in depth and 3.4 ± 1.0 min in length, while between 00:00 and 01:00, they had decreased to 40.5 ± 18.0 m and 1.3 ± 0.4 min, respectively (Fig. 8).

Discussion

Despite the large degree of variability in individual dive patterns, several features were consistent among animals. All sea lions dived in bouts, a continuous series of dives separated only by brief surface intervals. Bouts were separated by comparatively long periods of swimming during which time few, if any, dives occurred. The majority of all dives were relatively shallow and of short duration. Dive duration was positively correlated with depth, indicating that sea lions spend less time underwater on shallower dives than on deeper ones. Finally, all animals were active throughout virtually the entire period at sea. Resting accounting for only 3% of the average animal's time.

Although the results of this study only provide a record of diving behavior, there is little doubt that feeding occurred during these offshore periods. Doubly labeled water measurements have shown that nursing sea lions consume approximately 6.5% of their body weight per day while at sea (Costa 1986). Scat samples obtained from animals in this study also indicate that feeding occurred (R. L. DeLong, unpublished data). It seems reasonable to conclude, therefore, that the TDR records demonstrate the manner in which female sea lions locate and pursue prey.

Dive bouts are the most conspicuous feature of sea lion diving patterns. Several lines of indirect evidence suggest that these represent active feeding on individual prey patches. During short bouts (<3 h), dives were usually made to a specific depth that often varied less than 20–30 m. For example, short bouts by ZC-12 had a mean variance in dive depth of 23 m, while between-bout dives had a mean depth variance of 44 m, a statistically significant difference (t-test, p < 0.05). This is consistent with the hypothesis that interbout dives may serve an exploratory function, while dives within bouts represent feeding. Additionally, during longer bouts, dives gradually changed depth in a manner suggesting pursuit

of vertically migrating prey, similar to that observed for Antarctic fur seals feeding on krill (Croxall et al. 1985). Bouts that began during daylight hours and extended into the evening often became shallower as the night progressed (Fig. 9).

The observation that most diving effort was concentrated in bouts also suggests that they indicate foraging. Dive bouts averaged 3.3 h in length with mean interbout intervals of 2.9 h (Table 4); 86% of all dives made at sea occurred within these bouts. If dive bouts represent foraging, then animals spent an average of 50% of their total time at sea engaged in this activity (Table 5), with the remaining time spent resting, in travel between bouts, and in transit to and from the rookery.

The distribution of dive bouts throughout the day and night is a pattern consistent with the behavior of their prey. California sea lions feed primarily on hake (Merluccius productus), market squid (Loligo opalescens), juvenile rockfish (Sebastes spp.), and northern anchovy (Engraulis mordax) during the spring and summer breeding season (Antonelis et al. 1984). All are schooling, vertically migrating species that occur over the continental shelf and slope (Vaughan and Recksiek 1978; Dark et al. 1980; Gunderson and Sample 1980). These schools are generally compact and patchily distributed, a fact that may account for the discrete, discontinuous nature of diving bouts. It may also account for the observation that bouts occur at all hours and that interbout intervals are highly variable in length.

A comparison of the records obtained in 1982 and 1983 suggests that dive bout length may be dependent on prey density within these patches. During 1983, the Southern California Bight experienced a major influx of warm water attributed to a strong El Niño. This correlated with a 20-fold reduction in zooplankton biomass and a marked decrease in commercial catches of market squid, salmon, and other fish species (McGowan 1984). Presumably, this decrease extended to the prey of Zalophus as well. The longest dive bout recorded for any animal was from 1983 (ZC-17). Dive bouts were also significantly longer (t-test; p < 0.05) for animals in 1983 ($\bar{x}$ = 4.6 ± 4.3 h; N = 41) (ZC-17 and ZC-20) than for those in 1982 ($\bar{x}$ = 2.9 ± 2.9 h; N = 115). From these data, it appears that sea lions may compensate for a reduced prey encounter rate by increasing the number of dives during a foraging bout.

