

Three-dimensional movements and swimming activity of a northern elephant seal[☆]

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Abstract

We attached a video system and data recorder to a northern elephant seal to track its three-dimensional movements and observe propulsive strokes of the hind flippers. During 6 h of recording, the seal made 20 dives and spent 90% of the time submerged. Average dive duration, maximum depth and swimming speed were 14.9 min \pm 6.1 S.D., 289 m \pm 117 S.D. and 1.1 m s⁻¹ \pm 0.12 S.D., respectively. The distance swum during a dive averaged 925 m \pm 339 S.D., and the average descent and ascent angles were 41° \pm 18 S.D. and 50° \pm 21 S.D., respectively. Dive paths were remarkably straight suggesting that the seal was navigating while submerged. We identified three modes of swimming based on the interval between propulsive strokes: continuous stroking; stroke-and-glide swimming; and prolonged gliding. The seal used continuous stroking from the surface to a mean depth of 20 m followed by stroke-and-glide swimming. Prolonged gliding started at a mean depth of 60 m and continued to the bottom of dives. For dives to depths of 300 m or more, 75% of the descent time was spent in prolonged gliding and 10% in stroke-and-glide swimming, amounting to 5.9–9.6 min of passive descent per dive. Average swimming speed varied little with swimming mode and was not a good indicator of propulsive effort. It appears that the seal can use prolonged gliding to reduce the cost of transport and increase dive duration. Energetically efficient locomotion may help explain the long and deep dives that routinely exceed the theoretical aerobic dive limit in this species. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Elephant seal; Swimming; Diving; Three-dimensional; Navigation; Orientation; Locomotion

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1. Introduction

The northern elephant seal (*Mirounga angustirostris*) is a pelagic marine mammal that spends most of the year in the eastern North Pacific Ocean. At Año Nuevo Point (37° 8.0'N Lat., 122° 20.0'W Long.), California, adult females come ashore between mid-December and mid-February to give birth and breed and in April to molt (Le Boeuf et al., 1994). At sea, females migrate long distances (up to 10 800 km round-trip) in a broad expanse of the eastern Pacific as far north as 60° N Lat., and from near the coastline to as far west as 172.5° E Long. (Le Boeuf et al., 1993; Stewart and DeLong, 1993, 1994; Le Boeuf et al., 2000). During the 10-week foraging trip after the breeding season, females older than 2 years dive for an average duration of 20.8 min \pm 4.1 S.D. (range = 16–23 min), swim at routine speeds of 0.9–1.7 m s⁻¹, and reach an average maximum depth of 509 m \pm 147 S.D. (range = 325–550 m) (Le Boeuf et al., 1992; Crocker et al., 1994; Le Boeuf, 1994). Stewart and DeLong (1994) reported similar results for females breeding on San Miguel Island in southern California. During the 8-month foraging trip to sea after molting, which coincides with gestation, average dive duration of females in the third trimester of pregnancy is 39% longer than in non-pregnant females (Le Boeuf, 1994), possibly due to an increase in blood volume (Danforth, 1977) and total body oxygen stores. For both non-pregnant and pregnant females, intervals at the surface between dives are generally short (approx. 2.1 min \pm 0.5 S.D.), and approximately 90% of the total time at sea is spent submerged (Le Boeuf, 1994; Le Boeuf et al., 2000).

Our knowledge of the underwater behavior of elephant seals is based primarily on indirect information provided by dive depth and duration statistics and estimated swim speeds. In an attempt to elucidate the underwater behavior of these animals, these data have been used to identify several dive types that occur during transit, benthic or pelagic foraging, and food processing (Le Boeuf et al., 1988, 1992, 1993; Hindell et al., 1991; Asaga et al., 1994; Crocker et al., 1997). The data supporting these putative dive types are not empirical but circumstantial. To provide a better understanding of elephant seal diving behavior, we attached a small video system and data recorder to a female elephant seal in Monterey Bay, California. We use this new and highly de-

tailed information to describe diving behavior, evaluate potential energy-saving locomotor strategies, and comment on diving physiology and navigation.

2. Methods

2.1. Animal

We used the translocation–homing paradigm to study diving behavior of an elephant seal as it returned to the beach from which it was displaced (Oliver et al., 1998). Most seals return to the capture site in approximately 4 days after being translocated to sea by approximately 50 km. Diving performance in this situation is similar to that of migrating seals (Le Boeuf et al., 1996; Oliver, 1997).

