Locomotion in diving elephant seals: physical and physiological constraints

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To better understand how elephant seals (*Mirounga angustirostris*) use negative buoyancy to reduce energy metabolism and prolong dive duration, we modelled the energetic cost of transit and deep foraging dives in an elephant seal. A numerical integration technique was used to model the effects of swim speed, descent and ascent angles, and modes of locomotion (i.e. stroking and gliding) on diving metabolic rate, aerobic dive limit, vertical displacement (maximum dive depth) and horizontal displacement (maximum horizontal distance along a straight line between the beginning and end locations of the dive) for aerobic transit and foraging dives. Realistic values of the various parameters were taken from previous experimental data. Our results indicate that there is little energetic advantage to transit dives with gliding descent compared with horizontal swimming beneath the surface. Other factors such as feeding and predator avoidance may favour diving to depth during migration. Gliding descent showed variable energy savings for foraging dives. Deep mid-water foraging dives showed the greatest energy savings (approx. 18%) as a result of gliding during descent. In contrast, flat-bottom foraging dives with horizontal swimming at a depth of 400 m showed less of an energetic advantage with gliding descent, primarily because more of the dive involved stroking. Additional data are needed before the advantages of gliding descent can be fully understood for male and female elephant seals of different age and body composition. This type of data will require animal-borne instruments that can record the behaviour, three-dimensional movements and locomotory performance of free-ranging animals at depth.

Keywords: diving; locomotion; gliding; aerobic dive limit; elephant seal

1. INTRODUCTION

A controversy exists about the apparent ability of some diving mammals and seabirds to routinely exceed their theoretical aerobic dive limit (ADL; Ponganis *et al.* 1992; Boyd & Croxall 1996; Butler & Jones 1997; Ponganis *et al.* 1997a). The ADL is defined as the longest dive that an air-breathing animal can make while relying on oxygen stored in the lungs, blood and muscles to maintain aerobic metabolism (Kooyman *et al.* 1980). Historically, the ADL was determined by measuring the maximum voluntary dive duration without a post-dive increase in blood lactic acid concentration. However, this measurement has been possible for only a few species (Kooyman *et al.* 1980, 1983; Ponganis *et al.* 1997b). More commonly, a theoretical ADL is calculated (cADL) by dividing a species' body oxygen stores by an estimate of diving metabolic rate (Ponganis *et al.* 1993; Butler & Jones 1997). Based on this approach, Boyd & Croxall (1996) observed that many endothermic divers regularly exceed their cADL, suggesting that assumptions about body oxygen stores or metabolic rate must be incorrect. Although our ability to estimate the body oxygen stores available to support aerobic metabolism

during a dive is improving (Butler & Jones 1997; Kooyman & Ponganis 1998; Davis *et al.* 1999), direct measurement of metabolic rate during natural dives (excluding swimming and other activities at the surface) remains difficult (Butler & Jones 1997). Investigators have used estimates of diving metabolism ranging from 0.7 to 5 times the allometric basal metabolic rate (BMR; Kleiber 1975) in calculations of the cADL for various species (Le Boeuf *et al.* 1992; Ponganis *et al.* 1992; Boyd & Croxall 1996; Butler & Jones 1997). In many cases, a diving metabolic rate greater than one to two times BMR results in a cADL that is too low to account for a high percentage of normal dive durations. Values less than BMR represent hypometabolism, a suppression of metabolic rate below normal resting levels that could theoretically result from the dive response (i.e. bradycardia and peripheral vasoconstriction) or a decrease in core body temperature (Butler & Jones 1997). If assumptions about body oxygen stores are correct, hypometabolism would allow many of the observed dive durations to fall within the cADL. However, it is difficult to reconcile hypometabolism with the energetic costs of normal activities such as foraging. Furthermore, it is questionable whether physiological homeostasis could be sustained under hypometabolic conditions during the continuous prolonged diving characteristic of many species. An alternative explanation is that a large percentage of dives involve significant anaerobic metabolism (Ponganis *et al.* 1992). However, the normally short

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Figure 1. Reconstructed three-dimensional dive path for a 263 kg elephant seal showing the spatial distribution of swimming modes. Prolonged gliding dominated the descent and continuous stroking was used principally during ascent. Stroke-and-glide swimming was used in horizontal swimming (Davis *et al.* 2001).

surface intervals between dives do not allow enough recovery time for processing the high concentrations of lactic acid that would result from a heavy reliance on anaerobic metabolism. Consequently, neither of these two explanations is completely satisfactory.

Calculation of the energetic cost of a dive assumes that changes in the rate of energy expenditure while submerged can be estimated indirectly. The depth and duration of dives and the manoeuvrability of marine mammals and birds limit direct observation of locomotory behaviour. Animal-borne time–depth recorders and acoustic tracking document dive depth, duration and swimming speed, but not locomotory mode or effort. Nevertheless, swimming speed has been assumed to directly reflect metabolic rate (Le Boeuf *et al.* 1992; Ponganis *et al.* 1992). The validity of this assumption has not been tested for most free-ranging marine mammals or diving birds. It has been shown that different swimming modes, such as dive gliding and burst-and-glide swimming in fishes (Weihs 1973, 1974), may result in significant energy savings over continuous swimming without an apparent difference in average speed. There is a critical lack of behavioural and physiological information on which to base estimates of diving metabolism for most species, and this may be the cause of the cADL paradox.