The observation that dives within bouts were shallower and

TABLE 4. Diving bout characteristics

Animal	Recorded time at sea (h)	Bout-ending criteria (min)	No. of dive bouts per trip	Mean dive bout length (h)	Mean interval between dive bouts (h)*	Dive bouts per day	Mean dives per bout
ZC-5	28.1	8.0	6	2.4	1.8	5.1	43
ZC-6	83.3	11.0	12	2.3	4.4	3.5	29
ZC-7	—†	10.0	14‡	4.7	—†	—	51
ZC-8	74.4	10.0	15‡	2.5	0.7	4.9	55
ZC-9	66.2	10.0	14	2.8	1.8	5.1	45
ZC-10		7.5§					
1st trip	16.5		2	2.8	3.7	2.9	57
2nd trip	38.0		3	3.7	7.2	1.9	62
3rd trip	41.4		6	1.6	6.0	3.5	29
ZC-11	156.7	7.0	23	2.0	4.6	3.1	35
ZC-12		11.0§					
1st trip	76.2		10	3.9	1.6	3.2	67
2nd trip	84.7		13	2.9	3.0	3.7	57
ZC-17		11.0§					
1st trip	84.1		11	2.7	4.8	3.1	36
2nd trip	42.3		9	3.0	1.2	5.1	39
3rd trip	30.9		3	6.7	3.7	2.3	66
4th trip	21.3		2	9.6	0.2	2.3	98
5th trip	68.8		9	6.9	0.8	3.1	89
ZC-20	58.2	10.0	7	4.0	1.5	2.9	64
$\bar{x}$	60.7		9.2	3.3	2.9	3.5	54.2
SD	34.7		5.3	1.5	1.8	1.0	19.4
N	16		17	159	129	16	17

*Excluding transit times to first dive bout.
†May have returned to shore during the recording period.
‡May have made an earlier, shallow dive bout.
§BEC was calculated using all dives made by the animal.
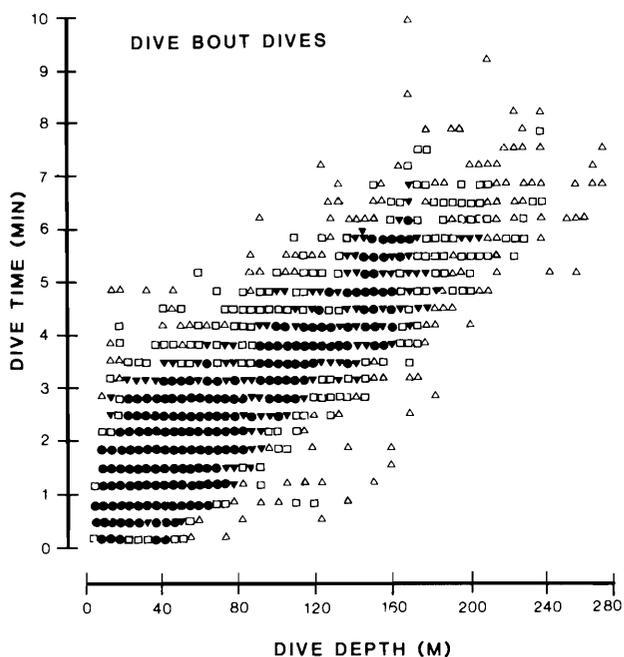
FIG. 5. The relation between depth and duration for dives occurring within dive bouts. A positive correlation was observed ($R^2 = 0.73$). Dive time can be predicted from the following equation: Dt $=$ 0.409 + 0.0262 depth, where Dt is in minutes and depth in metres. Symbols refer to the number of observations at each point. △, 1 observation; □, 2−5 observations; ▼, 6−9 observations; ●, 10 or more observations.
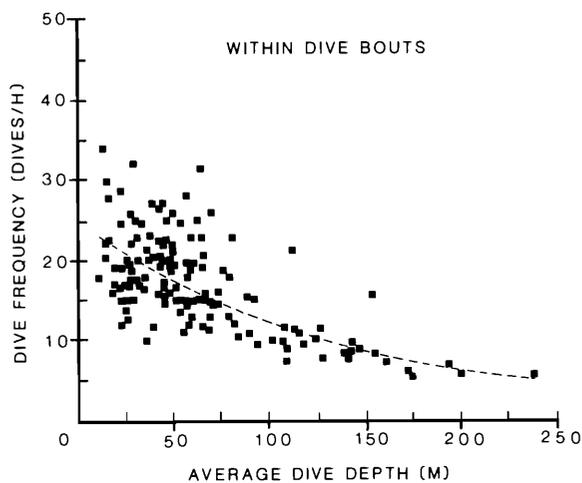
FIG. 6. Plot of dive frequency (dives/h) within dive bouts vs. the average depth (m) of those dives. Frequency showed an exponential decline with depth. The best fit equation determined from least squares analysis was as follows: frequency $= 24.8$ e$^{-0.007\ \text{depth}}$. The relatively low correlation ($R^2 = 0.57$) is due to the scatter present for shallow bouts.