We captured a 27-month-old female northern elephant seal that weighed 263 kg (Identification Number GJ904R; standard length = 201 cm; axillary girth = 165 cm) at Año Nuevo Point, California, on 2 April 1996 and transported it 30 km south to the Long Marine Laboratory at the University of California at Santa Cruz. The seal was immobilized with an intramuscular injection of ketamine hydrochloride (2 mg kg⁻¹). After cleaning the fur in the mid-dorsal area with acetone, a piece of neoprene rubber (0.5-cm thick, 30 cm in diameter) was glued to the fur along the dorsal midline above the shoulders with neoprene rubber cement. The video system was attached with hose clamps to small brass rings sewn to the rubber. The video camera faced rearward so that we could observe the propulsive strokes of the hind flippers during dives. The antenna for a Global Positioning System (GPS) was glued to the fur on the top of the seal's head, and a satellite telemeter (Wildlife Computers, Redmond, WA, USA) and VHF radio (Advanced Telemetry Systems, Bethel, MN, USA) were glued to the neoprene rubber on its back. The seal was allowed to recover from the sedative overnight. It was then transported offshore and released beyond the continental shelf in northern Monterey Bay (36° 46.428' N Lat., 122° 1.053'W Long.) at 11.45 PST on April 3. Video and data were recorded from 11.38 to 17.38 PST. The seal returned to Año Nuevo Point 1 week later and the instrument was recovered.

2.2. Video system and data recorder

The video system and data recorder were fabricated by Pisces Design (San Diego, CA, USA). The torpedo-shaped, aluminum housing was 30-cm long, 13 cm in diameter and pressure rated to a depth of 2000 m. The instrument weighed 6.2 kg in air and 2.2 kg (less than 1 % of the seal's body mass) in water. The cross-sectional area of the housing was 6% of the maximum cross-sectional area of the seal. The wide angle (80° horizontal, 60° vertical) low-light sensitive (0.3 lux), black and white CCD camera (Chinon GX060, Mountainside, NJ, USA) was encircled by an array of blue light emitting diodes (LEDs) (Ledtronics, Torrance, CA, USA). The blue LEDs provided sufficient illumination for the camera to record objects at a distance of 2 m in complete darkness. When additional ambient light was available, objects were visible at much greater distances. The aluminum housing contained an 8-mm video tape recorder (Sony EVO-220 VTR), lithium batteries, and a microprocessor for programming camera functions and encoding data from transducers. A data encoder received digital signals directly from transducers or from the 14-bit A/D board (Maxim, Sunnyvale, CA, USA) and encoded them into the vertical blanking interval of the videotape. The signal from the hydrophone was recorded on the VTR's audio track. The video system was activated by an external switch on the housing or by a programmable microcontroller. Maximum recording duration was 6 h. Onboard transducers sampled once per second. A pressure transducer (Series-20, Keller-PSI, Hampton, VA, USA) was used to record depth. Swimming speed through the water (water speed) was measured with a miniature, vertical axis impeller transducer (Ultramarine, Galveston, TX, USA) that had excellent linearity and was able to record from 0.3 m s⁻¹ (stall speed) to over 3.5 m s⁻¹ ± 0.045 S.D. It was calibrated in situ using the method of Hill (1986) and Blackwell et al. (1999) in which the rate of change in depth (m s⁻¹) was plotted against the output from the speed sensor and a linear equation was fitted to the upper edge of the data. This line represents vertical movements in which depth change and speed are equal. Using computed positions in three spatial dimensions (see Section 2.3, below), there were 140 observations for which the seal was moving at an angle > 80° from horizontal. The flux-gate com-

pass (KVH, Middletown, RI, USA) was fully gimballed (± 95°) and had a mean standard deviation for any compass bearing of 0.38°. Rolls or pitches more than ± 95° exceeded the gimbaling and were recorded as an error to indicate unreliable bearing data. Location at the surface was determined with a GPS (GPS 25, Garmin, Lexena, KS, USA) and 6-cm diameter submersible antenna (Applied Ocean Physics, San Diego, CA, USA). The hydrophone (Pisces Design, San Diego, CA, USA) had a frequency response of 50–16 kHz. The data encoder superimposed time, date, depth (m), swimming speed (m s⁻¹) and compass bearing (0–360°) on the video image during playback.

2.3. Data analysis

Three-dimensional dive paths were computed from depth, compass bearing, and swimming speed using standard 'dead reckoning' methods (Bowditch, 1995). Dead reckoning enabled us to compute the animal's position at any time during a dive from knowledge of a known position (i.e. GPS position prior to diving), time, water speed, and bearing. Initial dive path calculations produce the 'course steered', which reflects the result of only the animal's swimming. Ocean currents and accumulated sensor errors also affect calculation of the animal's position. The direction and speed of these external effects are called 'set' and 'drift,' respectively, and are calculated from the difference between the end of the course steered and the GPS position at the end of each dive. The final dive path, called the 'course made good,' is computed by applying the set and drift equally throughout the dive, thereby assuming uniformity in space and time (Bowditch, 1995). The corrected coordinates of the course made good enable calculation of the speed of the seal relative to a fixed position in space (ground speed). This is different from the speed reported by the onboard flow meter, which reports water speed.

The digitized video image, synchronous three-dimensional dive path, and numerical data (time, depth, water speed and compass bearing) were integrated and displayed simultaneously on a personal computer using software developed at Texas A&M University. This type of analysis enabled us to relate the seal's movements in space with flipper strokes and water speed. Flipper stroke interval was calculated as the time between maximum left and maximum right excursions of the flippers

as seen on the digitized video record. These points were recorded as video frame numbers, giving a resolution of 0.033 s. Stride length is defined as the distance the seal traveled during a single flipper stroke (i.e. left-to-right or right-to-left). It was determined from the onboard flow meter data and not corrected for set and drift because stride calculations pertain to swimming effort and the movement of the seal with respect to the water, rather than with respect to a fixed position on the ground. Straightness of swimming paths and surface GPS positions was quantified using the net-to-gross displacement ratio (NGDR), the net distance between two endpoints divided by the total distance swum between those points. NGDR takes a value of 1.0 when the animal swims in a straight path between the endpoints. Any deviation from a straight path decreases the ratio.

