

Swimming speed and foraging strategies of northern elephant seals

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Abstract

We investigated swimming speed, a key variable in both the management of oxygen stores and foraging strategies, and its relationship to diving behaviour in northern elephant seals, *Mirounga angustirostris*. Swimming speed significantly reduced the dive duration and time at depth for presumed foraging dives, but increased with dive depth. This suggests that the extended duration of deep dives is made possible by physiological adjustments and not by changes in swimming speed or effort. Swimming speeds were similar across sex and age classes despite different predicted minimum cost of transport speeds.

All seals exhibited characteristic dive shapes and swimming speed patterns that support their putative functions, but two-dimensional dive shapes and swimming angles varied between sexes and age classes. Mean dive angles on descent were markedly shallow, suggesting use of negative buoyancy to cover horizontal distance while diving. Buoyancy also appeared to affect two-dimensional dive shapes and ability to use extended gliding behaviours between surface and deep foraging zones. Significant differences in diving behaviour between sexes and between young and adult females were evident for various phases of the dive cycle, potentially resulting from physical constraints or differences in dive functionality.

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1. Introduction

A fundamental constraint on the foraging behaviour of most air-breathing marine vertebrates is the

need to dive underwater to obtain food. Whether a dive is aerobic or anaerobic, the primary determinant of how long an animal can dive is its diving metabolic rate. The primary determinant of diving metabolic rate is the speed at which it swims (Williams et al., 2000). Successful foraging is, therefore, a complex interaction between where the prey is located in the water column and how

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hard and/or fast the animal must swim to catch it. While swimming is less energetically expensive than running or flying (Schmidt-Nielsen, 1972), there remains an interplay between swimming speed, dive duration, and dive depth (Williams et al., 2000).

The aerobic dive limit (ADL) is the maximum breath-hold threshold without an increase in blood lactic acid concentration during or after a dive (Kooyman et al., 1980). Clearance of lactic acid build-up from anaerobic processes requires extended time intervals for respiration at the surface and ultimately leads to increased exposure to surface zone predators and reduced time for foraging at depth. While diving is constrained by the physiological limitation of oxygen stores, seals can modify the depth, duration, swimming speed and descent/ascent angles of dives relative to foraging tactics in order to most effectively acquire prey. The energetic cost of transport (COT) is primarily determined by swimming speed due to the combined effects of drag (Vogel, 1996). Investigations of drag, energetic cost, and efficiency have shown that swimming speed exponentially affects rates of oxygen consumption while diving (Davis et al., 1985; Williams and Kooyman, 1985; Feldkamp, 1987; but see Rosen and Trites, 2002). Foraging swimming speeds influence prey encounter rates and impact both the efficiency and rate of net energy intake.

Thompson and Hiby (1993) have developed a behavioural model that describes the energetic implications of swimming speed during descent, ascent, and foraging. Their model suggests that there should be a narrow range of minimum cost of transport (MCT) speeds that will reduce oxygen consumption for a given distance travelled. To optimize energy efficiency, divers should descend vertically to depth at MCT swimming speeds and then forage at speeds necessary to provide the most energy gain relative to that expended. If the net rate of energy intake is maximized, divers should decrease speed during descent and ascent on deeper foraging dives. Northern elephant seals, *Mirounga angustirostris*, have been shown to dramatically increase dive duration for deeper dives (Le Boeuf et al., 1988, 1989, 2000) and maintain bottom time despite increased travel time to depth. It is unknown whether this is accomplished through behavioural or physiological adjustments.

Northern elephant seals exhibit distinct sex differences with respect to their diving behaviour and migration patterns (Le Boeuf et al., 1993).

Females and juveniles forage in pelagic waters throughout the Pacific Ocean on prey associated with the deep scattering layer (Le Boeuf et al., 2000). In contrast, males undergo an initial period of rapid transit to foraging areas along the North American continental margin from Puget Sound, along the Gulf of Alaska, extending to the Aleutian Islands (Le Boeuf and Crocker, 1996). Once on foraging grounds, males appear to feed demersally, based on a correlation between the depth of benthos and foraging depths (Le Boeuf et al., 2000). Energy expenditure in transit to focal foraging areas and back affects net rates of energy gain during foraging migrations. While in transit, males travel on average 24% farther than females and 66% farther than juvenile females. This difference, in theory, could result from faster swim speeds or changes in the directionality, shape, and temporal patterns of dives.

The diving behaviour of northern elephant seals has been classified into five dive patterns or shapes: A, B, C, D, and E (Le Boeuf et al., 1988, 1992, 2000; Crocker et al., 1994, 1997), and it is thought that these shapes are associated with different functions or activities. Spiked (A) and U-shaped (B) dives indicate travelling or searching for a prey patch. Foraging (D) dives are thought to be dives where prey is being actively pursued, while E dives are consistent with demersal foraging along the bottom. The best studied are C dives, where swim velocity data coupled with the temporal pattern of these dives suggests that seals are processing food while drifting through the water column (Le Boeuf et al., 1992, 1994; Crocker et al., 1994, 1997). While the characteristics of C dives have been well studied, the putative role of the other four dive types has received less attention. Further, variation in these different dive types with respect to age, size and sex has not been examined.

Although juveniles follow a diel pattern of prey movement at similar depths to adults, they are faced with additional physiological constraints while foraging. Juveniles have a lower predicted ADL, resulting from both higher mass-specific metabolic rates and smaller proportional blood-oxygen and myoglobin reserves (Burns and Castellini, 1996). Larger blubber stores render them closer to neutral buoyancy and reduce their ability to use prolonged gliding on descent, but appear to be of some service to stroke and glide swimming on ascent (Webb et al., 1998). Finally, juveniles cannot regulate heart rate, respiration rate, vasoconstriction, or body

temperature as well as adults, which could potentially elevate diving metabolic rates, thereby impacting time spent foraging (Kodama et al., 1977; Schmitz and Lavigne, 1984; Schmidt-Nielsen, 1990; Rea and Costa, 1992; Cherapanova et al., 1993; Ponganis et al., 1993; Thorson and Le Boeuf, 1994; Burns and Castellini, 1996; Butler and Jones, 1997; Rutishauser et al., 2004).

The focus of this study was to gain insight into the possible functions of the five different dive patterns observed in elephant seals with respect to swimming speed, dive geometry, and swimming effort. Variations in swimming speed can indicate how swimming effort is managed over the course of a dive and provide information on foraging tactics. Our aims were to: (1) determine dive function from patterns of swimming speed and acceleration associated with recurring dive shapes; (2) compare the relationship between swimming speed, dive duration, and depth with model predictions; and (3) describe developmental and sex differences in swimming speed and dive behaviour.

