

RESEARCH ARTICLE

Sink fast and swim harder! Round-trip cost-of-transport for buoyant divers

Patrick J. O. Miller^{1,*}, Martin Biuw¹, Yuuki Y. Watanabe², Dave Thompson¹ and Mike A. Fedak¹

¹Sea Mammal Research Unit, School of Biology, University of St Andrews, Fife KY16 9QQ, UK and ²National Institute of Polar Research, 10-3, Midori-cho, Tachikawa, Tokyo 190-8518, Japan

*Author for correspondence (pm29@st-andrews.ac.uk)

SUMMARY

Efficient locomotion between prey resources at depth and oxygen at the surface is crucial for breath-hold divers to maximize time spent in the foraging layer, and thereby net energy intake rates. The body density of divers, which changes with body condition, determines the apparent weight (buoyancy) of divers, which may affect round-trip cost-of-transport (COT) between the surface and depth. We evaluated alternative predictions from external-work and actuator-disc theory of how non-neutral buoyancy affects round-trip COT to depth, and the minimum COT speed for steady-state vertical transit. Not surprisingly, the models predict that one-way COT decreases (increases) when buoyancy aids (hinders) one-way transit. At extreme deviations from neutral buoyancy, gliding at terminal velocity is the minimum COT strategy in the direction aided by buoyancy. In the transit direction hindered by buoyancy, the external-work model predicted that minimum COT speeds would not change at greater deviations from neutral buoyancy, but minimum COT speeds were predicted to increase under the actuator disc model. As previously documented for grey seals, we found that vertical transit rates of 36 elephant seals increased in both directions as body density deviated from neutral buoyancy, indicating that actuator disc theory may more closely predict the power requirements of divers affected by gravity than an external work model. For both models, minor deviations from neutral buoyancy did not affect minimum COT speed or round-trip COT itself. However, at body-density extremes, both models predict that savings in the aided direction do not fully offset the increased COT imposed by the greater thrusting required in the hindered direction.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/215/20/3622/DC1>

Key words: drag, buoyancy, cost-of-transport, swimming gait.

Received 10 January 2012; Accepted 1 June 2012

INTRODUCTION

Total cost-of-transport (COT) is the amount of energy expended by an organism moving a unit of mass a given distance, which also specifies the amount of oxygen consumed (Tucker, 1975). Energetic expenditure during swimming locomotion is commonly divided into basal metabolism and locomotion cost incurred due to thrust generated to overcome forces resisting locomotion, such as drag (Williams et al., 2004). Both modelling (Thompson et al., 1993) and empirical research on swimming mammals (Sumich, 1983; Feldkamp, 1987; Videler and Nolet, 1990) indicate that COT is minimized at an intermediate travel speed. At lower speeds, basal metabolism dominates energy expenditure during transport, whereas at higher speeds drag dominates because it increases non-linearly with speed. Deep-diving animals should benefit by transiting to and from depth at the minimum COT speed, because this strategy maximizes the amount of oxygen available for efficient aerobic metabolism at depth (Thompson et al., 1993).

In addition to drag, buoyant forces generated by the difference in density of a diver's body and the surrounding medium should have an important influence on the energetics of vertical transit. Buoyant forces act vertically, adding to (or subtracting from) drag forces during dives to and from depth (Webb et al., 1998; Beck et al., 2000). In breath-hold divers, which carry air in the lungs and fur or plumage (Miller et al., 2004; Sato et al., 2006), the force of buoyancy can exceed drag (Løvvorn and Jones, 1991). Air carried by a diving animal is compressed at depth, reducing its effect on

buoyancy, while the effect of tissue density on buoyancy is relatively constant across depth. Changes in buoyancy have been shown to influence the stroking patterns of swimmers, with more gliding observed when buoyancy aids movement (Williams et al., 2000; Skrovan et al., 1999; Miller et al., 2004). Buoyancy forces also modulate the terminal speed obtained during prolonged glides, with higher speeds obtained when stronger buoyancy forces aid the glide (Biuw et al., 2003; Miller et al., 2004; Watanabe et al., 2006). A key question we address here is whether changes in buoyancy, which do have consequences for locomotion behaviour, also have energetic consequences for divers (Fahlman et al., 2008). Although gliding can reduce COT relative to active swimming (Williams et al., 2000), the key consideration for round-trip COT in divers is that any buoyancy force that aids movement in one direction of the transit to/from depth will hinder movement in the opposing direction (Hays et al., 2007).

Many marine divers, such as phocid seals, are known to undergo substantial changes in body condition over annual cycles. Energy stores lost during fasting periods associated with breeding and moult are replenished prior to the subsequent fast. Because lipid, the main body energy reserve, is less dense than seawater whereas the remaining lean body is slightly more dense than seawater, changes in body composition strongly influence net buoyancy in seawater. The cost of maintaining energy reserves [e.g. predation risk in flying birds (Gosler et al., 1995)] may influence the body condition maintained by animals, but it is largely unknown whether there is a

locomotion cost to varying fat reserves in divers (Houston et al., 2007; Fahlman et al., 2008). However, there is evidence that changes in body density leads to changes in diving behaviour in seals. Webb et al. (Webb et al., 1998) found that descent rates were higher in northern elephant seals (*Mirounga angustirostris*) with weights added to increase negative buoyancy, but that ascent rates were unchanged. Beck et al. (Beck et al., 2000) described how diving behaviour changed in relation to seasonal changes in buoyancy in free-ranging grey seals (*Halichoerus grypus*). Although common dive parameters such as dive depth and shapes remained unchanged, both descent and ascent rates were higher during periods when seals were relatively lean (Beck et al., 2000). Also, the difference between ascent and descent rates was greatest when seals were lean, and decreased when animals were fatter and therefore less negatively buoyant [fig. 2 in Beck et al. (Beck et al., 2000)]. Although higher descent rates observed in both these studies could be explained simply by faster terminal descent glides during high-density lean periods, it is not clear why ascent rates were either unchanged (Webb et al., 1998) or increased (Beck et al., 2000) as the ascending seals had to counter the combined forces of drag and buoyancy during ascent. In addition to assessing the potential influence of buoyancy changes on round-trip COT, the present study also assesses how buoyancy conditions might affect the minimum COT speed ($U_{COT,min}$) in both transit directions.