3. Results

During the 6 h of continuous video and data recording, the seal made 20 dives and spent 90% of the time submerged (Table 1). Average dive duration was 14.9 min \pm 6.1 S.D. (range = 0.6–22.2 min), and average maximum depth was 289 m \pm 117 S.D. (range = 14–430 m). Swimming

speed (water speed) while submerged averaged 1.1 m s⁻¹ \pm 0.12 S.D. The distance swum along the course steered averaged 925 m \pm 339 S.D., ranging from 41 to 1273 m ($N = 20$ dives). Surface intervals between dives averaged 1.8 min \pm 0.4 (range = 0.4–2.3 min). While at the surface, the seal rested in an upright or prone position, being carried by the current at approximately 0.3–0.4 m s⁻¹. No vocalizations or other distinguishable sounds were heard on the audio recording.

3.1. Three-dimensional movements during dives 1–8

Three-dimensional dive paths (course made good) were calculated for dives 1–8 (Fig. 1). The GPS antenna cable failed after dive 8, so the seal's surface location at the beginning and end of dives 9–20 could not be determined. Although this prevented computation of the course made good for the later dives, depth, speed, bearing, and stroke data were collected for all 20 dives.

Net horizontal displacement based on the first and last GPS positions (point-to-point) for dives 1–8 was 3.3 km along a west–northwesterly heading of 297°. The path through the animal's surface positions was remarkably straight (Fig. 1), with a horizontal net-to-gross displacement ratio (NGDR) of 0.91. The courses steered while sub-

Table 1
Summary statistics for the series of 20 dives by the elephant seal

Dive	1	2	3	4	5	6	7	8	9	10	
Pre-dive interval (min)	2.23	1.75	1.37	2.02	2.15	1.90	1.65	2.28	1.87	2.00	
Duration (min)	9.42	0.63	7.65	10.38	12.78	13.27	15.50	17.85	18.45	15.00	
Mean depth (m)	150	8	69	113	163	153	192	221	228	231	
Maximum depth (m)	260	14	115	173	247	229	333	325	343	402	
Distance steered (m)	708	41	550	777	946	961	1097	1038	996	939	
Mean speed (m s ⁻¹)	1.3	1.0	1.2	1.2	1.2	1.2	1.2	1.0	0.9	1.0	
Maximum speed (m s ⁻¹)	2.2	1.3	1.5	1.7	1.7	1.7	1.7	1.7	1.7	1.5	
Total propulsive strokes	531	34	456	602	723	676	723	715	667	656	
Time gliding (min)	3.47	0.1	2.28	3.47	4.38	5.33	6.93	9.18	10.9	6.9	
Dive	11	12	13	14	15	16	17	18	19	20	Mean
Pre-dive interval (min)	1.87	1.7	2.03	1.37	0.42	1.45	2.02	1.77	2.13	1.98	1.8
Duration (min)	14.97	18.97	19.43	18.72	2.23	21.58	22.23	19.00	19.57	20.38	14.90
Mean depth (m)	205	240	242	223	32	257	258	223	244	259	186
Maximum depth (m)	333	352	361	323	58	384	394	332	374	430	289
Distance steered (m)	940	1004	1133	1049	156	1229	1258	1162	1245	1273	925
Mean speed (m s ⁻¹)	1.1	0.9	1.0	0.9	1.2	1.0	0.9	1.0	1.1	1.0	1.1
Maximum speed (m s ⁻¹)	1.6	1.7	1.5	1.6	1.4	1.6	1.7	1.5	1.5	1.5	1.6
Total propulsive strokes	609	655	729	638	101	769	798	725	820	783	621
Time gliding (min)	7.53	11.13	10.38	11.10	1.03	12.07	12.53	10.27	9.68	10.63	7.47

merged in each dive averaged $283^\circ \pm 9.0$ and were significantly less linear than the GPS path, with an average horizontal NGDR of 0.69 ± 0.12 . However, the effect of currents was to straighten the actual dive paths (mean horizontal NGDR for course made good = 0.78 ± 0.08 S.D.).

The seal descended to depths of more than 100 m in all but dive 2, a dive that was very short (38 s) and which will be excluded from further analysis. Dives 3, 4, 5, and 6 included more than one descent and ascent, whereas dives 7 and 8 involved a single descent to the bottom of the dive, followed by an ascent to the surface. Mean total distance traveled over the course made good (906 m \pm 179 S.D., 7 dives) was 1.9 (\pm 0.4 S.D.) times the net displacement (476 m \pm 101 S.D.) between the surface positions at the start and end of dives. This ratio is a measure of the additional distance that the animal traveled by descending to depth rather than swimming directly between the endpoints at the surface. The mean horizontal transit

speed (net displacement per dive divided by elapsed time) was $0.7 \text{ m s}^{-1} \pm 0.18$ S.D.