2. Materials and methods

2.1. Subjects and instrumentation

A total of 16 swimming speed recorders were deployed over three field seasons. Six recorders were deployed during the moult haul-out in late April to early May 2002 on known age 1.4-year-old female northern elephant seals and recovered the following October at Año Nuevo State Reserve. Four recovered instruments were immediately re-deployed on a separate group of 1.8-year-old females and recovered the following April–May of 2003. Age was determined from known cohorts of animals that were flipper tagged at weaning. As benthic foragers, males do not exhibit the same degree of complexity in their dive profiles and were thus excluded from a developmental analysis of diving ability. We used three types of swimming speed instruments: Mk6 and Mk8 time-depth recorders (Wildlife Computers, Redmond, WA), and custom-built Blackwell–Haverl (B–H) data recorders. B–H swimming speed/time-depth recorders were deployed on five adult female and five adult male elephant seals on foraging trips in 1995 and 1996. Adult females, 6–7 years old, carried instruments during the post breeding season foraging trip and adult males, 8 or more years old, carried instruments during the post moult foraging trip.

Instruments measured swimming speed via water movement of an impeller and depth via a pressure transducer. The stall speed of the instruments was determined experimentally in a flume to be 0.22 ms^{-1} . Each B–H data logger had 512 K–1.0 Mbytes of memory. The Mk6 and Mk8 data loggers had 2 and 16 Mbytes of memory, respectively. Prior to attaching instruments, subjects were immobilized with an intramuscular injection of tiletamine hydrochloride and zolazepam hydrochloride (Telazol, Fort Dodge Laboratories, Fort Dodge, IA, USA; dosage: 1 mg kg^{-1} for females and juveniles, and 0.3 mg kg^{-1} for males). Immobilization was maintained using intravenous injections of 100 mg ketamine hydrochloride (Ketaset, Fort Dodge Laboratories, Fort Dodge, IA, USA) into the extradural vein. Instruments were attached to a VHF radio transmitter to facilitate recovery. The package was glued to the pelage of the seal, on the dorsal midline between the shoulders, with 5-min waterproof epoxy (Loctite[®] Quick Set[™] Epoxy, Henkel Consumer Adhesives Inc., Avon, OH, USA) and nylon mesh.

Instruments on juveniles were programmed to sample depth and impeller rotations at 5- or 15-s intervals, depending on memory and battery life. Instruments deployed on adult females recorded depth and impeller rotations every 20 s until the memory was full or the battery ran out. Instruments on males had an identical sampling regimen for the first 30 days, a 10-s sampling interval for 14 days, and then a 20-s interval until the memory was full or the battery ran out. Instruments that sampled over longer intervals can potentially bias surface intervals or miss features associated with the bottom of dives. For example, if errors are randomly distributed, the animal does not swim at the surface and we overestimate the duration of a dive by one 20-s sampling interval, this would result in 2% underestimate of overall swim speed in a typical 20-min dive and as much as a 3% underestimate of swimming speed during descent or ascent. However, these errors should be distributed randomly and our large sample size should allow for meaningful comparisons between sexes and age classes.

Adult seals carried 0.5-W Argos-linked ST6 platform terminal transmitters (PTT) (Telonics, Mesa, AZ, USA) that were attached to the head using nylon mesh and marine epoxy (Le Boeuf et al., 2000). The satellite tracking data have been reported earlier (Le Boeuf et al., 2000) and are included here to provide a location context for the

diving and swimming speed data and for comparison with transit rates calculated from dive profiles and swimming speed.

To obtain mass, juvenile and adult female seals were placed in a sling and weighed using a tension dynamometer accurate to ± 1 kg suspended from an aluminium tripod. The mass of males was estimated from morphometric measurements (Le Boeuf et al., 2000). Males were not immobilized for recovery of instruments, thus morphometric measurements were not collected upon their return to the breeding colony. Body composition was determined using a combination of ultrasound and morphometric measurements. This method requires six dorsal, lateral, and ventral measurements of blubber depth using an ultrasound scanner (Ithaco Scanprobe, Ithaca, NY, USA), and eight measurements of length and girth that correspond to the six ultrasound locations along the body, ear, and ankle girths. These measurements were used to model a seal as a series of truncated cones. The volumes of the blubber and non-blubber compartments of each cone were calculated and summed to estimate total body composition (Gales and Burton, 1987; Webb et al., 1998; Crocker et al., 2001) and buoyancy (Webb et al., 1998). Briefly, body composition from the truncated cones method was used to calculate buoyancy using the equation from Webb et al. (1998):

$$B_T = (0.8871M_T^*A) + (-0.6689M_T^*L),$$

where B_T is total buoyancy (N), M_T is total body mass (± 1 kg), A is the percentage of adipose tissue, L is the percentage of lean tissue, 0.8871 is the mass specific buoyancy of adipose tissue (N kg^{-1}), assuming an adipose density of 0.94 g cm^{-3} (from Worthy et al., 1992), and -0.6689 is the mass specific buoyancy of lean tissue (from Nordøy and Blix, 1985). The mean error associated with ultrasound methods relative to a tritium dilution method was 0.01 ± 4.25 (S.D.)% (Webb et al., 1998). This method of estimating buoyancy has not been validated empirically.

2.2. Calibration and summary data

On recovery, each instrument was calibrated using the method described in Blackwell et al. (1999). This method assumes vertical swimming occurs on some dives where swimming speed is equal to the change in depth. Only dives below 6 m were included in the analysis. The animal was

considered to be at the surface above 1 m. The time period within a dive between the end of descent and the beginning of ascent was set manually by inspection for adults or using a custom written program (Dive, by Stewart Greenhill, Murdoch University, Perth, Australia) for juveniles. To validate the program against manual inspection, all adult dive records were processed through the program, resulting in greater than 90% agreement between the two methods. Bottom time was defined as the amount of time within 95% of maximum depth. Swimming speed data were rounded to the nearest 0.1 m s^{-1} to match the sampling resolution of the instruments. Initial and return transit periods over the continental shelf were removed from this analysis to remove effects of benthic constraints on diving. A dive also was removed from analysis if swimming speed dropped below corresponding descent rates when the impeller was clogged from debris.

Swimming speed data were analysed using custom written C⁺⁺ and BASIC programs. Swimming speeds were calculated for all descent, ascent, and bottom time segments of dives and surface intervals. Acceleration between each swimming speed measurement was derived from the difference between speeds calculated for each sampling interval. MCT speed was estimated as $0.5 \text{ Mass}^{0.27} \text{ m s}^{-1}$ (Videler and Nolet, 1990). This estimate was based on a variety of diving species ($r^2 = 0.85$, $n = 30$).