of shorter duration at night than during the day (Fig. 8) is further evidence that these large scale diving patterns are strongly influenced by prey distribution. Vertical migrations of the prey would appear to account for diel variations in dive depth. Twilight peaks of diving activity (Fig. 9) may also
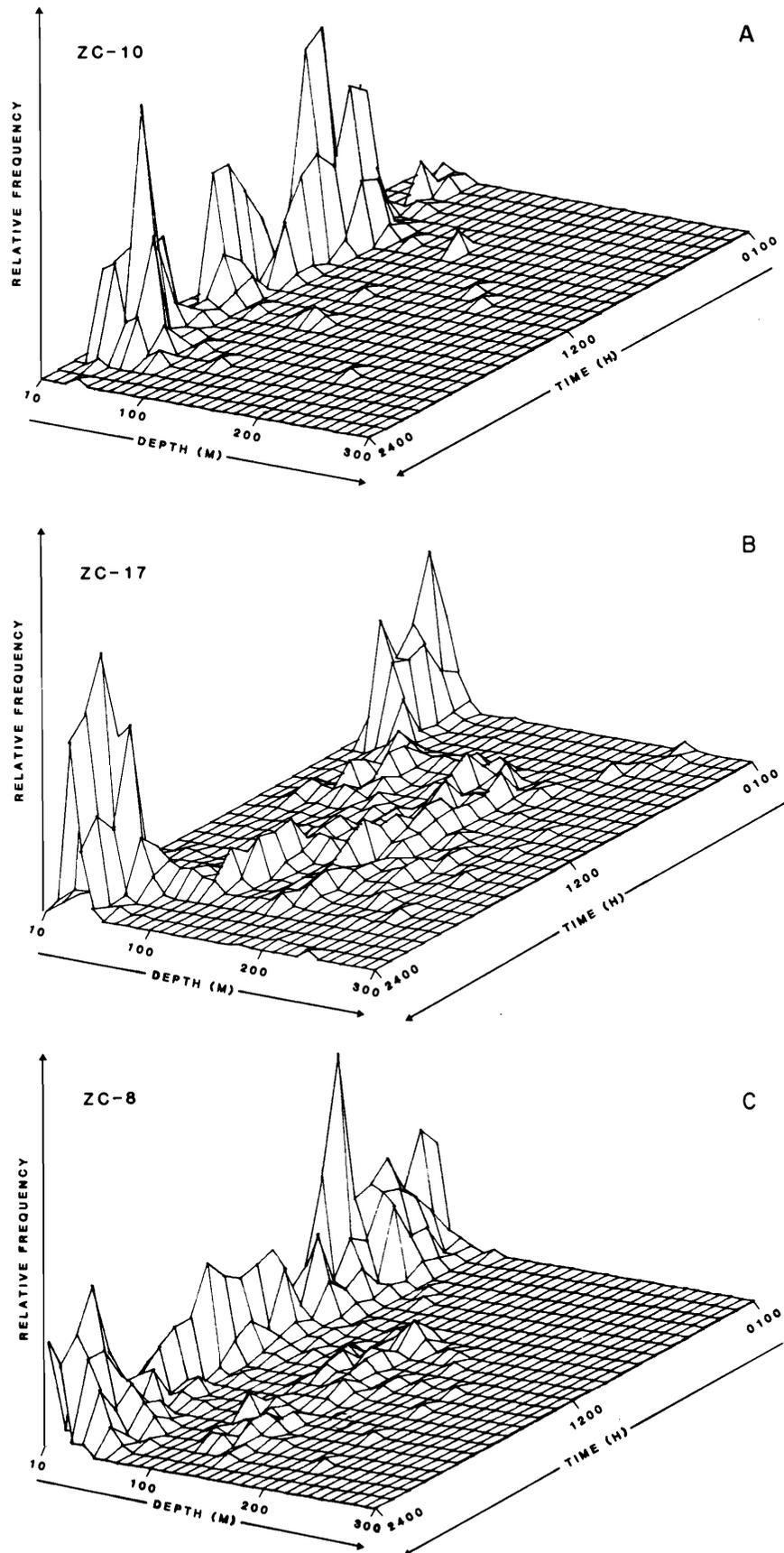
FIG. 7. Three dimensional plots of representative dive patterns. The relative frequency of dives is plotted as a function of both depth and time of day. (A) ZC-10 exhibiting a diurnal diving preference, (B) ZC-17 showing nocturnal preference, (C) ZC-8 exhibiting no clear preference for dive occurrence.