Angles of descent and ascent (dives 1, 3–8) were calculated from the three-dimensional position data and smoothed using an 11-s moving average to reduce the error arising from the 1-m precision of the depth sensor. Mean (smoothed) descent angle was $41^\circ \pm 18$ S.D. and was not significantly different during the first 60 m of descent ($42^\circ \pm 17$ S.D.) or when the seal was deeper ($40^\circ \pm 18$ S.D.). The mean ascent angle was $50^\circ \pm 21$ S.D. Ascent angles during the last 60 m were steeper ($55^\circ \pm 23$ S.D.) than they were for deeper portions of ascents ($48^\circ \pm 20$ S.D.). All pairwise differences in these four mean angles (shallow and deep during descent and ascent) were highly significant ($P < 0.001$, Student's *t*-test) except shallow (≤ 60 m) vs. deep dive angles during descent ($P = 0.049$). Calculating average descent and ascent angles from swim speed, time, and depth data alone, rather than using the

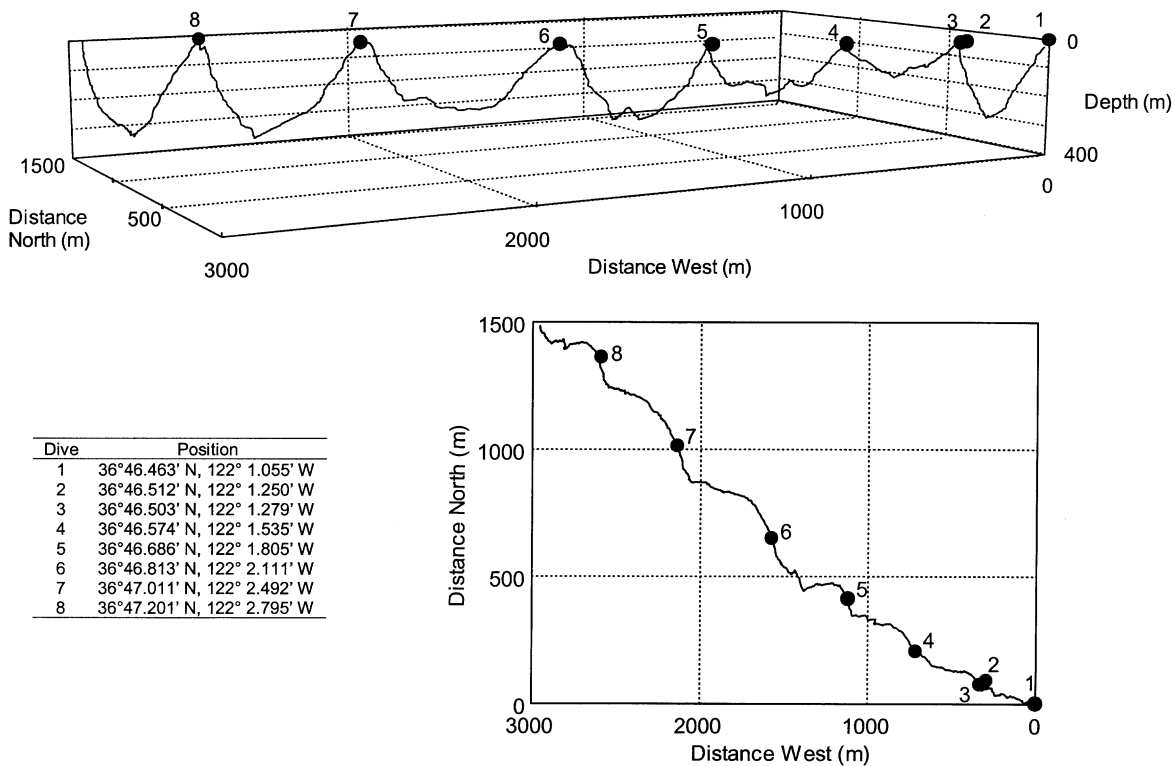


Fig. 1. Reconstructed three-dimensional dive path of an elephant seal during the first eight dives of the deployment. Surface GPS positions prior to the beginning of each dive are shown in the figure. Submerged positions are plotted at 1-s intervals computed by dead-reckoning techniques and corrected for the effects of currents. The lower panel (aerial view of the same series of dives) shows the relatively straight path swum by the seal. The depth of water at this location was approximately 1000 m.

three-dimensional position data, yielded lower values. For example, mean (smoothed) descent angle was $34^\circ \pm 18$ and mean ascent angle was $34^\circ \pm 20$ S.D.

3.2. Locomotor activity

Analysis of the interval between propulsive strokes of the hind flippers in all 20 dives revealed three modes of swimming: continuous swimming; stroke-and-glide swimming; and prolonged gliding. The division between continuous stroking and stroke-and-glide swimming was at a local minimum (2.5 s) in the frequency distribution for tail beat interval (Fig. 2). The division between stroke-and-glide swimming and prolonged gliding was where the declining trend of stroke-and-glide swimming met the level distribution for prolonged gliding (see inset of Fig. 2). Using these divisions, the mean tail beat interval was 0.76 s (± 0.19 S.D.) for continuous stroking, 5.7 s (± 2.28 S.D.) for stroke-and-glide swimming, and 51.6 s (± 67.8 S.D.) for prolonged gliding. Many episodes of prolonged gliding lasted for 1–2 min and some as long as 6 min.