2.3. Dive classification and two-dimensional analysis

The dives of all juveniles (16,034 dives) were classified using discriminant functions that were built from previous records typed by visual inspection. This method resulted in a 93% correct bootstrapped estimate of reclassification of those records. Adult dive types (15,040 dives) were classified individually by visual inspection based on time-depth profiles as in Le Boeuf et al. (1993, 2000). The major dive types were: A dives (and their U-shaped variant, B dives): direct descent to a sharp or rounded inflection point followed by direct ascent to the surface; C dives: direct descent to a depth at which point the descent rate decreased to near the stall speed of the instrument and then continued to the bottom of the dive, followed by direct ascent to the surface; D dives: direct descent to a depth at which point there occurred two to twelve vertical excursions, followed by a nearly vertical ascent to the surface; and E dives: direct

descent to a flat bottomed dive, followed by nearly vertical ascent to the surface. E dives were further classified as E_f dives, where the bottom of the dive was perfectly flat, and E_b dives, where there were slight variations in depth which appeared to follow bottom topography (see Le Boeuf et al., 1993).

For each sampling interval, swimming speed was paired with depth change to draw two-dimensional vector triangles. The horizontal distance calculated from this analysis was summed for the descent, ascent, and if applicable, bottom segments of dives. These horizontal distances were then used to calculate average angles of descent and ascent for each dive. Total horizontal distance was calculated for adult males and females based on the two-dimensional shapes of all dives and compared to the cumulative calculated great circle distance between all locations of class “0” or better. Less accurate locations were excluded in order to minimize inflation of path lengths due to location error.

2.4. Statistical analysis

Data were analysed using SAS 8.02, SYSTAT 10.2 and JMP 4.0. We used linear mixed-effects models to control for individual variation and test for significance of fixed effects and differences in diving parameters between adult and juvenile females and adult males. Mixed models were used for all comparisons using data from individual dives. Interaction terms between all fixed effects were included in the models and removed if they lacked significance. Means are presented as \pm one standard deviation.

3. Results

Swimming speed and time-depth records were obtained from all but one 1.4-year-old juvenile from the 2002 spring deployments, and from one of the following four fall deployments of a 1.8-year-old female. Mean record duration for the four juveniles was 87 ± 51 days, yielding a mean of 4008 (range 1290–10,066) useable dives. Two of the missing animals from the spring were seen the following fall without instruments. Instruments were recovered from four of the five adult females and three contained data. Mean record duration for the three females was 54 ± 22 days, yielding a mean of 3014 (range 1938–4907) useable dives. Instruments were recovered from all five adult males. In two of the instruments the impeller had become blocked

shortly after deployment and no swimming speed data were obtained. Mean record duration for the three remaining males was 51 ± 6 days, yielding a mean of 2000 (range 1532–2241) useable dives. Matched swimming speed and depth change data yielded reasonable vector triangles (i.e. swimming speed was greater than or equal to descent rate) on 98% of dive segments. Mean descent and ascent angles, swimming speed, and horizontal distance covered for all segments of dive types for each age class are shown in Table 1. Consistent patterns of swimming speed and acceleration were associated with each dive type (Figs. 1–3).

3.1. Swimming speed and dive function

3.1.1. Transit dives (Type A)

Transit dives represented 35% of the dive record in juveniles, 36% of recorded dives in adult females, and 64% of recorded dives in adult males. These dives often exhibited an initial burst of acceleration followed by two to five cycles of acceleration and deceleration (Fig. 1A). There was usually a strong deceleration at the bottom of the dive followed by a rapid acceleration upon ascent. Swimming speed was generally more constant during ascent in adults. Juveniles exhibited similar cycles of acceleration and deceleration on ascent as on descent. There was always a rapid deceleration when seals approached the surface. This pattern was altered when dives lacking bottom time were constrained by the benthos in males. When males were in transit, on the continental margins just prior to reaching their foraging areas, dives became shallower and more rounded, lacking a strong deceleration at the bottom, but retained cycles of acceleration and deceleration on descent and more constant speed during ascent (Fig. 1B).

3.1.2. Pelagic foraging dives (Type D)

Descent angles were always considerably less than 90° on presumed foraging dives (Fig. 4). For juveniles, D dives represented 58% of dive records, and 57% and 7% of dive records in females in males, respectively. D dives revealed a similar pattern to transit dives during descent, but always exhibited wide oscillations in swimming speed at the bottom of dives (Fig. 2A). Changes in swimming speed coincided with inflection points of vertical excursions. The magnitude and frequency of accelerations and decelerations at the bottom of D dives

Table 1
Summary statistics for diving behaviour across dive types in *Mirounga angustirostris*

Dive type	A		C		D		<i>p</i> < 0.01
	Mean	S.D.	Mean	S.D.	Mean	S.D.	
<i>Juveniles</i>							
Descent speed (m s ⁻¹)	2.00	(0.50)	0.95	(0.65)	2.04	(0.38)	AC, AD, CD
Ascent speed (m s ⁻¹)	2.02	(0.38)	1.88	(0.38)	2.06	(0.34)	AC, AD, CD
Descent angle (°)	42	(10)	46	(13)	41	(9)	AC, AD, CD
Ascent angle (°)	44	(11)	41	(11)	43	(11)	AC, AD, CD
Descent rate (m s ⁻¹)	1.30	(0.30)	0.62	(0.35)	1.31	(0.23)	AC, AD, CD
Ascent rate (m s ⁻¹)	1.35	(0.25)	1.12	(0.32)	1.37	(0.24)	AC, AD, CD
Horizontal descent distance (m)	434	(228)	288	(148)	401	(248)	AC, AD, CD
Horizontal ascent distance (m)	405	(224)	361	(177)	364	(233)	AC, AD, CD
Horizontal total distance (m)	1186	(514)	960	(430)	1407	(631)	AC, AD, CD
<i>Adult females</i>							
Descent speed (m s ⁻¹)	2.09	(0.50)	0.38	(0.24)	2.21	(0.33)	AC, AD, CD
Ascent speed (m s ⁻¹)	1.77	(0.40)	1.34	(0.31)	1.75	(0.34)	AC, AD, CD
Descent angle (°)	30	(8)	43	(23)	39	(9)	AC, AD, CD
Ascent angle (°)	33	(12)	33	(11)	46	(13)	AC, AD, CD
Descent rate (m s ⁻¹)	1.03	(0.31)	0.31	(0.05)	1.37	(0.25)	AC, AD, CD
Ascent rate (m s ⁻¹)	0.92	(0.23)	0.74	(0.22)	1.20	(0.16)	AC, AD, CD
Horizontal descent distance (m)	985	(344)	541	(294)	657	(237)	AC, AD, CD
Horizontal ascent distance (m)	889	(339)	656	(274)	529	(274)	AC, AD, CD
Horizontal total distance (m)	1877	(582)	1241	(499)	1546	(496)	AC, AD, CD
<i>Adult males</i>							
Descent speed (m s ⁻¹)	1.88	(0.29)	0.70	(0.35)	2.03	(0.34)	E _b A, E _b C, AD, AC, CD
Bottom speed (m s ⁻¹)	N/A	N/A	N/A	N/A	1.64	(0.38)	E _b D
Ascent speed (m s ⁻¹)	1.81	(0.25)	1.61	(0.19)	1.89	(0.32)	E _b A, E _b C, AD, AC, CD
Descent angle (°)	18	(7)	38	(14)	27	(7)	E _b A, E _b C, E _b D, AD, AC, CD
Ascent angle (°)	19	(9)	26	(10)	30	(9)	E _b A, E _b C, AD, AC, CD
Descent rate (m s ⁻¹)	0.55	(0.21)	0.40	(0.12)	0.91	(0.23)	E _b A, E _b C, E _b D, AD, AC, CD
Ascent rate (m s ⁻¹)	0.57	(0.23)	0.68	(0.20)	0.91	(0.23)	E _b A, E _b C, E _b D, AD, AC, CD
Horizontal descent distance (m)	1248	(403)	724	(208)	654	(220)	E _b A, E _b C, E _b D, AD, AC, CD
Horizontal bottom distance (m)	N/A	N/A	N/A	N/A	1333	(455)	E _b D
Horizontal ascent distance (m)	1195	(432)	901	(258)	608	(215)	E _b A, E _b C, E _b D, AD, AC, CD
Horizontal total distance (m)	2444	(619)	1640	(402)	2596	(674)	E _b A, E _b C, E _b D, AD, AC, CD