In 1996, we captured a 263 kg female elephant seal (*Mirounga angustirostris*) on the rookery at Año Nuevo Point, California, attached a video and data recorder to its back, and released it approximately 50 km away in Monterey Bay (Davis *et al.* 2001). The seal returned to the rookery one week later and the instrument was recovered. The video camera faced rearward so that we could observe the propulsive strokes of the hind flippers during dives. In addition, we recorded data from sensors (pressure, water speed and compass bearing) and global location at the surface (global positioning system) that enabled us to compute the three-dimensional movements of the seal underwater (Davis *et al.* 2001; figure 1). The videotape showed that the seal stopped stroking below a depth of approximately 25 m during descent. After analysing the video-recorded behaviour and dive paths, we hypothesized that the seal used negative buoyancy due to lung compression to glide for extended periods

(approx. 90% of descent). This locomotor strategy was later confirmed for other species of marine mammals (Williams *et al.* 2000). Gliding appeared to be an energy-conserving locomotory strategy that could potentially reduce diving metabolic rate, conserve oxygen stored in the blood and skeletal muscle, and extend the ADL. For Weddell seals (*Leptonychotes weddellii*) making foraging dives from an isolated ice hole in Antarctica, the energetic savings (estimated by indirect respirometry) from gliding during descent ranged from 9 to 60% (Williams *et al.* 2004). Whether a similar energetic savings occurs during non-foraging (e.g. transit) dives, while theoretically feasible (Weihs 1973), remains unknown. One problem with reconciling the energy saved by negative buoyancy for gliding during descent is that the same force will augment the energetic cost of ascent. Therefore, the energy saved during descent may have to be repaid, at least partially, during ascent. The residual gain results mainly from the fact that active drag is much larger than passive (gliding) drag. To better understand how marine mammals use negative buoyancy to reduce energy metabolism and prolong dive duration, we modelled the energetic cost of transit and deep foraging dives in a hypothetical elephant seal similar in size and shape to the animal we studied in 1996 (Davis *et al.* 2001).

2. MATERIAL AND METHODS

Numerical integration was used to calculate the effects of swim speed, descent and ascent angles, and modes of locomotion (i.e. stroking and gliding) on diving metabolic rate, ADL, vertical displacement (maximum dive depth) and horizontal displacement (MHD along a straight line between the beginning and end locations of the dive) in a model elephant seal making aerobic transit and foraging dives. The model was based on the three-dimensional movements and swimming activity of a 263 kg female elephant seal that had been studied previously by attaching a video and data recorder to its back (Davis *et al.* 2001). Many of the variables used in the model were based on measurements from that study or from previously published results.

(a) Assumptions and equations

This model considers only dives that are within the seal's ADL (Kooyman *et al.* 1980). Body oxygen stores were confined to the blood and skeletal muscle in this model, since no oxygen storage capability exists in the splanchnic organs (Dodd *et al.* 1987) and the heart represents less than 2% of the total muscle mass. We assumed that lung oxygen was not available during a dive due to the complete functional pulmonary shunt that occurs in elephant seals at pressures greater than 3–5 atmospheres (2280–3800 mm Hg; 1 mm Hg = 0.133 kPa; approx. 30–50 m deep; Falke *et al.* 1985; Reed *et al.* 1994). The increased ambient pressure during a dive causes the respiratory bronchioles and alveoli to collapse which forces air into the bronchi and prevents gas exchange between the lungs and blood. Since elephant seals spend much of their time at depths greater than 50 m (Le Boeuf *et al.* 1986, 1988, 1996), this assumption is generally valid during foraging and transit dives. Even if lung oxygen were available during a dive, it represents only 5% of the total body oxygen store in elephant seals (Kooyman & Ponganis 1998).

To calculate total oxygen stores in the blood, we assumed that the blood volume was 66 l (25% of body mass (M_b); Ponganis *et al.* 1993; Kooyman *et al.* 1999) and that 33% of

this volume was arterial blood and 67% was venous blood (i.e. venules, small and large veins, hepatic sinus and spleen; Rowell 1986; Hurford *et al.* 1996). The blood haemoglobin concentration (assuming complete splenic contraction) was 250 g l^{-1} , and the oxygen-binding capacity of Hb was $1.34 \text{ ml O}_2 \text{ g}^{-1} \text{ Hb}$ (Kooyman *et al.* 1980, 1999; Qvist *et al.* 1986; Ponganis *et al.* 1993). This gave a capacitance coefficient of oxygen in blood (β_{O_2}) of $335 \text{ ml O}_2 \text{ l}^{-1} \text{ blood}$ ($250 \text{ g Hb l}^{-1} \text{ blood} \times 1.34 \text{ ml O}_2 \text{ g}^{-1} \text{ Hb}$). At the beginning of a dive, we assumed that the arterial blood was 100% saturated with oxygen due to pre-dive hyperventilation (Kooyman *et al.* 1980; Qvist *et al.* 1986; Ponganis *et al.* 1993). Mixed venous blood ($\bar{S}\bar{V}_{\text{O}_2}$) was calculated from equation (2.1) to be 85% saturated at the beginning of a dive assuming an oxygen content that was 5% by volume less (Ponganis *et al.* 1993) than an initial arterial oxygen content (Ca_{O_2}) of $335 \text{ ml O}_2 \text{ l}^{-1} \text{ blood}$.

$$\bar{S}\bar{V}_{\text{O}_2} = \left[\frac{(335 - 50)}{335} \right] \times 100 = 85\%. \quad (2.1)$$