To investigate how buoyancy might affect the vertical COT of divers, as well as $U_{COT,min}$, we extend an existing external-work steady-state COT model (Sato et al., 2010) to include the direction of movement aided as well as that resisted by buoyancy. The model (see Eqn 4) uses power=work (force \times distance) per unit time, which can also be expressed as power=force \times speed, to calculate net external work per unit time, a predictor of the internal power required (Sato et al., 2010) to maintain kinetic energy (speed) against drag and to change potential energy during ascent and descent. Sato et al. (Sato et al., 2010) found that this model predicts that $U_{COT,min}$ is neither affected by buoyancy nor pitch angle when divers move against buoyancy (i.e. descent phase of penguin dives). We start by extending this 'external-work' model to also include the opposite transit direction, in which buoyancy aids movement, so that round-trip COT can be predicted for divers under varying buoyancy forces.

A different modelling approach to estimate the power consumed in order to counter gravity and drag forces employs actuator-disc theory, which has been widely used for flying animals and helicopters (Weis-Fogh, 1972; Ellington, 1984; Wakeling and Ellington, 1997). Thrust force for weight support, climbing, acceleration and to overcome drag is generated by acceleration of the fluid medium across the idealised disc, and power is the product of thrust force and speed of the medium across the disc (Johnson, 1994). By focusing upon the work done to the fluid medium in swimming, this approach overcomes an unsatisfactory aspect of the external-work model: it cannot predict power requirements for hovering when speed is zero. In the case of a diver maintaining its position against a strong buoyancy force, for example, the 'external-work' model would predict zero locomotion cost, which is clearly unrealistic (Lovvorn et al., 1991) (see Fig. 1). Actuator-disc theory provides a solution for estimating power requirements for hovering and climbing flight in air (Johnson, 1994). A marine diver vertically moving against net buoyancy corresponds well to a flying animal (or helicopter) supporting its weight in air by accelerating the surrounding fluid to climb against gravity. Therefore, the application of actuator-disc theory to study power requirements of vertical transit in buoyant divers is appropriate.

Using the 'external-work' and 'actuator-disc' models, we explore how buoyancy influences the predicted $U_{COT,min}$, and the COT itself

to and from depth in diving animals in both travel directions under the influence of varying levels of buoyancy forces. Qualitative predictions from the models of how buoyancy might influence $U_{COT,min}$ are then compared with data on the dive behaviour of southern elephant seals (*Mirounga leonina*) affected by natural changes in body density, collected using satellite relay data loggers (SRDLs) (Fedak et al., 2002). Changes in buoyancy of the seals were tracked using changes in vertical drift rate (Biuw et al., 2003), and vertical transit (ascent and descent) rates were evaluated using compressed dive records (Fedak et al., 2001). The models appear to predict many aspects of observed behaviour, and may be a useful technique for exploring the influence of buoyancy on the energetics of diving animals as well as tracking their changes in relative body composition over time.

MATERIALS AND METHODS

The 'external-work' steady-state COT model

The 'external-work' model is equivalent to the mechanical model presented by Sato et al. (Sato et al., 2010), which calculates the mechanical work required of the animal to carry out the external movements of the animal. During the transit phases of dives, energy and oxygen consumption can be divided into maintenance costs and locomotion expenditures:

$$GMR = a + C_L, \quad (1)$$

where GMR is the gross metabolic rate, a is the basal metabolic rate and C_L is locomotor cost, i.e. energy expended by the animal in generating thrust (Williams et al., 2004). In steady-state, where velocity (u) is constant, thrust forces from swimming must equal all resistive forces, which include drag (which always acts in a direction opposite that of the movement) and buoyancy (which can act either with or against movement in a diving animal). COT can be derived by dividing GMR by u and body mass. Our goal is to explore the influence of buoyancy independent of mass changes, so we specified body mass to remain constant. As our goal is to consider vertical COT only, diving angles are assumed to be perfectly steep.

In the drag-only case, Eqn 1 can be simplified to:

$$GMR = a + \epsilon_{pA} F_d u, \quad (2)$$

where a is a constant basal metabolic rate, and ϵ_{pA} is the product of propeller efficiency and efficiency of converting chemical energy into muscular work. The term F_d is the total resistive force of drag, which changes with speed according to the drag equation:

$$F_d = 0.5 A_{body} \rho_w u^2 \lambda C_d, \quad (3)$$

where A_{body} is the surface area of the body, ρ_w is the density of the surrounding fluid and C_d is the drag coefficient. The drag coefficient may differ in active and passive glide phases by factor λ . Multiplying drag forces by (u) in Eqn 2 derives the power output associated with swimming at speed (u) against the resistive drag force per unit distance per unit time (F_d) (Videler and Nolet, 1990).