Letters corresponding with travelling dives (A), drift dives (C), and foraging dives (D and E_b) also indicate significant differences between dive types (*p* < 0.01).

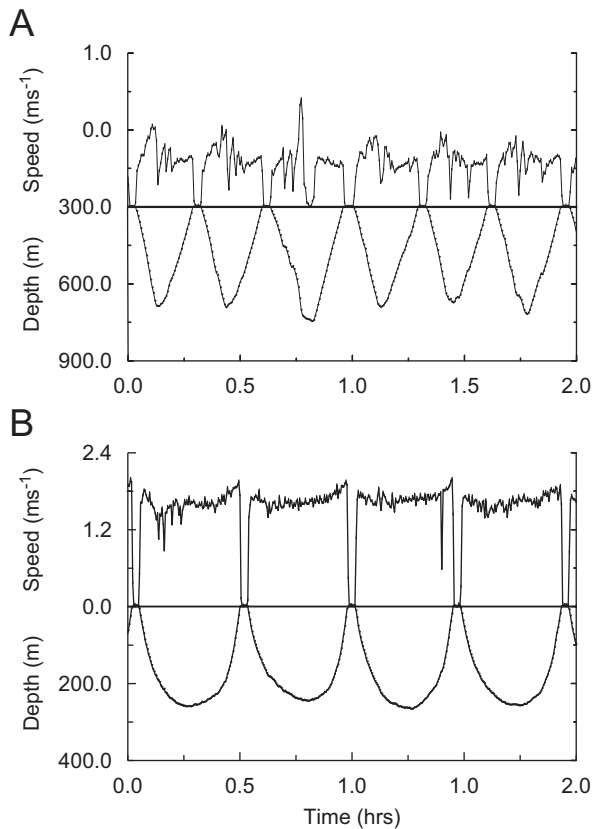


Fig. 1. (A) Depth versus time profile of a representative bout of transit dives (type A) from an adult female northern elephant seal. Corresponding swimming speeds (m s^{-1}) overlay the depth profile (m) illustrating the cycles of acceleration/deceleration that accompany inflection points, suggesting intermittent burst and glide swimming on descent to depth. (B) A bout of transit dives (type B) for a male northern elephant seal prior to reaching his focal foraging area. Unlike type A dives, swim speeds are consistent throughout the course of a dive.

were more exaggerated than any segment of any other dive type.

3.1.3. Drift dives (Type C)

Both sexes exhibited ‘drift’ or C dives, where swimming speed on descent was reduced significantly to near the stall speed of the instrument (Fig. 3A). These dives were much more common in juveniles and females than males (8%, 6% and 1%, respectively). Juvenile seals were occasionally observed exhibiting reverse C dives, where drifting occurred during ascent from the bottom of a dive before swimming resumed. Males exhibited C dives only during periods of transit to and from their foraging grounds. C dives, in which the duration of

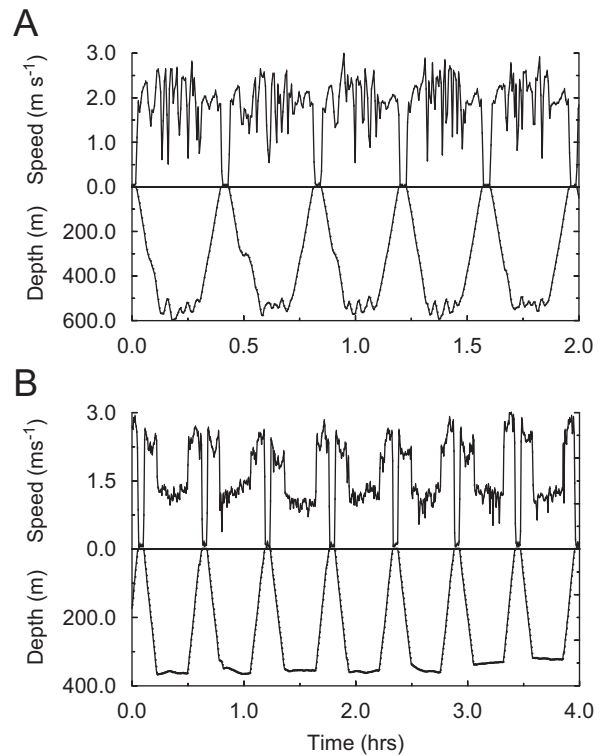


Fig. 2. (A) Changes in swimming speed associated with bottom phases of type D dives support their function as pelagic foraging behaviours of a representative adult female northern elephant seal. (B) Demersal foraging of a representative male where the seal appears to follow the contours of the benthos. These E_b dives appear to be analogues of D dives exhibited by females.

the drift phase increased linearly across a bout (Crocker et al., 1997), exhibited a corresponding linear increase in the period of reduced swimming speed within this phase (Fig. 3A).