TABLE 5. Mean diving effort

	Over entire period at sea			Within diving bouts	
	% total time spent diving	% dives occurring within dive bouts	% total time engaged in dive bouts	% time spent diving	Dive frequency (dives/h)
$\bar{x}$	32	86	50	54	16.4
SD	12.2	8.4	20.4	9.2	3.1
N	16	17	16	17	17

NOTE: N, Number of trips to sea. Where N = 17, 11 animals are represented; where N = 16, 10 animals are included.
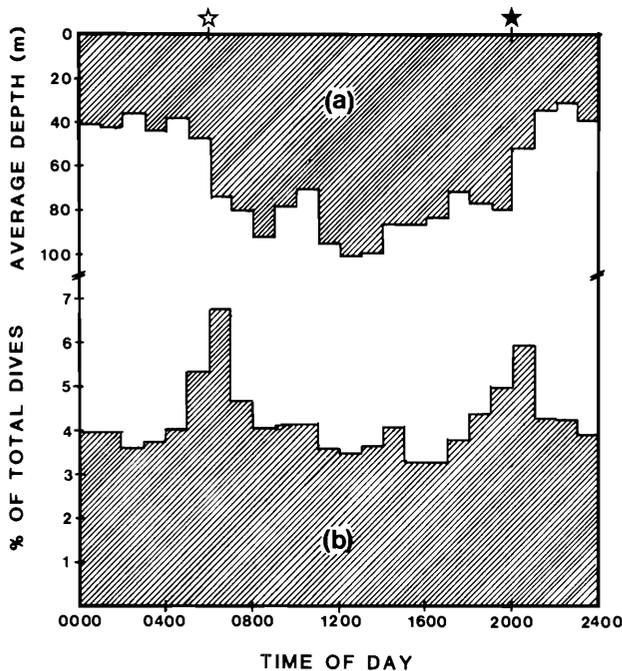
FIG. 8. Plot of all recorded dives as a function of the hour of day. (a) Diel variation in dive depth. (b) Diel variation in the relative frequency of dives. Stars represent local sunrise and sunset.

reflect a greater likelihood of foraging success during these times. Prey may remain clumped as they rise toward the surface before dispersing (Bailey et al. 1982), and shallower prey might be better silhouetted against the brighter surface during twilight than at night, making detection easier (Gentry et al. 1986a). Some fish may also be more susceptible to predation during this time when ambient light wavelengths rapidly shift out of their peak spectral sensitivity range (McFarland and Munz 1975; Hobson et al. 1981).