We assumed that 28% of the seal's body mass was skeletal muscle with a myoglobin concentration of 65 g kg^{-1} muscle (Kooyman *et al.* 1999), an oxygen-binding capacity of $1.34 \text{ ml O}_2 \text{ g}^{-1}$ myoglobin, and complete saturation at the beginning of a dive (Gayeski *et al.* 1987; Schenkman *et al.* 1997). Arterial, venous and muscle oxygen stores were calculated as

$$\text{Arterial blood oxygen (ml)} = 66 \times 0.33 \times 335 = 7269, \quad (2.2)$$

$$\text{Venous blood oxygen (ml)} = 66 \times 0.67 \times 335 \times 0.85 = 12592, \quad (2.3)$$

$$\text{Skeletal muscle oxygen (ml)} = 263 \times 0.28 \times 65 \times 1.34 = 6414. \quad (2.4)$$

The elephant seal therefore had a total oxygen store of $26\,275 \text{ ml O}_2$ (approx. $100 \text{ ml O}_2 \text{ kg}^{-1}$): 28% in the arterial blood, 48% in the venous blood and 24% in skeletal muscle. This is the maximum amount of oxygen that the seal can store in its blood and muscle. However, Davis & Kanatous (1999) showed that only 63% of the blood oxygen but all of the muscle oxygen in Weddell seals were available to support metabolism during an aerobic dive. Therefore, we assumed that the total oxygen available during a dive was $18\,926 \text{ ml O}_2$.

To estimate diving metabolism, we calculated the energetic cost of locomotion based on estimates of hydrodynamic drag and buoyancy. Passive drag was calculated as

$$D_p = 0.5 S_w \rho C_d U^2, \quad (2.5)$$

where D_p is passive drag in Newtons; ρ is the density of seawater (1020 kg m^{-3}); S_w is the wetted surface area of the seal; C_d is the drag coefficient (0.005; Williams & Kooyman 1985); and U is swimming speed. To calculate wetted surface, we modelled the seal as two cones joined at their bases using the equation

$$S_w = 2\pi R(R + S), \quad (2.6)$$

where R is the base radius of a cone (maximum girth/ 2π) and S is the length of the side of the cone (square root of ($\text{radius}^2 + (0.5 \times \text{SL})^2$)). The standard length (SL, 2.01 m) and maximum girth (1.65 m) were actual measurements for a 263 kg elephant seal (Davis *et al.* 2001). Therefore,

$$S_w = 2 \times 3.142 \times 0.263(0.263 + 1.039) = 2.2 \text{ m}^2. \quad (2.7)$$

Active drag (D_A) was taken as three times passive drag (Weihs 1974; Fish *et al.* 1988). Total buoyancy (B_T) in

Newtons was calculated as

$$B_T = (0.8771 M_T \times 0.36) + (-0.6689 M_b \times 0.64)$$

$$+ [0.0227 g \rho M_b / (1 + D/10)], \quad (2.8)$$

where M_b is body mass; 0.36 is the fraction of M_b that is adipose tissue; 0.64 is the fraction of M_b that is 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 metres (m); 0.8771 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}); 1 is the atmospheric pressure at the surface; and 10 is the factor for converting depth in meters to atmospheres of pressure (Webb *et al.* 1998). We assumed that the body composition for the 263 kg elephant seal modelled in this study was similar to the body composition (i.e. 36% adipose tissue and 64% lean tissue) of other juvenile northern elephant seals returning from their pre-moult foraging trip (Webb *et al.* 1998). We modified equation (2.8) to include the estimated buoyancy at depth due to gas remaining in the lungs (Kooyman *et al.* 1999). Depending on depth, the seal will be either positively or negatively buoyant. In this case, the transition from positive to negative buoyancy occurred at a depth of 15 m. For depths shallower than this, the buoyancy vector along the descent path augmented drag force and required additional thrust for the animal to descend. For depths deeper than 15 m, the buoyancy vector along the descent path increasingly offset drag force. At a depth of 25 m, the buoyancy vector exceeded passive drag, which enabled the seal to cease stroking and glide during the remainder of descent as observed in the experimental animal. The buoyancy vector along the dive path was calculated as

$$(\sin(\text{angle} \times 3.142/180)) \times B_T, \quad (2.9)$$

where angle refers to the angle of descent or ascent. Most (95%) of the buoyancy change takes place between 15 and 140 m, below which there is little further change in lung volume. During ascent, additional thrust was required to offset the combination of drag (which depended on ascent speed) and negative buoyancy until the seal was shallower than 15 m and could glide to the surface.

Locomotory power (J s^{-1}) was calculated each second as the product of the instantaneous thrust and speed, and then converted into a rate of oxygen consumption ($\dot{V}_{\text{O}_2}$, $\text{ml O}_2 \text{ min}^{-1}$) assuming a metabolic efficiency of 0.25 (Kleiber 1975, p. 311) and using the conversion factors of 0.239 cal J^{-1} and $0.208 \text{ ml O}_2^{-1} \text{ cal}^{-1}$ (Schmidt-Nielsen 1979, pp. 162 and 163). To calculate the rate of oxygen consumption during diving, the oxygen consumption resulting from locomotion was added to the basal rate of oxygen consumption (BMR; Kleiber 1975), which was estimated as $\text{BMR} = 9.98 \times M_b^{-0.25} = 2.5 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$. (2.10)