3.1.4. Benthic foraging dives (Type E)

Once on their foraging grounds, E dives represented the majority of dives for males (91%). After reaching deep water on departure, females and juveniles exhibited no E dives. Two subclasses of E dives were found in males. E_b dives had a flat bottom with some variation in depth that appeared to follow the contours of the floor of the continental shelf (Fig. 2B). These dives accounted for 22% of the male dive record. Mean swimming speed was $1.29 \pm 0.53 \text{ m s}^{-1}$ during the bottom of E_b dives. Swimming speed was reduced and more consistent at the bottom of E dives than in D dives. Males ceased swimming for the majority of the bottom segment of E_r dives, resulting in a mean swimming

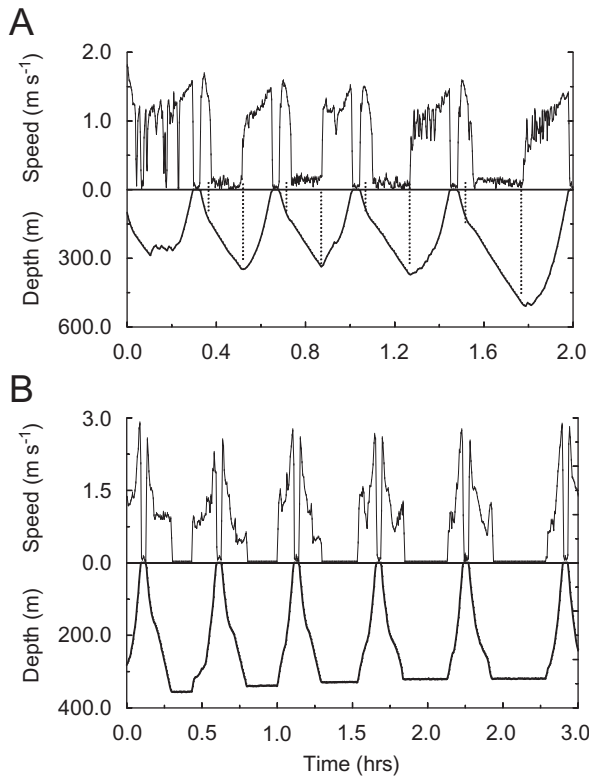


Fig. 3. (A) Depth versus time profiles of drift dives (type C) in adult females and (B) flat bottomed dives (type E_f) in adult male northern elephant seals appear to serve an analogous, non-active function. Dashed lines correspond with patterns of increased periods of reduced swimming speeds shown over the depth profiles for drift dives.

speed of $0.11 \pm 0.10 \text{ m s}^{-1}$. E_f dives were relatively rare, representing 6% of the dives made over foraging grounds. The duration of the stationary bottom period of E_f dives increased linearly across a bout (Fig. 3B).

3.2. Swimming speed

Histograms of swimming speeds for each individual are presented in Fig. 5. No surface swimming was observed in any of the seals. Increased overall swimming speed had a significantly negative impact on dive duration ($F_{30,836,1} = 1932.1$, $p < 0.01$). Dive duration also declined with increased swimming speeds for foraging and travelling type dives, respectively ($F_{15,251,1} = 86.7$, $F_{9,907,1} = 81.05$, $p < 0.01$). Despite significant individual variation for all of the following models ($p < 0.05$), overall swimming speed did not vary between adult males,

adult females, and juveniles, hereafter referred to as classes ($p > 0.05$). Swimming speed on descent to maximum depth and on ascent to the sea surface did not vary between classes ($p > 0.05$). Within foraging type dives, swimming speed across the bottom segments of dives did not vary between classes ($p > 0.05$).

Estimates of buoyancy for all classes are presented in Table 2. Upon departure, buoyancy was significantly different between classes ($F_{61,509,2} = 113.7$, $p < 0.01$). Adult female northern elephant seals were significantly less buoyant than juvenile females ($t = 11.9$, 8.8 , $p < 0.01$). In turn, adult male northern elephant seals were significantly less buoyant than adult females ($t = 8.0$, $p < 0.01$).

3.2.1. Effects of depth on swimming speed

Swimming speed on descent significantly increased with depth ($F_{28,165,1} = 1087.6$, $p < 0.01$). These findings were identical when presumed foraging and transit type dives were considered separately ($F_{14,988,1} = 376.0$, $F_{11,406,1} = 1988.4$, $p < 0.0001$). Ascent swimming speed was not significantly impacted by diving depth and did not significantly vary between classes ($p > 0.05$). The relationship between ascent speed and depth also did not vary significantly between classes for foraging or transit type dives ($p > 0.05$).

3.2.2. Bottom time

Within pelagic foraging type dives (type D), we used data from adult females and juveniles to examine the effect of age class, maximum depth of a dive, descent speed, and bottom speed on bottom time. Results from this analysis are shown in Table 3. The model revealed significant positive effects of age class and depth and significant negative effects of the interaction of descent speed with depth on bottom time of D dives. Swimming speed during the bottom phase of dives had a significant negative effect on bottom time. Thus, larger animals exhibited longer bottom times and all classes were able to extend time in the foraging zone on deeper, longer dives. However, when controlled for these factors, the increase in swimming speed with depth reduced time at the bottom of dives.

3.3. Dive angles

Dive angles on descent were significantly different between classes ($F_{28,165,2} = 12.3$, $p < 0.01$) (Table 1). Ascent angles were also significantly different