Although sea lions have the physiological capacity to reach depths of at least 250 m with durations longer than 9 min, dives rarely approached these limits (Figs. 3 and 4). Approximately 75% of all dives were less than 100 m in depth and 3 min in length. Moreover, shallow dives were invariably short, while deeper dives were longer, presumably reflecting increased travel time to and from depth. Do these observations reflect small scale diving patterns that are also structured by the distribution and abundance of prey, or ones that are determined more by the physiological constraints of breath hold?

The most efficient foraging strategy for any aquatic mammal is one that allows it to spend maximum time underwater in search of food. This is achieved by reducing time spent on the

surface, rather than by making the longest possible dives. Previous studies on Weddell seals have shown that surface time can be minimized if dives are sustained by aerobic metabolism (Kooyman et al. 1980). When anaerobic metabolism supplements energy production during a dive, lactic acid (LA) is formed. If LA accumulates over time, animals must extend their surface time to process it and return the body's acid−base balance to predive conditions (Kooyman 1985). In Weddell seals, dives up to 20 min can be supported aerobically. Beyond this, increasing dive durations lead to increasing surface periods (Kooyman et al. 1980; Kooyman 1981). The point at which LA begins to appear in the blood stream has been termed the aerobic dive limit (ADL) (Kooyman et al. 1980). For any species, if serial dives are to be useful for foraging, surface intervals must be brief to enable a quick return to the prey patch. For this reason, the ADL is more important than the maximum breath hold in structuring overall diving patterns during foraging (Kooyman 1985; Gentry et al. 1986a).

Based on estimates of body O_2 stores, we have calculated the ADL of a 90-kg sea lion as approximately 5.8 min (Table 6). This calculation makes several assumptions, the least certain of which is the diving metabolic rate. At the minimum cost of transport speed, metabolism is roughly 2.5 times the resting value (Feldkamp 1987). Upon submergence, however, changes occur that may lower this rate. Ventilation ceases, heart rate slows, and cardiac output is reduced from nondiving conditions (Kooyman 1975; Sinnett et al. 1978). For this reason, we use 2 times the predicted resting value as an estimate of diving metabolism. Because of the uncertainties in these assumptions, 5.8 min should be viewed as only an approximate value.

Sea lions exceeded this predicted ADL on only 4% of their dives (Fig. 3). Similar findings have been reported for Weddell seals and fur seals that remain within their ADL on over 95% of their free-ranging dives (Kooyman et al. 1980; Gentry et al. 1986a). Sea lions, in fact, rarely approached this limit. Of all dives, 57% were less than 2 min in length, while 18% were between 2 and 3 min (Fig. 3).