The occurrence of these swimming modes var-

ied with depth and whether the seal was descending or ascending (Fig. 3). The seal used continuous stroking as it descended from the surface down to a mean depth of 20 m (range = 6–34 m), then began using a stroke-and-glide swimming mode. Prolonged gliding started at a mean depth of 60 m (range = 5–177 m) and continued to the bottom of the dive. For the 13 dives to depths of 300 m or more, 75% of the descent time was spent in prolonged gliding (range = 54–85%) and 10% in stroke-and-glide swimming (range = 2–27%) (Fig. 4). This amounted to 5.9–9.6 min of passive descent (during stroke-and-glide swimming and prolonged gliding) per dive.

Swimming (water) speeds varied slightly with swimming mode and whether the seal was ascending or descending, as exemplified by data for dives 1–8 (Fig. 5). Overall mean speed was 1.2 m s^{-1} (± 0.23 S.D.); continuous stroking yielded the fastest speeds and prolonged gliding the slowest. Stride length for continuous stroking averaged 0.8 m (± 0.13 S.D.) overall. During descent, stride length for continuous stroking was slightly greater than during ascent (0.9 ± 0.13 S.D. vs. 0.8 ± 0.11 S.D.). Continuous stroking during ascent was vigorous and produced noticeable yaw in the dive

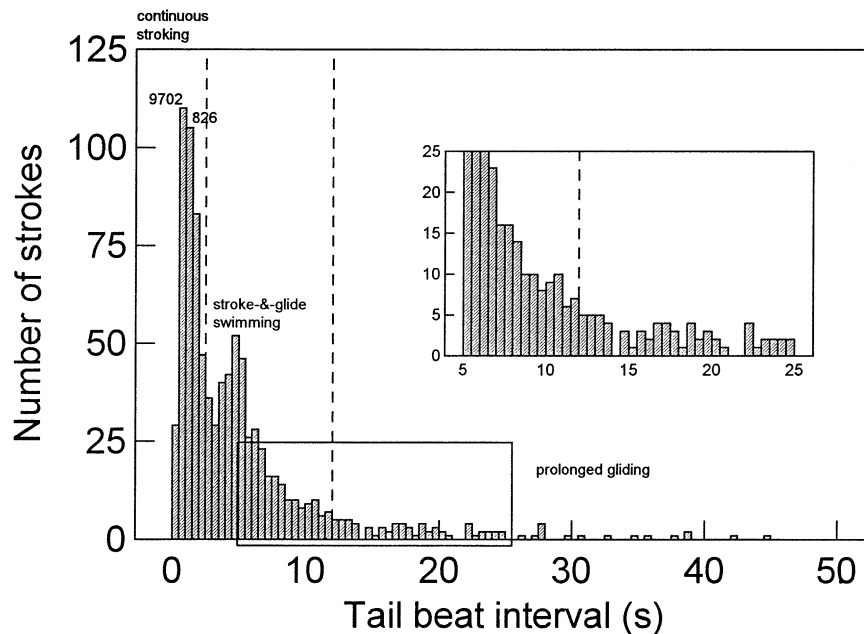


Fig. 2. The frequency distribution for intervals between consecutive propulsive strokes during 20 dives shows three modes of swimming. The limits of these swimming modes are at 2.5 and 12 s (dashed lines). Inset shows area of larger distribution enclosed by the rectangle. Bar width for both plots is 0.5 s. The two highest bars in the larger plot exceed the scale on the y-axis; numbers show actual frequencies.

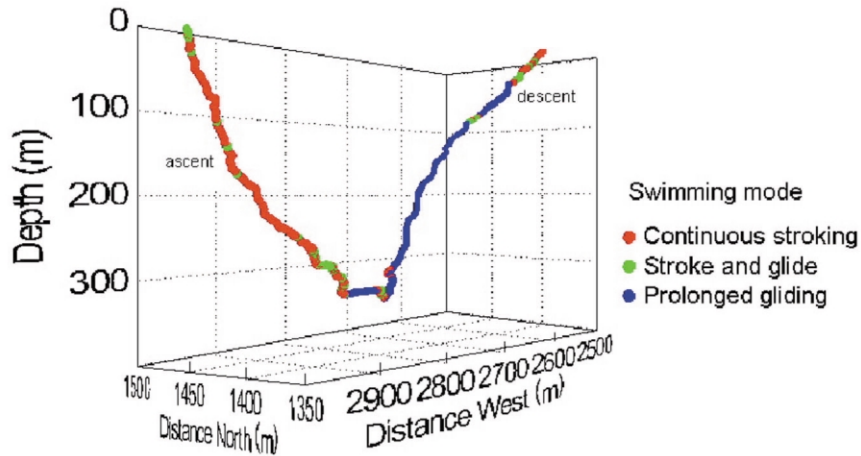


Fig. 3. Reconstructed three-dimensional dive path for dive 8 showing the spatial distribution of swimming modes. Prolonged gliding dominated the descent and continuous stroking was principally used during ascent. Stroke-and-glide swimming was used in horizontal swimming.