(b) Computations

We modelled three types of dives: transit and two types of deep foraging dives. For the transit dives, we kept descent and ascent speed constant at 1.2 m s^{-1} , which was the routine speed measured for the 263 kg elephant seal (Davis *et al.* 2001). At the beginning of a dive, the seal descended vertically and stroked continuously (active drag) to a depth of 25 m, at which point negative buoyancy was equal to passive drag. The seal then glided (passive drag) for the remainder of descent. As the seal became heavier with increasing depth, it began to accelerate. We kept the speed constant during transit dives by reducing the angle of descent so that the buoyancy vector along the dive path was always equal to passive drag. This meant that the angle decreased

throughout descent, causing the seal to move forward. In this manner, the seal converted the vertical force of gravity into horizontal movement. The trajectory was maintained by assuming that the forward speed produced sufficient hydrodynamic lift to counteract the vertical component of the buoyancy force (figure 1). This will define a minimum speed, much like the minimum speed for tuna (Magnuson 1978). The lift can be enhanced by flipper orientation and postural characteristics (e.g. cambered body).

Once the curvilinear descent path was determined empirically, the ascent angles were varied from 5 to 90°. Instantaneous metabolic rate was calculated each second and summed to give the oxygen consumption for the dive, which could not exceed the total available oxygen stores (i.e. 18 926 ml O₂). The duration of descent and, therefore, the maximum depth were adjusted empirically so that the dive remained within the ADL. The optimum angle of ascent was determined based on the maximum horizontal displacement (MHD) along a straight line. For comparison, we calculated the metabolic cost (E_D , ml O₂) for the seal to cover the horizontal distance during a transit dive versus the metabolic cost (E_H , ml O₂) that would be incurred while swimming three body diameters beneath the surface at 1.2 m s⁻¹ (i.e. same active drag) over the same horizontal distance. This enabled us to determine whether it was more cost-efficient for seal to make transit dives as opposed to swimming just below the surface to cover the equivalent horizontal distance.

The second model was a vertical foraging dive. For simplicity, we assumed 90° ascent and descent angles. At the beginning of a dive, the seal descended vertically and stroked continuously (active drag) until a depth of 25 m, at which point negative buoyancy was equal to passive drag. The seal then stopped stroking and glided (passive drag). As the seal became heavier during descent, it accelerated to a terminal velocity (approx. 2.2 m s⁻¹) that was obtained when the passive drag equalled the submerged weight. Ascent speed with stroking was varied from 0.4 to 3.0 m s⁻¹. Metabolic rate was calculated each second and summed to give the oxygen consumption for the dive, which could not exceed the total available oxygen stores (i.e. 18 926 ml O₂). The duration of descent and the maximum depth were adjusted empirically so that the dive remained within the ADL. The optimum speed of ascent was based on the maximum vertical displacement (maximum dive depth).

The third model was a flat-bottom foraging dive at a depth of 400 m. We assumed 90° ascent and descent angles. At the beginning of a dive, the seal descended vertically and stroked continuously (active drag) until a depth of 25 m, at which point negative buoyancy was equal to passive drag. The seal then stopped stroking and glided (passive drag). As the seal became heavier during descent, it accelerated to a terminal velocity (approx. 2.2 m s⁻¹) that was limited by passive drag until a depth of 400 m was reached. The seal then swam horizontally at a speed ranging from 0.4 to 3.0 m s⁻¹, and then ascended vertically at the same speed. Metabolic rate was calculated each second and summed to give the oxygen consumption for the dive, which could not exceed the total available oxygen stores (i.e. 18 926 ml O₂). The duration of horizontal swimming at a depth of 400 m was adjusted empirically so that the dive remained within the ADL. The optimum speed was based on either the time or the distance travelled at 400 m.

The models were run on a standard spreadsheet program (EXCEL for Windows) for transit dives with 10 ascent angles and foraging dives with 6 ascent swim speeds. This produced 60 combinations of dives. The general procedure was to select

Figure 2. Optimum descent angle as a function of depth for transit dives. The angle of descent decreased asymptotically as the seal became more negatively buoyant so that speed was maintained at 1.2 m s⁻¹.

Figure 3. Maximum horizontal displacement (MHD) travelled as a function of ascent angle during a transit dive. Descent angle was the same for each transit dive and is shown in figure 1.

a dive type and then vary the ascent angle (transit dives), ascent speed (deep foraging dives) or time at 400 m (flat-bottom foraging dives). Descent duration was adjusted empirically so that all available oxygen was consumed for each ascent angle, ascent speed or duration at 400 m.

3. RESULTS

(a) *Transit dives*

We assumed that the optimum transit dive was one that gave the maximum horizontal displacement (MHD) along a straight line for a fixed amount of energy, i.e. the lowest cost of transport (COT) in the horizontal plane. To accomplish this, the seal glided during descent below a depth of 25 m, and the angle of descent decreased asymptotically as the seal became more negatively buoyant so that speed was maintained (i.e. no acceleration) at 1.2 m s⁻¹ (figure 2). By making the descent angle increasingly shallow (range 90–18°) and holding speed constant, the component of the vertical gravity force, in the direction of motion, enables horizontal motion without stroking. At a depth of 28 m, 50% of the change in descent angle had occurred, 95% had occurred at a depth of 141 m (figure 2).