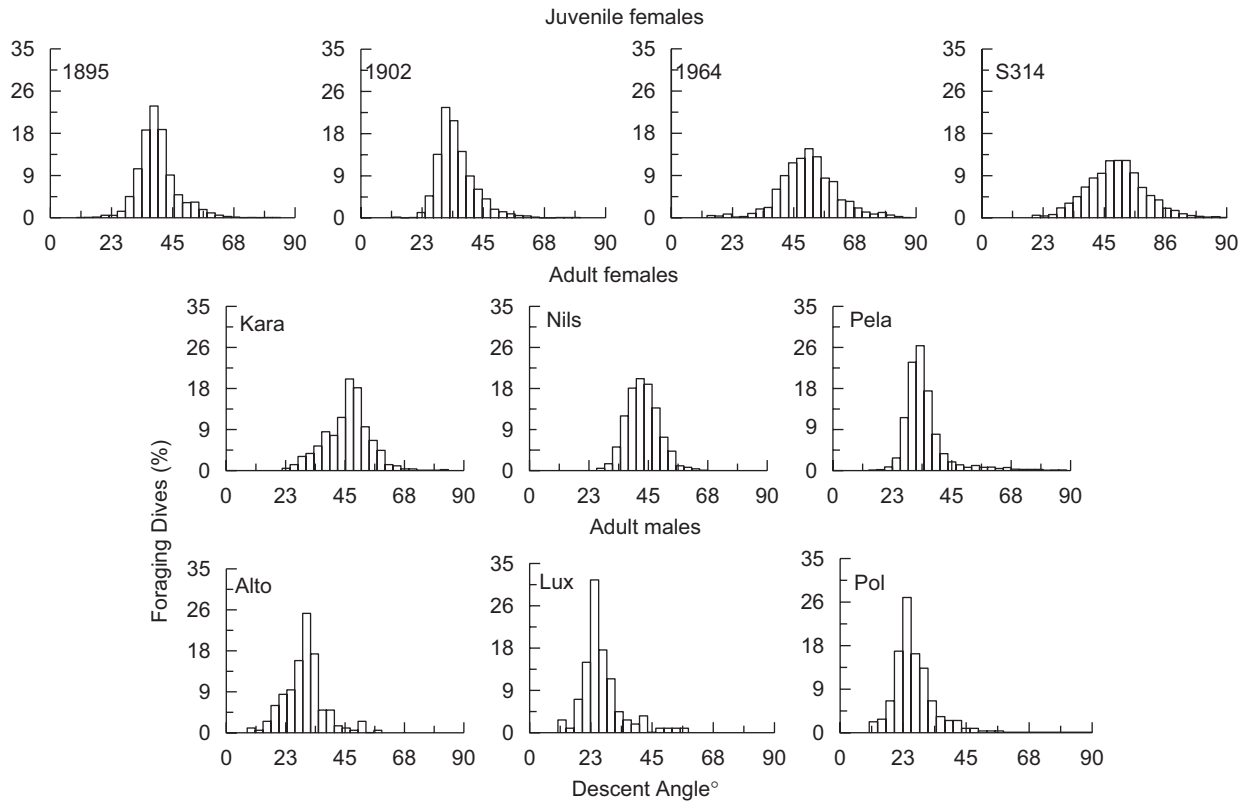


Fig. 4. Histograms of descent angles (degrees) of foraging dives in northern elephant seals, *Mirounga angustirostris*. Rather than use the most direct approach to access prey patches by diving vertically, all seals used oblique angles on descent to foraging depths.

between classes ($F_{28,165,2} = 7.1$, $p < 0.05$). Within foraging type dives, descent and ascent angles were significantly different between classes ($F_{14,989,2} = 6.9$, 4.4 ; $p < 0.01$). Similarly, descent and ascent angles of transit type dives were significantly different between classes ($F_{11,405,2} = 18.0$, 13.4 ; $p < 0.01$).

Adult females and juveniles exhibited similar dive angles on descent ($p > 0.05$). However, mean angle of descent between foraging type dives ($40 \pm 9^\circ$) and transit type dives ($37 \pm 10^\circ$) were significantly different ($F_{22,920,1} = 1166.1$, $p < 0.01$). The interaction term between age class and dive type was also highly significant ($F_{22,920,1} = 1666.4$, $p < 0.01$). Adult females and juveniles exhibited similar dive angles on ascent ($p > 0.05$). Again, mean angles of ascent between foraging type dives ($44 \pm 11^\circ$) and transit type dives ($39 \pm 12^\circ$) were significantly different ($F_{22,920,1} = 1286.04$, $p < 0.01$). The interaction term between age class and dive type was also highly significant ($F_{22,920,1} = 1837.33$, $p < 0.01$).

3.4. Horizontal distance and transit

Estimated horizontal distances of dives, actual transit distance measured by Argos satellite tracks, and associated rates are shown in Table 4. During the rapid transit phases of their foraging trips, horizontal distance covered was on average $95.8 \pm 2.3\%$ of actual transit distance as measured by satellite tracks for males. This value was $67.4 \pm 7.2\%$ for the outward legs of females' foraging trips.

4. Discussion

4.1. Swimming speed

In order to maximize net rate of energy increase, swimming speed may decrease with increased depth of dives (Thompson and Hiby, 1993). In contrast to this prediction, northern elephant seals exhibited significant increases in swimming speed with depth. Studies on several species of diving vertebrates have