It is possible that drag arising from the instrument package may have led to a greater metabolic rate, thereby reducing this predicted ADL. Laboratory studies showed that drag attributable to the TDR increased with higher velocities (Appendix). At faster speeds, which might occur during pursuit of rapidly moving or evasive prey, greater drag would necessitate increased metabolic power requirements. However, if metabolism was elevated to 4 times resting (equivalent to juvenile sea lions swimming at 2.2 body lengths/s; Feldkamp 1987), dives up to 3 min could still be supported aerobically. Moreover, all animals but one (ZC-10) made serial dives that exceeded 5 min in length, implying that these too were
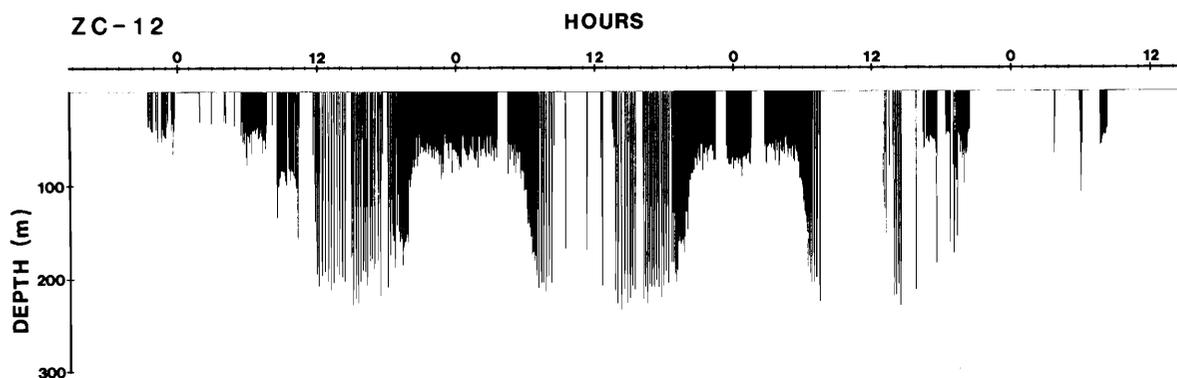
FIG. 9. Segment of the diving record of ZC-12 showing vertical changes in dive depth as a function of time of day. This pattern suggests pursuit of vertically migrating prey.

TABLE 6. Predicted aerobic dive limit for a 90-kg sea lion

Stores	Reference
Lungs	
Total lung capacity (TLC): 8.5 L	Kooyman 1973
Diving lung volume: 50% TLC	Kooyman and Sinnett 1982
Alveolar O_2 concn.: 15%	Kooyman 1973
Available O_2: 0.64 L	
Muscle	
Estimated mass: 0.3 × body mass	Lenfant et al. 1970
Myoglobin (Mb) concn.: 3.2 g/kg muscle	Castellini and Somero 1981
Combining capacity (mL O_2/g Mb): 1.34	Kooyman and Sinnett 1982
Available O_2: 1.16 L	
Blood	
Total blood volume: 9.81 L	Lenfant et al. 1970
Arterial volume: 0.33 × total	Lenfant et al. 1970
Venous volume: 0.67 × total	Lenfant et al. 1970
Hemoglobin (Hb) content (g %): 16.5	Kooyman and Sinnett 1982
Hb combining capacity (mL O_2/g Hb): 1.34	Kooyman and Sinnett 1982
Arterial stores (95 to 20% saturation): 0.54 L	Lenfant et al. 1970
Venous stores (90 to 15% saturation): 1.09 L	Lenfant et al. 1970
Available O_2: 1.63 L	
Summary	
Total available O_2: 3.43 L	
Estimated metabolic rate:	
2 × 0.0101 mass$^{0.75}$ = 0.59 L/min	Kleiber 1975
Predicted ADL: 5.8 min	

aerobic. It therefore appears that the majority of dives did not exceed the ADL.

These findings suggest that within the physiological limits to duration and depth, individual dives are also strongly influenced by prey location and availability. While the majority of dives were shallow and short (Figs. 3 and 4), sea lions have the capacity to sustain longer breath holds, as evidenced by the correlation between depth and duration. If shallow prey are abundant, animals may make short dives to minimize time spent loading oxygen at the surface. On these dives, an oxygen reserve could be maintained to provide the flexibility needed to make extended pursuits if necessary. If prey are unavailable at the surface, or deeper prey are of a higher energy content or encountered more frequently, sea

lions may extend their search time by diving deeper at the risk of reducing the time available for pursuit (Dunstone and O'Connor 1979a). The abundance of shallow prey may therefore be an important factor structuring the observed patterns.