Following Sato et al. (Sato et al., 2010), the forces required to overcome buoyancy are added to those required to overcome drag, resulting in:

$$GMR = a + \epsilon_{pA} (F_d + F_b) u, \quad (4)$$

where F_b is equal to $\sin(\theta)g(\rho_{animal}-\rho_{sw})V_{animal}$, where θ is pitch angle and $\sin(\theta)$ is +1 during vertical (+90 deg) ascent and -1 during vertical descent, g is gravitational acceleration (9.8 ms^{-2}), ρ_{animal} and ρ_{sw} are the densities of the total animal and surrounding seawater, respectively, and V_{animal} is the volume of the animal body.

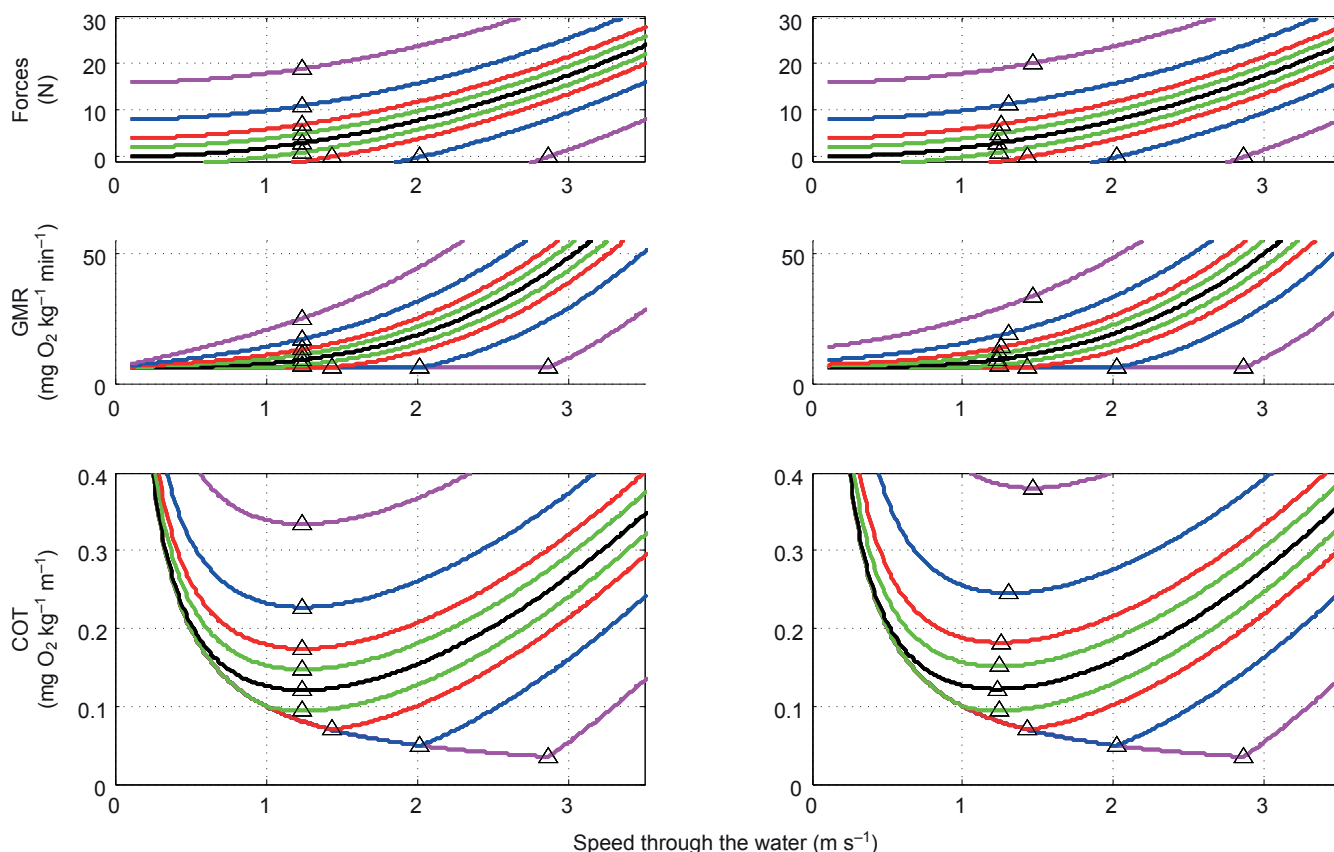


Fig. 1. Predictions from the external-work (left) and actuator-disc (right) cost-of-transport (COT) models for a vertically diving animal affected by a specified buoyancy force. For both panels, the central black line is the neutral buoyancy curve, with coloured curves at ± 2 , 4, 8 and 16 N. Each line represents model results for a single transit direction, e.g. the red lines above and below the black line represent the results when movement is hindered and aided by 4 N buoyant force, respectively. In all graphs, black triangles mark the value at the minimum COT speed for the external-work and actuator-disc models. Top: total force versus speed. Middle: gross metabolic rate (GMR) versus speed. Note that GMR is set to be equal to the basal metabolic rate at any combination of drag and buoyancy forces at which total forces are ≤ 0 . Bottom: COT (GMR/u) curves versus speed for each buoyancy level.

Note that F_b will be a positive value when movement is hindered by buoyancy, and a negative value when it is aided by buoyancy, irrespective of transit direction. When total forces ($F_d + F_b$) are ≤ 0 , the animal is expected to glide continuously and GMR is set to be equal to the basal metabolic rate (a) for that combination of speed and buoyancy force.