MHD was greatest at ascent angles ranging from 20 to 30° (figure 3; table 1). These were also the angles in which descent and ascent distances were about the same, which gave the dives a symmetrical appearance similar to three-dimensional transit dive recorded for an elephant seal in the wild (figure 1; Davis *et al.* 2001). At ascent angles less than this, the seal spent a greater percentage of the dive (greater ascent distance)

Table 1. Characteristics of transit dives with different ascent angles computed by the model. (Descent angle was the same for each ascent angle and is shown in figure 1. Swim speed during descent and ascent was constant at 1.2 m s^{-1} . ADL is the aerobic dive limit, MHD is the maximum horizontal displacement, $\dot{V}_{\text{O}_2}$ is the average rate of oxygen consumption during a transit dive and COTMHD is the cost of transport for maximum horizontal displacement.)

ascent angle (°)	90	80	70	60	50	40	30	20	10	5
ADL (min)	22.78	22.75	22.70	22.58	22.43	22.18	21.82	21.25	20.28	19.50
maximum dive depth (m)	420	418	413	403	388	364	329	274	179	104
descent distance (m)	1220	1213	1195	1162	1110	1031	913	731	428	205
ascent distance (m)	420	425	439	464	505	566	658	799	1032	1199
MHD (m)	1124	1191	1250	1300	1344	1378	1401	1409	1387	1355
$\dot{V}_{\text{O}_2}$ ($\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$)	3.2	3.2	3.2	3.2	3.2	3.3	3.3	3.4	3.6	3.7
COTMHD ($\text{ml O}_2 \text{ m}^{-1}$)	16.9	15.9	15.2	14.6	14.1	13.8	13.5	13.5	13.7	14.0

Figure 4. Rate of oxygen consumption ($\dot{V}_{\text{O}_2}$) as a function of ascent angle during transit dives.

Figure 5. Maximum depth as a function of ascent angle during transit dives.

stroking, which increased $\dot{V}_{\text{O}_2}$ and decreased the ADL and the MHD (table 1; figure 4). At ascent angles greater than 20–30°, the seal spent a smaller percentage of the dive (shorter ascent distance) stroking, which decreased $\dot{V}_{\text{O}_2}$, increased the ADL slightly (a maximum of 4%) and enabled a longer duration of the gliding descent phase. However, this resulted primarily in a greater maximum depth but smaller MHD (figures 3 and 5; table 1). The optimum ascent angle was a balance between the duration of gliding during descent and the duration of stroking during ascent, the latter being a direct result of ascent angle. Nevertheless, horizontal displacement was relatively insensitive (i.e. less than a 5% difference in the MHD) to ascent angles ranging from 5 to 50° (figure 3).

In the model for a transit dive, we kept the descent and ascent speed constant at 1.2 m s^{-1} , even though the seal spent most of descent gliding and all of ascent stroking. We kept speed constant based on actual measurements from a free-ranging elephant seal making transit dives, which showed that speed remained constant at approximately 1.2 m s^{-1} and was a poor indicator of the mode of locomotion (Davis *et al.* 2001). At an optimum angle of ascent

Figure 6. Ratio of the cost of transport for maximum horizontal displacement (COTMHD) for transit dives to that of horizontal submerged swimming as a function of ascent angle.

(based on MHD) of 20°, average $\dot{V}_{\text{O}_2}$ for the dive was $3.3 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ (1.4 times BMR). If the seal had stroked continuously at 1.2 m s^{-1} during the dive (assuming the same active drag and no effect due to buoyancy), then the $\dot{V}_{\text{O}_2}$ would have been $3.8 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$. By gliding during descent, the seal reduced its $\dot{V}_{\text{O}_2}$ by 13% and increased its ADL by 2.3 min. However, the seal travelled a greater total distance (i.e. the sum of descent and ascent distances) during a transit dive than it would by swimming submerged just below the surface (i.e. at a depth of approx. three body diameters to keep active drag the same) along a straight line from the beginning and end locations of the dive. The cost of transport for the maximum horizontal displacement (COTMHD, $\text{ml O}_2 \text{ m}^{-1}$) for transit dives reached a minimum ($13.5 \text{ ml O}_2 \text{ m}^{-1}$) for dives with ascent angles of 20–30° (table 1; figure 6). By comparison, the COTMHD for submerged swimming at 1.2 m s^{-1} was $13.9 \text{ ml O}_2 \text{ m}^{-1}$. Consequently, there was little difference (0–3%) in the COTMHD between transit dives with ascent angle of 5–45° and submerged swimming just below the surface (i.e. three body diameters) between the beginning and end locations of the dive. At ascent angles steeper than 45°, the COTMHD for transit dives was greater than that for submerged swimming (figure 6). At an ascent angle of 90°, the COTMHD was 22% greater than submerged swimming.

(b) Deep foraging dives

We used two criteria for determining optimality for foraging dives: (i) maximum depth for deep dives and (ii) time and distance travelled at a depth of 400 m for flat-bottom dives.

Table 2. Characteristics of deep foraging dives with different ascent speeds computed by the model. (Descent and ascent angles were vertical. Descent speed was 1.2 m s^{-1} while the seal was positively buoyant down to a depth of 25 m. When the seal became negatively buoyant, it accelerated until passive drag force equalled the negative buoyant force, which occurred at a terminal speed of approximately 2.2 m s^{-1} . ADL is the aerobic dive limit, $\text{D}\dot{V}_{\text{O}_2}$ is the average oxygen consumption during the foraging dive and $\text{S}\dot{V}_{\text{O}_2}$ is the oxygen consumption during continuous stroking at the average speed for the dive.)

ascent speed (m s^{-1})	0.4	0.8	1.2	1.8	2.2	3.0
ADL (min)	24.8	21.9	17.2	12.2	9.7	6.2
maximum dive depth (m)	495	722	780	700	609	440
average descent speed (m s^{-1})	2.0	2.0	2.0	2.0	2.0	1.9
average dive speed (m s^{-1})	0.7	1.2	1.5	1.9	2.1	2.3
descent time (min)	4.2	5.9	6.4	5.8	5.1	3.8
ascent time (min)	20.6	15.0	10.8	6.5	4.6	2.4
$\text{D}\dot{V}_{\text{O}_2}$ ($\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) for the dive	2.9	3.4	4.2	5.9	7.5	11.6
$\text{S}\dot{V}_{\text{O}_2}$ ($\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) for the dive	2.7	3.6	5.1	7.7	9.5	12.2
ratio dive: swimming $\dot{V}_{\text{O}_2}$	1.07	0.94	0.82	0.76	0.79	0.95

Figure 7. Maximum depth as a function of ascent swimming speed during deep foraging dives. Descent and ascent angles were 90° .