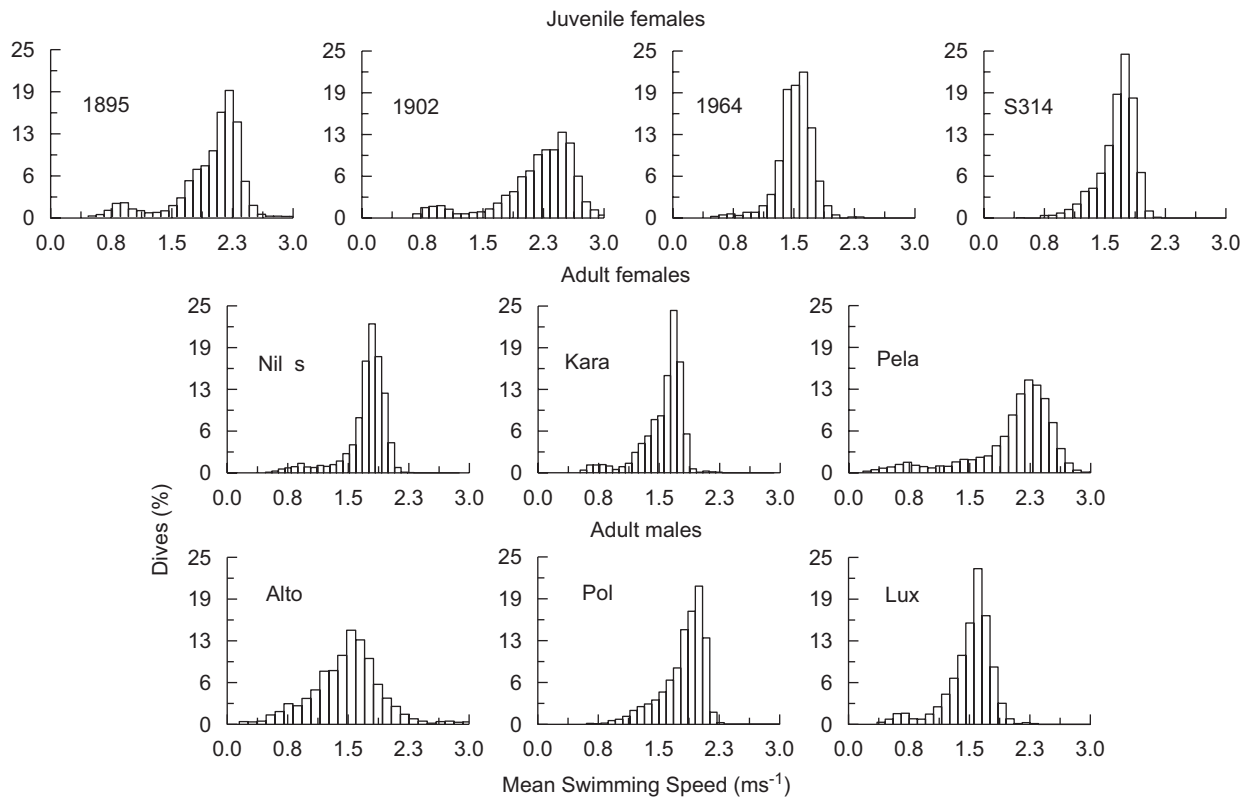


Fig. 5. Histograms of swimming speed over the entire dive in northern elephant seals, *Mirounga angustirostris*. Despite size differences, all age and sex classes used similar speeds.

Table 2

Mass, calculated buoyancy and minimum cost of transport (MCT) speeds, and mean descent/ascent speeds for *Mirounga angustirostris* equipped with speed time-depth recorders

Class	Seal	Mass _d (kg)	Mass _r (kg)	Buoyancy _d (N) ^a	Buoyancy _r (N) ^a	MCT _d (m s ⁻¹) ^b	MCT _r (m s ⁻¹) ^b	Mean descent speed (m s ⁻¹)	S.D.	Mean ascent speed (m s ⁻¹)	S.D.
Juvenile female	1895	92	186	-9.74	-26.59	1.70	2.05	2.06	(0.48)	2.11	(0.28)
	S314	117	197	-11.7	-19.58	1.81	2.08	1.59	(0.26)	1.68	(0.18)
	1902	110	183	-8.71	-22.46	1.78	2.04	2.18	(0.59)	2.37	(0.39)
	1964	162	240	-13.8	-33.19	1.97	2.2	1.47	(0.24)	1.61	(0.19)
Adult female	Nils	340	405	-83	-93.19	2.41	2.53	2.07	(0.29)	1.50	(0.17)
	Pela	307	426	-67.3	-94.05	2.35	2.56	2.28	(0.44)	1.94	(0.36)
	Kara	369	410	-71.1	-73.93	2.47	2.54	1.82	(0.30)	1.42	(0.15)
Adult male	Pol	1568	N/A	-321.8	N/A	3.65	N/A	1.90	(0.27)	1.79	(0.24)
	Alto	1339	N/A	-256.0	N/A	3.49	N/A	1.98	(0.50)	1.89	(0.44)
	Lux	1454	N/A	-241.8	N/A	3.57	N/A	1.68	(0.31)	1.37	(0.27)

All means comparisons of buoyancy and MCT speeds between classes were statistically significant ($p < 0.01$).

_d is the departure from the rookery and _r the return to the rookery.

^aWebb et al. (1998).

^bVideler and Nolet (1990).

Table 3

Linear mixed effects model summary with bottom time as the response variable and age class maximum depth of dive, descent swimming speed and bottom swimming speed as fixed effects

Fixed effect	F-value	p-value
Intercept	32.6	<0.01
Age class	96.1	<0.0001
Depth	149.5	<0.0001
Descent speed	1.2	0.27
Bottom speed	3.2	0.06
Descent speed*depth	100.9	<0.0001
Likelihood ratio (χ^2)	600.6	<0.0001

df = 7182 for all effects.

Table 4

Transit distances and rates calculated from Argos satellite locations and two-dimensional shapes of dives derived from swimming speed and depth change

	Satellite locations		Dive profiles		
	Distance (km)	Rate (m s ⁻¹)	Distance (km)	Rate (m s ⁻¹)	% Directed travel
<i>Female</i>					
Kara	2415	0.88	3230	1.17	74.7
Nils	2189	0.77	3125	1.09	70
Pela	2128	0.62	3813	1.1	57.7
<i>Males</i>					
Lux	4654	1.02	4735	1.03	98.3
Pol	4952	1.15	5132	1.19	96.4
Alto	792	1.02	854	1.1	92.7

Percent directed travel is the total estimated horizontal distance from dive profiles divided by satellite locations.

revealed similar increases in swimming speed with depth, including southern elephant seals (Hindell and Lea, 1997) New Zealand sea lions (Crocker et al., 2001), Rockhopper penguins (Cherel et al., 1999), and Antarctic fur seals (Boyd et al., 1995). It was suggested that the pattern in Antarctic fur seals resulted from an increase in faster transit speeds relative to slower foraging speeds when time spent in transit extended over a greater depth range (Boyd et al., 1995). We found a similar reduction in swimming speeds used at the bottom of presumed foraging type dives in northern elephant seals. However, overall swimming speeds used during presumed transit and foraging type dives were not significantly different. Although northern elephant seals significantly increased swimming speed with depth, our data support the assumption that swimming slower extends foraging time because of

the strong negative impact of the interaction of depth and descent speed on bottom time observed in foraging type dives.

Several studies also reported reduced foraging times associated with high swim speeds on deeper dives (Boyd et al., 1995; Crocker et al., 2001). Despite the effects of increased swimming speed on bottom time, longer overall dive durations associated with deeper dives in this species allow slight increases in bottom time with depth, even in the presence of significantly longer descent and ascent times. This suggests that elephant seals extend the duration on deep dives by using physiological adjustments rather than changes in swimming speed or effort. Previous studies have shown that the criteria by which individuals choose to forage depend on the energetic costs of deeper and longer dives and the benefits of increased energetic gains from higher quality prey (Houston and Carbone, 1992; Boyd et al., 1995). Variation in prey preference may drive variation in foraging tactics observed in individual elephant seals if there is a difference in the distribution or quality of prey higher in the water column relative to deeper depths. Thompson and Fedak (2001) suggest that seals foraging in a diffuse prey patch would benefit from using a simple rule of thumb approach by varying dive durations in response to some perceived correlate of prey density.

Despite large differences in body size which led to predictions of significantly different MCT speeds between classes (Table 2), overall swimming speed did not vary between classes and all seals appeared to swim within a narrow range of speeds. Videler and Nolet (1990) also found that despite a 20-fold increase in body mass and a 2.5-fold increase in size of *Palaemon adspersus*, empirically derived MCT speeds were virtually the same. However, Reynold's numbers associated with a 3- to 4-fold difference in body length between adult male and juvenile elephant seals suggest that juveniles expended more energy to achieve similar speeds. Adult elephant seals appeared to swim at lower than the predicted range of MCT speeds (Table 4). MCT models assume continuous swimming over a range of speeds, but our data show that elephant seals employ a burst and glide form of locomotion and that mean swimming speeds in transit to and from the foraging zone are actually an average of alternating periods of sustained swimming and gliding. Deep-diving New Zealand sea lions similarly employ a burst and glide form of locomotion

and also swam at lower than predicted MCT speeds (Crocker et al., 2001). Existing MCT models appear to be more suited to animals that exhibit a more constant swimming pattern such as observed in more neutrally buoyant juvenile elephant seals.