The 'actuator-disc'-based COT model including buoyancy forces

Actuator-disc theory quantifies a theoretical estimate of the induced power (P_{ind}) required to generate any given level of thrust *via* a uniform pressure gradient across an idealised disc of area A (Ellington, 1984). The mass flux through a disc moving parallel to its thrust direction is equal to $\rho_w A(v_i + u)$, where v_i is the induced velocity at the disc that generates thrust ($T = F_d + F_b$). The level of thrust is related to induced velocity as: $T = 2\rho_w A v_i^2$ from momentum theory, considering that the induced velocity in the far wake is twice that at the actuator disc (Johnson, 1994). Power is calculated as the thrust force times the fluid speed across the actuator disc: $P_{\text{ind}} = T(v_i + u)$. When the disc is transiting vertically (Wakeling and Ellington, 1997; Johnson, 1994), this is equivalent to:

$$P_{\text{ind}} = (F_d + F_b) \left(\frac{u}{2} + \sqrt{\frac{u^2}{0.25} + \frac{F_d + F_b}{2\rho_w A}} \right). \quad (6)$$

Induced power is added to basal metabolic rate to derive GMR. As with the external work model, when total forces ($F_d + F_b$) are ≤ 0 , the animal is expected to glide continuously and GMR is simply equal to the basal metabolic rate (a).

Initialization and implementation of both models

We used the two steady-state models to make predictions of how buoyancy might influence steady-state COT and $U_{\text{COT,min}}$ using numerical simulations in MATLAB (The Mathworks, Natick, MA, USA). We initialized the model using mass-specific power curves and drag coefficient values reported for a 37.5 kg California sea lion [*Zalophus californianus*; seal 1 in Feldkamp (Feldkamp, 1987)]. Area of the actuator disc, A , was estimated as ΦR^2 , where Φ is stroke amplitude in radians and R is effective flipper length (Ellington, 1984; Wakeling and Ellington, 1997). Effective flipper length for this seal was estimated to be 12.5 cm, and stroke amplitude was assumed to be $\pi/4$ radians (90 deg). Area of the actuator disc was doubled to account for use of both flippers. The basal metabolic constant (a) was set to $6.0 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$, and the efficiency and drag constants were specified using Videler and Nolet's (Videler and Nolet, 1990) values for the mass-specific locomotion cost of California sea lions. A similar curve has been reported for harbor seals (*Phoca vitulina*) (Williams et al., 1991). Mass-specific GMR ($\text{mg O}_2 \text{ kg}^{-1} \text{ min}^{-1}$) was calculated over a set of speeds (u ; m s^{-1}) at a specified buoyancy force; the COT

($\text{mg O}_2 \text{ kg}^{-1} \text{ m}^{-1}$) at each speed was determined as the minimum of GMR/u .

Buoyancy forces evaluated in the models were 0 (neutral buoyancy), ± 2 , ± 4 , ± 8 and $\pm 16 \text{ N}$. For each magnitude of buoyancy force, the model was evaluated for buoyancy aiding and hindering movement (subtracting from, or adding to, the drag force), simulating the ascent and descent behaviour of a diving animal. Speed was evaluated from 0.1 to 5.0 m s^{-1} at 0.1 m s^{-1} increments.

For any given buoyancy force, the cost of locomotion to a given depth is always smallest at vertical dive pitch angles (Thompson et al., 1993), and Sato et al. (Sato et al., 2010) showed that the minimum COT speed was unaffected by pitch angle. For simplicity, therefore, we only present the COT model at vertical pitch angles. As there is little agreement about an appropriate value for λ (Aoki et al., 2011), we used $\lambda=1.0$ (but see Discussion).

Satellite telemetry of southern elephant seal diving behaviour

To compare the model predictions with actual diving behaviour of a diver influenced by changes in body density and hence buoyant force, we made use of satellite-relayed diving behaviour of southern elephant seals. Seals were captured according to McMahon et al. (McMahon et al., 2000), and SRDLs (Sea Mammal Research Unit, St Andrews, UK) were glued to the fur on their heads using two-component epoxy glue (Fedak et al., 1983). All animal handling was carried out in accordance with applicable law. A description of the telemetry system and data compression is presented in Fedak et al. (Fedak et al., 2001; Fedak et al., 2002). Vertical rates of descent (ascent) were determined from the depth of the first (last) of the four inflection points relayed by the tag, divided by the time elapsed from the start of the dive to the first inflection point (from the last inflection point to the end of the dive).

Drift dives, which are dives in which the seal drifts passively at depth (Biuw et al., 2003), were extracted using a semi-supervised classification method (M.B., unpublished) based on the tree-based random forest algorithm (Breiman, 2001), and drift rates were calculated as described in Biuw et al. (Biuw et al., 2003). Smoothed time series of daily mean descent, ascent and drift rates were constructed using weighted constrained beta splines (Ng and

Maechler, 2007). Here, the weights for descent and ascent rates increased with the depth at which the descent ended or ascent began, to minimize the influence of shallow portions where air in the lungs has a large influence on buoyancy (Kooyman, 1989). A similar weighting scheme was applied to drift dives. To minimize the influence of erroneous drift rates calculated for dives with a low probability of actually being a true drift dive, weights based on the depth of the drift segment were multiplied by weights based on the classification probability from the random forest algorithm.