For both types of foraging dives, the seal glided vertically during descent below a depth of 25 m and accelerated until negative buoyancy was equal to passive drag and the seal reached a terminal speed (approx. 2.2 m s^{-1} at a depth of 380 m). For deep foraging dives, the greatest depth (780 m) was achieved when the seal ascended at 1.2 m s^{-1} (figure 7; table 2). However, this ascent speed did not coincide with the lowest $\dot{V}_{\text{O}_2}$ ($2.9 \text{ O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) and maximum ADL (24.8 min), which occurred for an ascent speed of 0.4 m s^{-1} . However, at this low speed, the seal required 18.4 min (74% of dive duration) to ascend. As a result, less time was available for descent to remain within the ADL, and the maximum depth was less (table 2). For ascent speeds greater than 1.2 m s^{-1} , the increasing $\dot{V}_{\text{O}_2}$ decreased the ADL and the time available for descent, so the maximum depth decreased (figure 8; table 2). In achieving the greatest depth, the optimum balance between speed and $\dot{V}_{\text{O}_2}$ ($4.2 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$; 1.7 times BMR) occurred for an ascent speed of 1.2 m s^{-1} . By gliding during descent, the seal reduced its $\dot{V}_{\text{O}_2}$ (except for an ascent speed of 0.4 m s^{-1}) compared with continuous stroking (same active drag) at the average speed for the dive (table 2). The greatest reduction (24%) in $\dot{V}_{\text{O}_2}$ compared to continuous stroking at the average speed for the dive occurred for an ascent speed of 1.8 m s^{-1} . For the optimum (i.e. maximum depth achieved) ascent speed of 1.2 m s^{-1} , the reduction in $\dot{V}_{\text{O}_2}$ was 18%, which increased the ADL by 3 min.

Figure 8. Rate of oxygen consumption ($\dot{V}_{\text{O}_2}$) as a function of ascent swimming speed during deep foraging dives.

During flat-bottom foraging dives, the seal glided vertically during descent below a depth of 25 m to a final depth of 400 m, at which point it began swimming horizontally at the same speed as during ascent. The maximum time (11.1 min) at 400 m occurred for a horizontal swimming and ascent (HS&A) speed of 0.8 m s^{-1} (figures 9 and 10; table 3). However, the greatest horizontal distance travelled (468 m) at a depth of 400 m occurred for a HS&A speed of 1.2 m s^{-1} (figures 9 and 10; table 3). Although the longest ADL (25.5 min) occurred for a HS&A speed of 0.4 m s^{-1} , the time (5.4 min) and distance travelled (78 m) at a depth of 400 m was significantly less because the duration of ascent occupied 65% of the dive. In addition, the estimated hydrodynamic lift at this low swimming speed was less than the negative buoyancy, so the seal would have sunk while swimming horizontally. Insufficient hydrodynamic lift was not a problem for HS&A speeds greater than 0.8 m s^{-1} . At a HS&A speed of 1.8 m s^{-1} , the time spent and distance travelled at 400 m decreased 50 and 24%, respectively, compared with values for a HS&A speed of 1.2 m s^{-1} . For HS&A speeds greater than 1.8 m s^{-1} , the increasing $\dot{V}_{\text{O}_2}$ further decreased dive duration and the amount of time and distance travelled at a depth of 400 m. At a HS&A speed of 3.0 m s^{-1} , the time and distance travelled at 400 m were a mere 0.3 min and 32 m, respectively. By gliding during descent, the seal reduced its $\dot{V}_{\text{O}_2}$ (except for an ascent speed of $0.4\text{--}0.8 \text{ m s}^{-1}$) compared with continuous stroking (same active drag) at the average speed for the dive (table 2). The greatest reduction (13%) in $\dot{V}_{\text{O}_2}$ occurred for an ascent speed of 1.8 m s^{-1} .

Figure 9. Amount of time spent at 400 m during flat-bottom foraging dives as a function of horizontal and ascent swimming speed.

Figure 10. Horizontal distance travelled at 400 m of depth during flat-bottom foraging dives as a function of horizontal and ascent speed.