path. During ascents, stroke-and-glide swimming and prolonged glides occurred at mean speeds that were 11–13% less than during descent. Lowest mean speeds were recorded during prolonged glides in ascents ($1.0 \text{ m s}^{-1} \pm 0.24 \text{ S.D.}$). However, such glides were rare (66 of 1938 s of ascent in dives 1–8), occurring mostly during the final approach to the surface when the animal was positively buoyant. By comparison, prolonged glides during descents averaged $1.1 \text{ m s}^{-1} (\pm 0.19 \text{ S.D.})$.

4. Discussion

4.1. Diving behavior

Dive depth as a function of time has been well

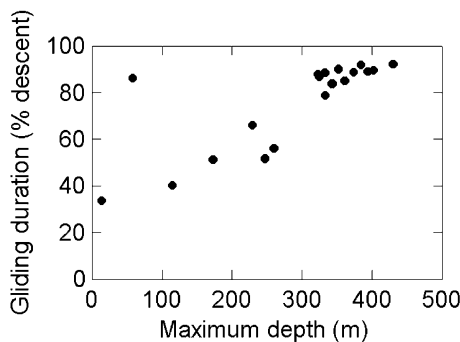


Fig. 4. Proportion of time spent gliding during descent in 20 dives. The seal used progressively more gliding to descend in deeper dives.

described for northern elephant seals based on data obtained from time–depth recorders (Le Boeuf et al., 1986, 1988; Le Boeuf, 1994). Although these time–depth profiles appear to give two-dimensional information, they provide only one spatial dimension (i.e. depth). In one study, depth and swim speed (water speed) were measured simultaneously providing information on two spatial dimensions (depth and horizontal displacement) so that descent and ascent angles could be estimated (Le Boeuf et al., 1992; Crocker et al., 1994). However, because of the absence of data for the third dimension, movements within the horizontal plane were neglected. The NGDR for course steered while submerged (0.69) reflects lateral meanders that contribute to a greater total distance traveled than would be estimated from

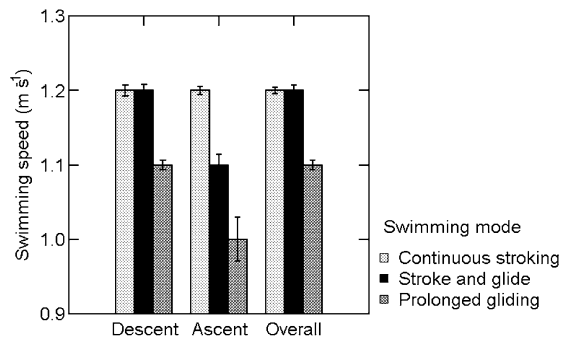


Fig. 5. Swimming speeds (water speeds) for each swimming mode and direction of movement. The seal maintained relatively consistent speeds in all swimming modes, even while passively gliding for prolonged periods.

depth and speed and which would result in an underestimate of computed angles of descent and ascent. In addition, the absence of GPS position at the surface precluded calculation of set and drift values that are necessary to convert water speed into ground speed (i.e. speed relative to a fixed position). As a result, true multi-dimensional spatial analysis of elephant seal dives has not been possible until now.

It was not possible to measure the potential effects of the video system and data recorder on the hydrodynamic drag of the seal in this study. However, the instruments were small relative to the size of the animal, representing less than 1% of the seal's body mass in water and 6% of maximum cross-sectional area. The depth, duration and average swimming speed of dives recorded were consistent with previous studies of female elephant seals using smaller time–depth recorders (Le Boeuf et al., 1996). We therefore consider the results to be comparable to previous studies of elephant seal diving behavior.

Most of the dives had the characteristics of Type A and B transit dives based on time–depth records (Le Boeuf et al., 1992, 1993; Asaga et al., 1994). In the present study, the seal descended at an average angle of 41° and ascended at an average angle 51°. These angles are similar to the those estimated by Le Boeuf et al. (1992) based on measurements of dive depth and swimming speed. However, this latter approach underestimates ascent and descent angle (see Section 3 above) relative to the more accurate, three-dimensional description of the dive path.