To examine whether vertical descent and ascent transit rates of dives were related to body composition (i.e. buoyancy), as predicted by our model, we ran a series of regressions with drift rate as the explanatory variable (i.e. a proxy for body composition/buoyancy), and where descent rate, ascent rate and the difference between them were used as response variables. The units for all rates were m s^{-1} . Because predicted values from the beta spline functions are likely to be temporally autocorrelated within individuals, standard regression methods are inappropriate. All models were therefore fitted to bootstrapped subsamples of the data. We created 1000 bootstrap samples, each with 500 data points randomly selected (without replacement) from the entire data set of 5908 days of data recovered from all seals. Furthermore, to avoid the error of inflated sample sizes due to repeated measures on individuals, we used linear mixed effects (LME) models (Pinheiro and Bates, 2000) rather than standard linear regression. Here, both the intercept and slope parameters were allowed to vary between individual seals by including individual as a random effect, thereby making the parameter estimates for the fixed effect (i.e. that of drift rate) more robust. The null hypothesis is that transit rate does not vary with drift rate, which would be reflected by an overall slope (drift rate/transit rate) not different from zero.

RESULTS

As expected, both forms of the model predict that, at any given speed, one-way GMRs are higher when buoyancy works with drag to hinder movement than at neutral buoyancy (Fig. 1). Likewise, GMR is lower when buoyancy acts against drag to aid movement (Fig. 1). A clear minimum in the COT curves (Fig. 1, bottom) could be identified for each buoyant force level for both models. Note

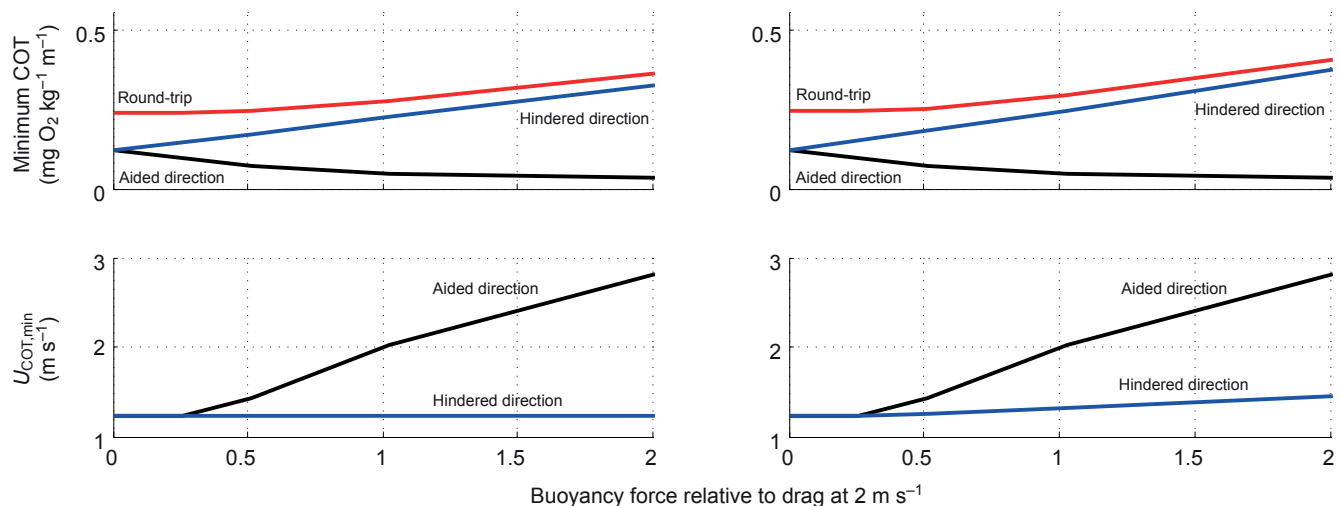


Fig. 2. Summary of the minimum COT values derived in the models shown in Fig. 1 for the external-work (left) and actuator-disc (right) COT models. Buoyancy force is scaled to the calculated drag force at 2 m s^{-1} , with 0 being neutral buoyancy, and the value at 2 being $\pm 15.6 \text{ N}$. Top: the predicted COT in the direction aided (black) and hindered (blue) by buoyancy. Round-trip COT (red) equals the sum of COT in each of two opposing transit directions. Note that round-trip COT increases with buoyancy under both models. Bottom: minimum COT speed ($U_{\text{COT,min}}$) versus buoyancy force. Note that $U_{\text{COT,min}}$ in the hindered direction increases with buoyancy under the actuator-disc model, but does not change under the external-work model.

that when buoyant force at a high level aids movement, such that $(F_d + F_b) \leq 0$, $U_{COT, \min}$ lies on the highest-speed point where total forces are equal to zero and GMR equals the basal metabolic rate (a). These are the conditions under prolonged gliding at terminal velocity (Williams et al., 2000). As buoyancy forces strengthen beyond this level, the model predicts that the minimum COT speed is always the glide terminal velocity for any specified buoyant force.

The model runs evaluate COT for each transit direction separately, and round-trip COT for each buoyancy condition is calculated by summing COT for the two transit directions. Both forms of the model predict that round-trip COT is lowest at neutral buoyancy, and increases non-linearly with larger deviations from neutral buoyancy. COT is predicted to increase more with stronger hindering buoyancy forces under the actuator-disc model than the external-work model (blue line in Fig. 2, top).