4. DISCUSSION

The northern elephant seal is a pelagic marine mammal that spends most of the year in the eastern North Pacific Ocean. While at sea, they make continuous deep dives for weeks or months, with occasional periods of rest at the surface (Le Boeuf *et al.* 1988). Since they gain weight while at sea, some of these dives are associated with feeding. However, many dives may be associated with transit as the seals migrate north. The 263 kg elephant seal that we studied in 1996, and on which the model in this study is based, had returned to the rookery at Año Nuevo Point to moult. We used the translocation–homing paradigm to study its diving and locomotory behaviour as it returned to the beach from which it was displaced by approximately 50 km (Oliver *et al.* 1998; Davis *et al.* 2001). Diving performance in this situation is similar to that of migrating seals, although feeding is not thought to occur. As a result, the dives that were recorded were considered transit dives (figure 1). The question arises, why would elephant seals dive to depth while transiting? One explanation is that they feed throughout migration, rather than waiting until they reach feeding grounds in the North Pacific Ocean. Another possible explanation is predator avoidance, especially for white sharks (*Carcharodon carcharias*) and killer whales (*Orcinus orca*) that prey on elephant seals and attack from below while the seal is at or near the surface (Le Boeuf *et al.* 2000; Klemley *et al.* 2001; Le Boeuf 2004). Descending to depth while transiting may

reduce the opportunity for attack. A third explanation is that there is an energetic advantage to diving while migrating. We examined the latter possibility in our model.

We knew from the three-dimensional dive profiles that elephant seals can use negative buoyancy to move horizontally without stroking during descent (figure 1; Davis *et al.* 2001). This means that they generate hydrodynamic lift while descending passively. We therefore examined under what circumstances the seal was able to travel the maximum horizontal distance (MHD). In the model, we used a constant average descent speed of 1.2 m s^{-1} , which was similar to what we recorded from the 263 kg seal (Davis *et al.* 2001). Since negative buoyancy increases down to a depth of approximately 141 m, the seal would accelerate unless it decreased descent angle, thereby converting the vertical force of gravity into horizontal displacement through hydrodynamic lift. Below 141 m in depth, there is little further change in buoyancy because the lungs are almost fully collapsed, and the hypothetical seal can maintain a speed of 1.2 m s^{-1} at a final descent angle of approximately 18° . This is shallower than the average descent angle of 41° that we recorded for the elephant seal in 1996 (Davis *et al.* 2001). The difference probably results from an underestimate of passive drag in the model, or the enhanced drag experienced by the seal when it had the video and data recorder attached. Regardless of descent angle, it is apparent that elephant seals can use negative buoyancy to move horizontally without stroking, thereby reducing the cost of locomotion and conserving oxygen. MHD was greatest with an ascent angle of $20\text{--}30^\circ$, but was relatively insensitive to angles ranging from 5 to 50° (figure 3). At very steep ascent angles (i.e. 90°), ascent distance was shorter, which meant that the seal spent less time stroking and average $\dot{V}_{\text{O}_2}$ was slightly lower (figure 4). As a result, the ADL and the maximum depth were greater (i.e. more time was available for passive descent) than for dives with a shallow ascent angle, but the MHD decreased 20% (table 1).

There was no energetic advantage in terms of MHD between diving and swimming submerged just below the surface (i.e. same active drag) while transiting. At the optimum angle of ascent (20°) that gave the greatest MHD, the average $\dot{V}_{\text{O}_2}$ for the dive was $3.3 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$, which is only 1.4 times the estimated BMR. If the seal had stroked continuously at 1.2 m s^{-1} while submerged (assuming the same active drag), then the $\dot{V}_{\text{O}_2}$ ($3.8 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) would have been 15% greater. However, the dive path was a greater distance than if the seal had swum a straight line between the beginning and end locations of the dive. As a result, the COTMHD ($13.5 \text{ ml O}_2 \text{ m}^{-1}$) for the dive was only 3% less than for submerged swimming ($13.9 \text{ ml O}_2 \text{ m}^{-1}$). For an elephant seal migrating across the North Pacific Ocean, our model indicates that there is little net energy savings in diving if the primary purpose is transiting. Therefore, there may be other reasons for the seal to dive. As mentioned previously, feeding along the way or avoiding predators are possible explanations, but additional data or video-recorded behaviour will be required.

Table 3. Characteristics of flat-bottom foraging dives to a maximum depth of 400 m with different ascent speeds computed by the model. (Descent and ascent angles were vertical. Descent speed was 1.2 m s^{-1} while the seal was positively buoyant down to a depth of 25 m. When the seal became negatively buoyant, it accelerated until passive drag force equalled the negative buoyant force, which occurred at a terminal speed of approximately 2.2 m s^{-1} . ADL is the aerobic dive limit, $\dot{V}\text{O}_2$ is the average oxygen consumption during the flat-bottom foraging dive and SVO_2 is the oxygen consumption during submerged swimming at the same average speed as occurred during the foraging dive.)

ascent speed (m s^{-1})	0.4	0.8	1.2	1.8	2.2	3.0
ADL (min)	25.5	22.7	18.2	11.7	8.8	6.0
average descent speed (m s^{-1})	1.9	1.9	1.9	1.9	1.9	1.9
average dive speed (m s^{-1})	0.6	1.0	1.3	1.8	2.1	2.4
descent time (min)	3.5	3.5	3.5	3.5	3.5	3.5
ascent time (min)	16.7	8.3	5.6	3.7	3.0	2.2
time (min) at 400 m of depth	5.4	11.1	9.0	4.5	2.3	0.3
horizontal distance travelled (m) at 400 m of depth	78	366	468	342	218	32
$\dot{V}\text{O}_2$ ($\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) for the dive	2.8	3.2	4.0	6.2	8.2	12.2
SVO_2 ($\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) for the dive	2.7	3.2	4.3	7.1	9.3	12.3
ratio dive: swimming $\dot{V}\text{O}_2$	1.06	1.00	0.92	0.87	0.88	0.99