Sea lions were active, engaged either in diving bouts or in travel, throughout their trips to sea (Table 2; Fig. 7). Continuous activity may reflect the importance of quickly returning to their dependent pup on shore. The observation that resting accounts for only 3% of a female's activity budget suggests that they may attempt to maximize energy intake while minimizing time spent away from the pup. The longer the pup must fast on shore, the more it will utilize stored energy reserves (Doidge et al. 1984a; Gentry et al. 1986a). In years of poor food availability, when females make longer trips to sea, sea

lion pups have lowered rates of milk intake, reduced growth rates, and suffer a greater mortality (Ono et al. 1987). Hungry pups also attempt to suckle more from unrelated females on the rookery and, in doing so, increase the risk of being injured (Doidge et al. 1984b; Ono et al. 1987). Sea lions that feed quickly and return to shore may, therefore, reduce the probability of mortality to their young.

Time spent in transit and in swimming between dive bouts provides an indication of distances sea lions travel while feeding. On average, animals swam an estimated 31 km before beginning their first dive bout and 42 km after finishing the last (Table 3). Between bouts they travelled a mean of 20 km, indicating active searching for prey patches. The percentage of total trip time spent in transit (16.5%) is similar to that observed for other otariid species. Fur seals and the Galapagos sea lion (Z. californianus wollebaeki) spend between 12 and 29% of their feeding trips in transit, although absolute transit durations vary greatly (Gentry et al. 1986a). This suggests that the duration of a feeding trip may be partially dependent on the distance animals swim to reach suitable feeding areas. For example, northern and Antarctic fur seals (Callorhinus ursinus and Arctocephalus gazella, respectively) have average transit times to the first dive bout of 15 − 16 h, with average trip durations of 128 − 165 h (Gentry et al. 1986b; Kooyman et al. 1986). The Galapagos sea lion spends only 16 h at sea and 0.5 h in transit from shore (Kooyman and Trillmich 1986). California sea lions appear to be intermediate between these, spending an average of 61 h at sea with a mean outward bound transit time of 3.4 h (Table 3).

Many aspects of California sea lion diving behavior are similar to those reported for other eared seals. Galapagos sea lions and all fur seals examined to date make dives that are generally shallow and of short duration, with average depths and durations comparable with those measured for sea lions (Gentry et al. 1986a). Maximum depths and durations are also in the range of sea lions, exceeding 200 m and 7 min in length. Dive durations correlate strongly with depth. All species partition diving activity into bouts, and diving frequency within these bouts shows little variation across species lines. Activity partitioning is also qualitatively similar among otariids, although absolute transit times vary greatly. All animals but the Galapagos sea lion spend the majority of time swimming. With the exception of the northern fur seal, rest accounts for only 5% or less of the total time at sea.

Comparisons such as these help to shed light on certain diving characteristics that may change as a consequence of environment or prey type and those that are constrained by the physiology, morphology, and behavior of these animals. For example, maximum depths and durations are similar among all otariid species and appear to be largely inflexible characteristics. The strong correlation between depth and duration also suggests a behavior constrained by the relatively short breath-hold duration of otariids. However, mean dive depths and durations, while shallow and short for most animals, can vary on an individual basis (Table 1; Gentry et al. 1986b) and may be partially dependent on prey availability. Similarly, variable transit times and feeding trip durations between habitats and large differences in the overall number of dives/h, imply that large scale activity patterns can be greatly modified to accommodate differences in local feeding conditions.

Although similar in many ways to other otariids, the patterns observed for sea lions are quite distinct from those described for phocid seals. In the two species for which comparable data are available, the Weddell and northern elephant seal, dives often exceed 300 m in depth and 20 min in length (Kooyman 1981; Le Boeuf et al. 1986; Le Boeuf et al. 1988). Elephant seals, unlike sea lions, also spend a considerable fraction of each dive at depth. If time at the bottom of a dive represents pursuit and (or) search time, then in general, phocids may spend a greater percentage of each dive engaged in this activity than do otariids (Le Boeuf et al. 1988). It is not clear whether these divergent patterns arise from differences in size and breath-hold capacity, methods of locomotion, or prey selection. While all are undoubtedly important, future studies are needed to help clarify the consequences of different adaptations to breath-hold foraging.