$U_{COT, \min}$ in the aided direction is predicted to increase as body density increasingly deviates from neutral buoyancy (Fig. 2, bottom). Near neutral buoyancy, $U_{COT, \min}$ does not change with buoyancy under the external-work model (black line in Fig. 2, left), but does increase slightly under the actuator-disc model (black line in Fig. 2, right). At greater non-neutral buoyancy, $U_{COT, \min}$ is predicted to increase strongly in the transit direction aided by buoyancy, as a consequence of a greater terminal speed during prolonged gliding (Fig. 2, bottom). COT savings in the direction aided by buoyancy largely balances losses in the direction hindered by buoyancy up to the level at which prolonged gliding is predicted to occur. At body densities highly deviant from neutral buoyancy, savings in the aided direction become smaller as terminal gliding speeds increase (black line in Fig. 2, top).

Predictions for $U_{COT, \min}$ under the two models differ increasingly as body density deviates from neutral buoyancy. Under the external-work model, transit rates in the hindered direction do not change at all with buoyancy (blue line in Fig. 2, left), as previously demonstrated by Sato et al. (Sato et al., 2010). However, under the actuator-disc model, $U_{COT, \min}$ in the direction hindered by buoyancy is predicted to increase as body density deviates from neutral buoyancy (blue line in Fig. 2, right). The COT under the actuator-disc model is somewhat greater than that for the external-work model, with the difference being greater at lower speeds and when higher buoyancy force is acting against movement (Fig. 1, bottom).

Transit rates of elephant seals during natural changes in buoyancy

The net buoyancy of southern elephant seals between the moult and breeding periods was monitored using the terminal drifting velocity obtained during drift dives (Fig. 3, green line). As expected, buoyancy was most strongly negative during transit to feeding grounds immediately following the moult in February, and moved closer to neutral buoyancy as the seals gained lipids during the migration. Closely matching the results of Beck et al. [see their table 3 (Beck et al., 2000)] with grey seals, ascent and descent rates were both greatest in the post-moult period, and less in the pre-breeding period. The difference between the descent and ascent rates was also smaller during the pre-breeding period than the post-moult [fig. 2 in Beck et al. (Beck et al., 2000)].

Summarizing the results from 36 adult southern elephant seals, we found that the difference in ascent and descent rates correlated strongly with buoyancy force (F_b) measured from drift rate. Model slope coefficients from subsamples of the data consistently deviated from zero, the predicted value if there were no correlation between buoyancy and ascent and descent rates (Fig. 4). From the 1000 bootstrap simulations, the LME model of descent rate as a function of drift rate had a mean slope coefficient of 0.96 (95% bootstrap

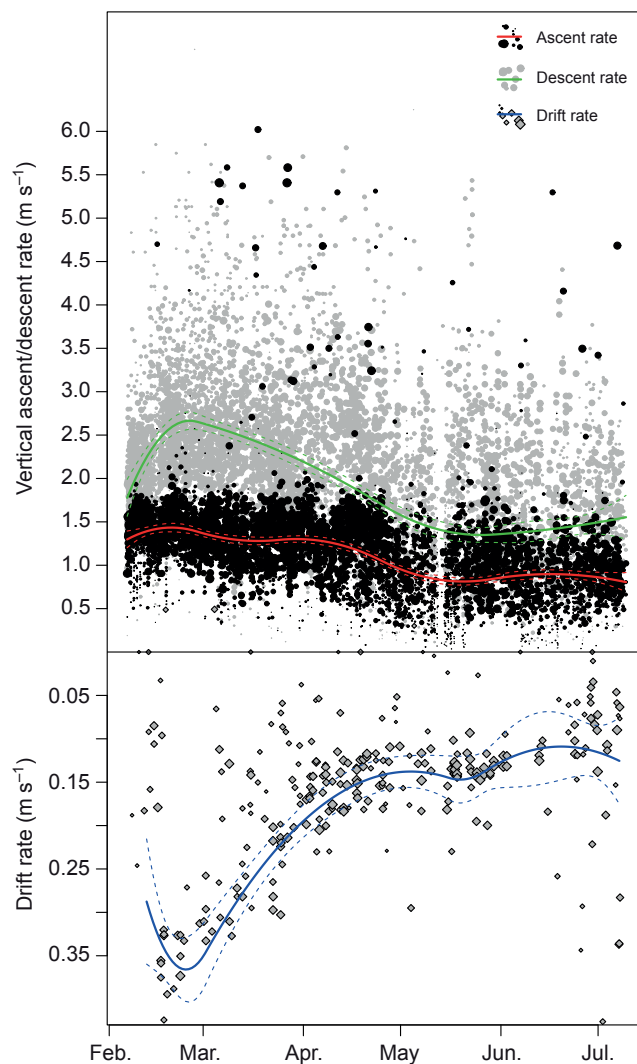


Fig. 3. Ascent and descent rates of a southern elephant seal during the migration between moult and breeding, monitored using a satellite relay data logger. Lines represent the weighted spline-fits (\pm s.e.m.) of ascent (red), descent (green) and drift (blue) rates. Note that descent and ascent rates are both plotted with speeds increasing towards the top of the graph, whereas drift rates are plotted in true direction, i.e. this animal was always negatively buoyant. Note also that descent transit rates were higher than ascent rates throughout, consistent with this negative buoyancy. Transit rates in both directions decreased as drift rates approach zero, as did the difference between ascent and descent rates.

confidence interval: 0.75–1.17), while the model for ascent rate had a mean slope coefficient of 0.74 (95% bootstrap confidence interval: 0.60–0.89). As indicated by the bootstrap confidence intervals (Table 1), both of these relationships were highly statistically significant.