Unlike transit dives in which we assumed no feeding, the factors we used for assessing optimality in foraging dives were the ability to reach great depths (access to deep living prey) or the amount of time and space searched at an intermediate (400 m) depth. These criteria were chosen based on the enhanced opportunity to encounter and capture prey. Elephant seals are thought to prey on mesopelagic squid and fishes, although male elephant seals may feed on benthic prey on sea mounts. In the model for deep mid-water dives, we assumed that the seal descended vertically while gliding, then ascended at different speeds. The seal was allowed to accelerate to a terminal speed of 2.2 m s^{-1} , at which point passive drag was equal to negative buoyancy. The maximum depth (780 m) was achieved with an ascent speed of 1.2 m s^{-1} . There was a trade-off between ascent speed and the duration of ascent. A lower ascent speed resulted in a lower dive $\dot{V}\text{O}_2$ and higher ADL (figure 8; table 2). However, the duration of ascent was longer, which meant less time was available for descent, so the maximum depth decreased. At higher ascent speeds, $\dot{V}\text{O}_2$ increased dramatically which decreased the ADL and the time available for descent (figure 8; table 2). Achieving the maximum depth was a balance between the duration and energetic cost of ascent. Overall, there was an energetic advantage to gliding during descent and ascending at 1.2 m s^{-1} in deep foraging dives. Using negative buoyancy during descent compared with stroking throughout the dive (a hypothetical situation that ignores buoyancy) at an average speed for descent and ascent (1.5 m s^{-1}), the seal reduced $\dot{V}\text{O}_2$ by 18% and increased its ADL by 3 min (21%; table 2). Greater relative savings (24 and 21%) in $\dot{V}\text{O}_2$ occurred at higher average dive speeds 1.9 and 2.1 m s^{-1} , respectively. However, the ADL and the maximum depth were much less than at the optimum ascent speed of 1.2 m s^{-1} (table 2).

The other type of foraging dive that we modelled was one in which the seal descended vertically while gliding (terminal speed 2.2 m s^{-1}) to a depth of 400 m and then swam horizontally (flat-bottom foraging dive) searching for prey before ascending vertically at the same speed. There were two ways to assess this type of dive: (i) the amount of time at a depth of 400 m or (ii)

the distance travelled at 400 m. We have no data to say whether seals use one or the other strategy in the wild, and it may depend on the size, motility and density distribution of the prey. The maximum amount of time (11.1 min) at a depth of 400 m occurred for a horizontal and ascent swim speed of 0.8 m s^{-1} (figure 9; table 3). The maximum horizontal distance travelled (468 m) at a depth of 400 m occurred for a horizontal and ascent swim speed of 1.2 m s^{-1} (figure 10; table 3). Interestingly, neither of these swim speeds gave the maximum ADL (25.5 min), which occurred for a speed of 0.4 m s^{-1} . However, the time available and distance travelled at a depth of 400 m was much less because the seal was moving so slowly while swimming horizontally and during ascent. In addition, the estimated lift at this speed was insufficient to allow the animal to swim horizontally without sinking (or colliding with the bottom). At speeds greater than 1.2 m s^{-1} , the increase in $\dot{V}\text{O}_2$ decreased the ADL and the amount of time or distance travelled at 400 m. Overall, there was little or no energetic advantage to gliding during descent compared with stroking at the average speed for the entire dive (table 3). The $\dot{V}\text{O}_2$ for the HS&A speed (0.8 m s^{-1}) that gave the maximum time at 400 m was the same as the $\dot{V}\text{O}_2$ for continuous stroking at an average speed for the entire dive (table 3). At an HS&A speed of 1.2 m s^{-1} , the energetic savings over continuous stroking was only 8% resulting in an increase in the ADL of 1.8 min.

In designing the model for this study, we had some data on the body morphology, three-dimensional movements and locomotory behaviour for a 263 kg elephant seal (Davis *et al.* 2001). However, we made many assumptions for calculating drag force and energetics. Despite these assumptions, the model produced estimates of maximum dive depths and durations, and optimum swim speeds that were consistent with values reported previously for elephant seals equipped with time–depth recorders and satellite telemeters (Le Boeuf *et al.* 1986, 1988, 1992, 1996). In addition, the assumptions used in calculating drag force produced estimates of diving metabolic rates that ranged from 1.3 to 1.7 times the allometric BMR. Hence, the estimated dive metabolism was low but not

less than BMR and produced theoretical values for ADL that account for a high percentage of normal dive durations for a 263 elephant seal. Overall, we think that the results from this model are useful in understanding the physical and physiological factors that influence elephant seal diving and locomotory behaviour.

In conclusion, our model indicates that any energetic savings from gliding descent depends on the characteristics of the dive. In terms of the energetic cost of migration, our results indicate that there is little advantage to transit dives with gliding descent compared with horizontal swimming beneath the surface. Predator avoidance may better explain why elephant seals make transit dives during migration. Alternatively, the seals may begin searching for prey and foraging as soon as the move beyond the continental shelf during migration, in which case the term transit dive may need to be reconsidered. Indeed, all deep dives may be potential foraging dives. However, gliding descent shows variable energy savings even for foraging dives. Deep mid-water foraging dives showed the greatest energy savings as a result of gliding during descent. In contrast, flat-bottom foraging dives with considerable amounts of horizontal swimming showed less of an energetic advantage with gliding descent, primarily because more of the dive involved stroking. Additional data are needed before the advantages of gliding descent can be fully understood for male and female elephant seals of different age and body composition. This type of data will require additional animal-borne instruments that can record the behaviour, three-dimensional movements and locomotory performance of free-ranging animals at depth.

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