Acknowledgements

Appendix

No studies have documented the average swimming velocity of California sea lions in the wild. We present here theoretical calculations of swim speed based on laboratory studies of juvenile animals. Feldkamp (1987) has shown that sea lions weighing 20−25 kg cover the greatest distance for the least amount of energy (minimum cost of transport speed) when travelling at 1.4 body lengths/s. The total length of eight adult female sea lions, measured on San Miguel Island, averaged 2.1 ± 0.1 m. If we assume similar relative transport costs as for juveniles, then adult sea lions should travel at speeds close to 3 m/s.

Swimming velocities were likely reduced as a result of increased drag caused by the TDR and harness (Wilson et al. 1986). To estimate this increase, drag studies with a 37-kg sea lion, 1.46 m in length, were undertaken. Resistance was measured by towing the animal through the water behind a moving cart (Williams and Kooyman 1985; Feldkamp 1987). At a speed of 1.4 body lengths/s, the presence of the TDR and harness increased drag by a factor of 1.65 (Fig. 10). While this value may decrease with larger body size, it does provide a first approximation of the recording system's hydrodynamic effect.

The extent that swimming speed was affected by drag from the instrument can be estimated from this augmentation factor. Feldkamp (1985) shows that the drag coefficient (Cd) of sea lions (based on wetted surface area) is a function of the Reynolds number (Re) (defined as the product of an animal's length and velocity divided by the fluid's kinematic viscosity; Hoerner 1958), where $Cd = 0.0464 Re^{-1/6}$. At 1.4 body lengths/s, swimming efficiency was roughly 10% (Feldkamp 1987). With these values, a number proportional to power input (P_i) can be calculated for a sea lion 2 m in length where:
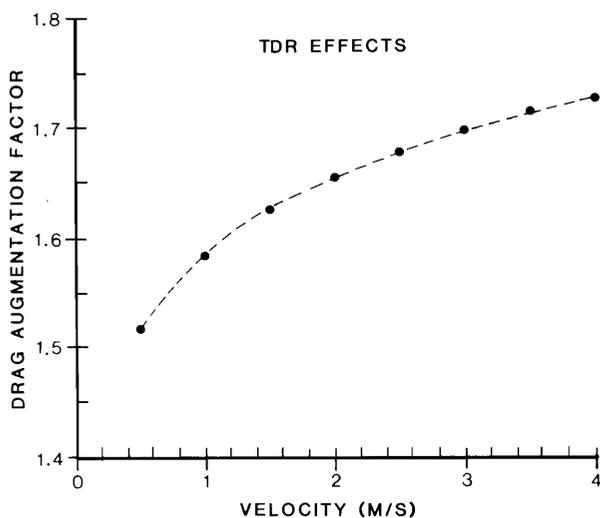
FIG. 10. An illustration of the increase in drag resulting from the TDR and harness for a 37-kg sea lion. Drag on the animal both with and without the recording system was obtained through towing experiments and the factorial increase plotted here as a function of velocity.

$$[1] \quad P_i = \frac{\text{drag} \times \text{velocity}}{\text{efficiency}}$$

and

$$[2] \quad \text{drag} = 0.5 \, p \times S \times U^2 \times Cd$$

(p = density; S = surface area; U = velocity) (Webb 1975). If drag is augmented by a factor of 1.65, then the power necessary to maintain a similar swimming speed also rises. For the same rate of energy expenditure, we predict that a sea lion encumbered by the TDR and harness would swim at 2.5 m/s (9 km/h) rather than the estimated value of 3.0 m/s. This speed is therefore taken as an estimate of the study animals' swimming velocity.

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