Because all observed drift rates were negative (i.e. all seals were negatively buoyant) these results demonstrate a strong positive correlation between the magnitude of the deviation from neutral buoyancy and the transit rates for descent as well as ascent. The LME model where the difference between the descent and ascent transit rates was used as response variable had slightly lower slope coefficients overall (mean: 0.20, 95% bootstrap confidence interval: 0.08–0.32). This positive coefficient demonstrates that descent rates were higher than ascent rates, and that this difference increased as the drift rates, and net buoyancy, became more negative. While this

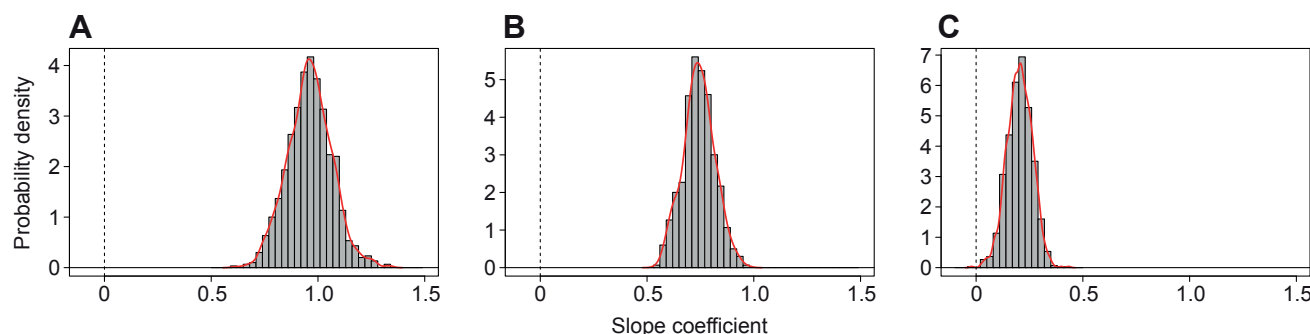


Fig. 4. Histograms of slope coefficients from bootstrapped linear mixed effects (LME) models of (A) descent rate, (B) ascent rate and (C) the difference between the two, as functions of drift rate (all in m s^{-1}). Each histogram represents the distribution of slope coefficients obtained from 1000 LME models, each fitted to a bootstrap sample from the original data. Note that none of the histograms straddles the broken vertical line indicating a slope coefficient of 0 (the expected value for no relationship between drift and vertical transit rates).

slope coefficient was smaller and more variable than the descent and ascent rate coefficients, the confidence intervals again demonstrates that this relationship is highly significant (less than 0.05% of the bootstrapped slope coefficients were less than or equal to zero). Therefore, we can conclude that descent rates, ascent rates and the difference between descent and ascent rates were strongly correlated with the net buoyancy of elephant seals as measured by drift rate.

DISCUSSION

As expected, both metabolic-cost models agree that one-way COT is reduced when buoyancy forces aids movement and COT is increased when buoyancy hinders movement (Figs 1, 2). They also agree that the minimum round-trip COT between the surface and a given depth is lowest at neutral buoyancy. The models predict that round-trip COT does not deviate much from COT at neutral buoyancy over a range of body densities close enough to neutral buoyancy that thrusting is required in both travel directions. As body density deviates more strongly from neutral buoyancy conditions, however, minimum round-trip COT increases in a non-linear fashion, driven by smaller benefits in the direction aided by buoyancy (Fig. 2, top).

It is indeed precisely once body density deviates so much from neutral buoyancy that prolonged gliding at higher speeds is predicted to occur in the aided direction that round-trip COT begins to increase strongly. This is because the concomitant level of increased metabolism entailed to move in the hindered direction cannot be increasingly recovered from the aided direction because the metabolic rate is already at basal values. The only benefit accrued in the aided direction is the increasing glide speed at terminal velocity, which reduces the duration of integrated basal metabolism over the transit. While prolonged gliding at terminal velocity is the minimum COT strategy, it does not benefit a diver sufficiently to offset the increased COT in the other direction (Figs 1, 2).

Both forms of the model match some behavioural predictions for efficient locomotion as body density deviates from neutral buoyancy. Once the force of buoyancy is equal to or exceeds the force of drag at the minimum COT speed, the minimum COT strategy in the

direction aided by buoyancy is to glide at terminal velocity. This corresponds to zero total forces being overcome by the animal, and GMR equivalent to the basal metabolic rate. Prolonged gliding during transit has been observed in a number of diving animals (Williams et al., 2000), and the proportion of time spent gliding increases with buoyant force in the aided transit direction (Miller et al., 2004). The metabolic rates of diving Weddell seals were lower during dives that contained long periods of gliding *versus* otherwise similar dives that did not contain as much gliding behaviour (Williams et al., 2000). Those observations support the prediction of our model that gliding is the minimum COT strategy in the travel direction aided by buoyancy. Additionally, the speed obtained by gliding divers has been shown to change when their movement is aided by buoyancy. The gliding speed of ascending sperm whales and penguins increases as they near the surface due to increasing positive buoyancy caused by expansion of gases carried to depth [figs 1, 3 in Miller et al. (Miller et al., 2004)] (Sato et al., 2011). In the opposite direction, the terminal gliding velocity of descending Baikal seals and northern elephant seals was higher when the seals were carrying a weight that experimentally increased its body density and net negative buoyancy (Watanabe et al., 2006; Aoki et al., 2011).