The use of gliding behaviour during descent has been described in numerous diving vertebrates including elephant seals (e.g., Williams et al., 2000; Davis et al., 2001). Intermittent propulsion reduces the number of strokes per dive and thus conserves oxygen reserves (Williams, 2001; Williams et al., 2004). The patterns of swimming speed and acceleration observed in the present study are consistent with several extended gliding phases during descent, particularly on transit type dives (Fig. 1). Less negatively buoyant juvenile northern elephant seals exhibited steeper, more symmetrical angles on descent and ascent than adults. They may not have been able to use gliding behaviours as effectively as adults in order to conserve oxygen for foraging at depth and, instead, maximized swimming angles to minimize descent times. Estimates of diving angles are highly dependent on the accuracy of swimming speed and descent rate. Calibration of swimming speed requires that at least some proportion of dives have a vertical profile, which is where the descent rate and swimming speed are equivalent. This assumption is supported by the distinct edges to the calibration plots (Blackwell et al., 1999). However, if there were no vertical profile dives, true swimming speed would be underestimated and diving angles would be even shallower. If the varied classes do not equally meet this assumption, this could potentially bias angles for a given class. The use of markedly shallower angles within transit dives by adult northern elephant seals is consistent with their faster rates of movement despite similar swimming speeds. Increased horizontal distances travelled by adult males relative to adult females on a dive per dive basis result in greater transit rates (Table 4). Males exhibited little foraging behaviour while in transit between the breeding colony at Año Nuevo and their foraging grounds off the Aleutian Islands. In contrast, females began exhibiting putative foraging behaviour as soon as they left the continental shelf.

Elephant seals invested roughly half of their swimming effort between the surface and the foraging zone in the horizontal direction, using a narrow range of dive angles that potentially reduced time that could have been spent foraging (Fig. 5). Although most individuals increased dive angles on

foraging dives, they remained far from vertical (Table 2). The use of shallower angles on descent than on ascent by adults may reflect use of negative buoyancy to minimize costs of horizontal transport. Transit dives likely represent a mixed purpose of directed travel and searching. The use of shallow angles on foraging dives is more puzzling because the most direct approach is vertical descent. Oblique dive angles would almost certainly reduce oxygen stores available at foraging depths. However, we note that this feature has now been reported for numerous species that forage at depth (e.g., Crocker et al., 2001; Davis et al., 2001, 2003; Weihs, 1973). The use of oblique descent angles in foraging dives may reflect the visual capabilities of the seals to detect the position of the prey in the water column. As squid photophores orient downward and match the colour of downwelling light (Young et al., 1979), oblique approach angles to prey may potentially aid in prey detection by maximizing any spectral mismatch between photophore and background light.

4.2. Dive function

Swim speed data support the proposed function of the different dive types observed in adult northern elephant seals. Transit dives in males are more efficient for covering horizontal distance and on average appear above the primary pelagic foraging depths for elephant seals. U-shaped transit dives with swimming throughout the dive were observed in males travelling over the continental shelf just prior to reaching their foraging areas (Fig. 1B). Transit dives in adult females and in juveniles are suited for a dual role in transit and searching for prey patches, sacrificing horizontal distance for a deeper dive that attains depths associated with the deep scattering layer. Foraging dives in adult females exhibit steeper angles on descent and ascent than transit dives, possibly to more directly attain foraging depths. Juveniles exhibit no such difference in dive angles between dive types, which may reflect an inability to effectively use efficient gliding behaviours due to increased buoyancy.

Similar to transit type dives, all age classes exhibited drift dives. A potential role in food processing has been suggested for these dives (Crocker et al., 1997). The drift segments of these dives coincided with periods of reduced swimming speed on descent at or near the stall speed of the TDR. Bouts of reverse C dives, where swimming

speed on ascent was reduced near the stall speed of the instrument, were only observed in juvenile seals in this study, although females late in pregnancy have also been observed drifting on ascent (Crocker et al., 1997). Periods of low swim speed corresponding with drift segments of C dives were observed to increase linearly within a bout of successive dives, suggesting a decreased rate of oxygen consumption across a bout (Crocker et al., 1997). Similar periods of increased periods of inactivity associated with the bottom of dives were also seen in type E_r dive bouts for males on the floor of the continental shelf. The striking similarity in the linear increase of non-swimming periods in E_r dives exhibited by males to that seen in C dives suggests that this behaviour may be an analogue of pelagic drift dives.

5. Conclusion

Elephant seals swam at similar speeds despite extreme differences in size between juveniles, adult females, and adult males. Variation in transit speed across sex and age classes appears to be largely the result of differences in two-dimensional shapes of dives and the sequence of particular kinds of dives. Two-dimensional dive shapes and speed profiles are consistent with the use of negative buoyancy to assist in efficient gliding behaviours on descent. Video footage obtained from a diving elephant seal revealed significant use of gliding behaviours during descent (Williams, 1999; Williams et al., 2000). The effects of buoyancy may have a significant influence on relative speeds throughout a dive. Patterns of acceleration in adults suggest the use of extended gliding at oblique angles on descent and steep burst and glide swimming on ascent. More buoyant juveniles appeared less able to use extended gliding behaviours on descent, exhibited symmetrical dive angles and employed more consistent swimming speeds on both descent and ascent. Further, variants of the flat-bottomed dive were observed in adult males where the seal apparently rested on the bottom. Given that these dives occurred after a series of foraging dives suggests this behaviour may be an analogue to pelagic drift or processing dives observed in female elephant seals.

Elephant seals significantly increased dive duration on deeper dives without extending surface intervals. Thus, a reduced metabolic rate from slower swimming could not account for increased dive durations. If active swimming is intermittent during descent, deeper dives may include a greater

number of active swimming phases, which could explain faster mean swimming speeds with increased depth. However, our data suggest that modifications to extend dive time on deeper dives are not related to reductions in swimming effort. Recent technological developments in data logging equipment have produced accelerometers with the capability of measuring stroke frequency. This resolution should allow future studies to quantify where energy is invested over the course of a dive, how overall swimming effort varies with depth, and provide new insights as to how northern elephant seals manage oxygen stores.

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