4.2. Energy-saving locomotor strategies

Stroke-and-glide swimming and prolonged gliding during descent can reduce the cost of transport in aquatic animals (Weihs, 1974) and, for air-breathing animals, may significantly increase dive duration (Williams et al., 2000). Both stroke-and-glide swimming and prolonged gliding incorporate periods of passive movement made possible as the ambient pressure compresses residual gas in the lungs to make the seal negatively buoyant (Williams et al., 2000). At a depth of 60 m, the negative buoyancy is greater than the seal's hydrodynamic drag when swimming at 1.0 m s⁻¹ (Appendix A) and this allows the animal to continue its descent by gliding, without incurring the

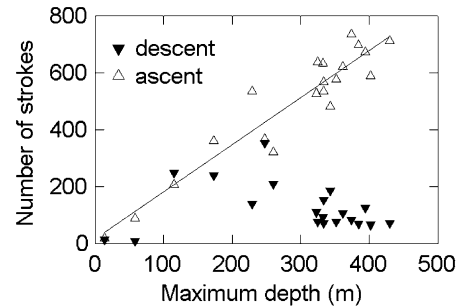


Fig. 6. Number of strokes used during a dive as a function of maximum depth. The number of strokes during ascent was proportional to the maximum depth ($Y = 16.76 + 1.65x$; $R^2 = 0.88$), whereas the number of strokes during descent was independent of dive depth.

additional cost of stroking and with no change in swimming speed.

Most of the cost of transport (excluding basal metabolism) arises from the propulsive strokes of the hind flippers. Williams et al. (2000) combined measurements of post-dive recovery oxygen consumption and distance swum over the course made good to estimate that Weddell seals can achieve an energy savings of 9–60% by incorporating prolonged gliding into dives. In the absence of recovery oxygen measurements in this study, the total number of propulsive strokes used during each of the dives provides a relative estimate of the energetic costs and possible energy savings incurred by gliding. The number of strokes used during ascents was directly proportional to maximum depth of the dive ($R^2 = 0.86$), whereas the number of strokes used during descents was independent of maximum depth ($R^2 = 0.01$) (Fig. 6). In 13 dives to depths exceeding 300 m, the seal used one-sixth as many strokes on descent as ascent. Indeed, the seal used fewer strokes (less than half as many) to descend to 300 m or deeper than it used in descents to shallower dives (< 250 m). Thus, the seal traveled farther and for a longer time using fewer strokes.

Another way to evaluate energy savings is to use the mean stride length (0.8 m) for continuous stroking to estimate the total number of strokes that would be required to cover the distance swum during a dive and to compare this with the actual number of strokes used. Such a comparison shows that the seal used 32–50% fewer strokes than predicted in the 20 dives. The savings were greatest in the deepest dives (> 300 m), where the seal spared 489–769 strokes, a savings

of 43–50% over continuous stroking throughout. If the number of strokes in a dive is a reasonable index of the cost of transport, these calculations suggest substantial energy savings by gliding.

Energy savings that arise from incorporating the stroke-and-glide and prolonged-gliding modes of locomotion into dives allow elephant seals and other diving mammals and birds to extend the length of time they are submerged. This helps resolve a paradox over the apparent ability of some diving animals to routinely exceed their theoretical aerobic dive limit (ADL) (Ponganis et al., 1992; Boyd and Croxall, 1996; Butler and Jones, 1997). The ADL is defined as the longest dive that an air-breathing animal can make while relying principally on oxygen stored in the lungs, blood and muscles to maintain aerobic metabolism (Kooyman et al., 1980). Most commonly, a theoretical ADL is calculated by dividing an animal's body oxygen stores by an estimate of diving metabolic rate which is assumed to be proportional to swimming speed (Le Boeuf et al., 1988; Ponganis et al., 1992; Butler and Jones, 1997). Based on such calculations, Hindell et al. (1992) observed that southern elephant seals (*Mirounga leonina*) regularly exceed their theoretical ADL and suggested that assumptions about body oxygen stores or diving metabolic rate must be incorrect. Boyd and Croxall (1996) came to a similar conclusion in a general review of routine dive durations for pinnipeds and seabirds.

Estimates of diving metabolic rate ranging from 0.7 to 5 times the mass-specific basal metabolic rate (BMR; Kleiber, 1975) have been used in calculations of the theoretical ADL for various species (Le Boeuf et al., 1988; Ponganis et al., 1992; Boyd and Croxall, 1996; Butler and Jones, 1997). In many cases, a diving metabolic rate greater than 1–2 times BMR results in an ADL that is too low to account for a high percentage of observed dive durations. These longer dive durations would be possible if diving metabolic rate were less than BMR (hypometabolism), which could theoretically result from the combined effects of the dive response (i.e. bradycardia and peripheral vasoconstriction) and hypoxic hypoxia (Butler and Jones, 1997). However, there is no experimental evidence for hypometabolism in pinnipeds during aerobic dives, and most organs and tissues probably receive adequate oxygen to maintain normoxic metabolic rates (Davis and Kanatous, 1999). Another explanation is that a

large percentage of dives involves significant anaerobic metabolism (Ponganis et al., 1992). However, the brief surface intervals between dives (Table 1), even following unusually long and deep dives (Le Boeuf et al., 1988), do not allow sufficient recovery time for processing the high concentrations of lactic acid that would result from significant anaerobic metabolism. Our observations and those of Williams et al. (2000) demonstrate that swimming speed overestimates diving metabolism because gliding is less costly than continuous stroking. During gliding periods, muscular activity for propulsion is near zero and the animal does not incur the added active drag resulting from the movements of its flippers, which may be as much as three to five times the passive drag of a gliding animal (Fish et al., 1988; Skrovan et al., 1999). We suggest that gliding during large portions of a dive may lower metabolic rate so that it approaches resting levels without invoking a generalized hypometabolism. Such a low metabolic rate would help reconcile the discrepancy between routine dive durations and theoretical ADL.

4.3. Orientation and navigation

Based on GPS positions at the surface, the elephant seal was able to maintain a consistent mean heading of 297° over a horizontal distance of 3.3 km. This compass heading was parallel to the coast and in the direction (320°) of the capture site at Año Nuevo Point. Oliver et al. (1998) observed that the initial orientation of translocated elephant seals is often in the direction of the rookery where they were captured. Although the seals may head home immediately, they often do not haul out immediately once they reach the rookery. This is consistent with the behavior of the seal in this study.

The capacity of marine mammals to find their way at sea and the cues they use are poorly understood. Although the data from this study are limited, the seal appears to have been using navigation, rather than orientation. Orientation is the skill of recognizing and maintaining a direction. In orientation, an animal displaced laterally continues in its original direction as if it had not been displaced. Navigation requires the identification of the direction for a given point in space (Bowditch, 1995). When displaced laterally, a navigating animal adjusts its direction so that it con-

tinues to move toward a specific point. During prolonged gliding descent, the elephant seal was displaced in the general direction of the average current (i.e. to the northwest, based on set and drift calculations) (Fig. 1). However, the seal made course changes when it began stroking at the bottom of several dives or during ascents, which put it on a more westerly heading. Some of these course changes were gradual while others were as much as 90° over several seconds, suggesting that the seal was correcting for current. These course changes were executed primarily when the seal was propelling itself and not simply gliding. The effect of these 'corrective' changes in course was a consistent mean heading at the surface even though the dive path was less linear.

If this elephant seal was navigating a course, the cues it used are unknown. Possible orientation or navigation cues include water-borne sounds, landmarks visible at the surface, and the geomagnetic field. Evidence weighs against some acoustic and visual cues. Seals have keen directional hearing (Wartzok et al., 1992), but the hydrophone attached to the seal detected no sounds at frequencies between 50 Hz and 16 kHz. The seal could have sighted features on the coastline 19 km to the north, but this does not explain its ability to maintain a relatively straight course while submerged. A geomagnetic sense seems most likely. Use of geomagnetic cues for spatial orientation is widely distributed in vertebrates (Walker et al., 1984; Kirschvink et al., 1985; Walker et al., 1985; Deutschlander et al., 1999; Salmon and Wyneken, 1994; Lohmann and Lohmann, 1996; Walker et al., 1997). There have been no psycho-physical experiments to demonstrate that marine mammals can sense a magnetic field. Magnetic material has been reported in several cetaceans, although it remains uncertain whether it is magnetite (Zoeger et al., 1981; Bauer et al., 1985). If marine mammals can sense direction relative to the earth's geomagnetic field, water speed (Dehnhardt et al., 1998), depth and time, then they have the information needed to navigate. The data in this study suggest interesting possibilities for submerged navigation that will require further research.

5. Conclusions

Our unexpected discovery that elephant seals

may spend long periods gliding during descent has important implications for our understanding of diving energetics. Dives to depths of more than 1000 m and migration distances of over 3000 km lasting up to months are energetically demanding. Better knowledge of the relationships among swimming activity, distance traveled, speed, and buoyancy is necessary before we can understand the full impact of gliding on energy budgets. It was equally unexpected that translocated seals would travel such direct return paths while submerged and in the presence of cross-currents. This observation points strongly toward a navigational capability. However, experiments will be necessary to verify this ability.

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Appendix A

The buoyancy of a 263-kg female elephant seal carrying the video system and data logger was estimated using the following equation modified from Webb et al. (1998):

$$B_T = (0.8871M_T \times A) + (-0.6689M_T \times L) \\ + [0.027g\rho M_T / (1 + D/10)] + (-21.6)$$

where B_T is total buoyancy in Newtons (N), M_T is total body mass, A is the percentage of adipose

tissue, L is the percentage of lean tissue, g is the acceleration due to gravity (9.8 m s^{-2}), ρ is the density of seawater (1.02 kg l^{-1}), D is the depth in meters, 0.8871 is the mass-specific buoyancy of adipose tissue (N kg^{-1}), -0.6689 is the mass-specific buoyancy of lean tissue (N kg^{-1}), 0.027 is the diving lung volume (l kg^{-1} ; Kooyman et al., 1999), 1 is the atmospheric pressure at the surface, 10 is a factor for converting depth in meters to atmospheres of pressure, and -21.6 is the buoyancy (N) of the video/data recorder. We assumed that the female elephant seal was 36% adipose tissue and 64% lean tissue (Webb et al., 1998). Based on this equation, the instrumented seal was 21.8 N positively buoyant at the beginning of a dive and was neutrally buoyant at a depth of 4 m. At a depth of 20 m, when the seal began stroke-and-glide swimming, it was 26.6 N negatively buoyant. At a depth of 60 m, we assume that the negative buoyancy of the seal (-40.1 N) carrying the video system and data logger was greater than its hydrodynamic drag allowing it to glide passively for the remainder of the descent.

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