The predictions of the two models have an important difference. Although the external-work model agrees with Sato et al. (Sato et al., 2010) that buoyancy does not influence $U_{\text{COT,min}}$ in the hindered direction, the actuator-disc model predicts that $U_{\text{COT,min}}$ should increase as body density deviates from neutral buoyancy. These predictions relate closely to published studies of the diving behaviour of grey seals (Beck et al., 2000) undergoing natural changes in body density and therefore buoyancy forces, and elephant seals whose buoyancy was experimentally manipulated (Webb et al., 1998). In both of those studies, vertical transit rates (vertical velocity) during descent correlated with buoyancy changes, likely driven by changes in the speed of gliding as descent is the direction aided by buoyancy. One interesting difference between the results of Beck et al. (Beck et al., 2000) and Webb et al. (Webb et al., 1998) was that ascent rates did correlate with buoyancy in grey seals undergoing natural changes in buoyancy (with ascent rates also increasing), while ascent rates were unchanged for elephant seals whose body density had been experimentally manipulated. However, in both studies, the transit rate during descent (aided by buoyancy) was greater than during ascent. These results for two species of phocid seal qualitatively match the predictions for minimum COT transit speeds generated by the actuator-disc-based form of the model presented here (Fig. 2, right), suggesting that it may be a better predictor of swimming energetic requirements than the external-work model.

Table 1. Summary of slope coefficients from 1000 bootstrap resamplings

Response	Mean slope coefficient	2.5% CI	97.5% CI
Descent rate	0.9616	0.7531	1.1708
Ascent rate	0.7428	0.5988	0.8908
Difference descent-ascent	0.2037	0.0852	0.3162

Indeed, we found that transit rates in the hindered direction (ascent) did correlate with natural fluctuations in southern elephant seal buoyancy estimated using the rate of depth changes (terminal velocity) during drift dives (Figs 3, 4) (Biuw et al., 2003). Our finding utilized a longer-duration data set than Webb et al. (Webb et al., 1998) and corresponds well with the observations of Beck et al. (Beck et al., 2000) in relation to natural changes in buoyancy. The discrepancy between our natural results and the experimental results of Webb et al. (Webb et al., 1998) suggests that divers may not always have the behavioural flexibility to alter swimming speeds in the short time scales used in Webb et al.'s (Webb et al., 1998) study (see also Aoki et al., 2011). Descent transit is aided by buoyancy, and requires less exercise by the seals. In contrast, ascent is hindered by buoyancy, and $U_{\text{COT,min}}$ requires higher levels of exertion by the seals that are predicted to increase sharply with buoyancy (Fig. 2, top). It is conceivable that slower processes, such as changes in muscle tissues, are required for the animals to be able to attain those higher levels of performance and thrust production in an efficient manner. In contrast, the rapid changes in buoyancy brought about by experimental manipulation (Webb et al., 1998) or from gas compression during dives (Lovvorn et al., 2004; Sato et al., 2011) may not allow for increased performance levels for swimming against buoyancy.

For deep-diving animals, the influence of gases on buoyancy over the entire transit may be of minor importance relative to constant body density evaluated here. However, in shallower phases of dives, the density of breath-hold divers changes with pressure at depth (Miller et al., 2004). As this effect increases with the volume of gas carried, it will be strongest for divers that depend upon lung O_2 stores and usually do not exhale before diving. The influence of this feature of the functional ecology of breath-hold divers should be further investigated (Hansen and Ricklefs, 2004). We might expect the effect of gases on buoyancy to match the predictions of our model, with the effect only observed over a relatively narrow range of depths for elephant seals and other deep divers. For shallow divers, however, non-neutral buoyancy may increase the cost of horizontal swimming because of body angle adjustments made to maintain a preferred depth (Ribak et al., 2005). Diving seabirds appear to alter the amount of air carried in their lungs depending on the corresponding depth of the dive (Sato et al., 2006; Sato et al., 2011; Cook et al., 2010). By inhaling less air, these divers may decrease the cost of maintaining a preferred depth position at shallow depths where air buoyancy is strong (Lovvorn and Jones, 1991; Lovvorn et al., 2004). It would be interesting to explore whether diving seals might compensate for extremes in body buoyancy by manipulating the quantity of air inhaled prior to diving (Fahlman et al., 2008), as has been documented for penguins (Sato et al., 2011). However, the inhalation behaviour of diving seals may be more tightly constrained by physiological challenges of breath-hold diving such as decompression sickness (Falke et al., 1985) or shallow-water blackout (Hooker et al., 2005).

As pointed out by Thompson et al. (Thompson et al., 1993) and Beck et al. (Beck et al., 2000), the interpretation of diving behaviour in free-ranging seals is potentially influenced by a number of motivational factors acting on the seals. It is important to note that swimming speed (u) used in this study and vertical transit rates reported by Webb et al. (Webb et al., 1998), Beck et al. (Beck et al., 2000) and ourselves here for elephant seals are related to each other as $u = \text{transit rate} / \sin(\theta)$, where θ is the animal's body angle during transit. Recent studies indicate that deep divers may only rarely make perfectly vertical dives (Miller et al., 2004; Tyack et al., 2006). A non-vertical pitch angle increases the overall COT to a given depth

layer, thus decreasing oxygen availability for aerobic metabolism at depth (see the Appendix) (see also Thompson et al., 1993). Therefore, other factors that compete with the benefits of optimal diving must drive pitch angle, such as the benefit of horizontal transfer toward feeding locations (Sato et al., 2003) or social group members (Miller et al., 2004). Over the feeding migration of a southern elephant seal (Fig. 3), the need for horizontal transfer is clear, though dives may become more vertical when high-quality prey patches are located (Davis and Weihs, 2007).

The substantial variations in ascent and descent rate throughout the migration of elephant seals (Fig. 3) are likely influenced by such factors. We assume here that the observed pattern of change in transit rates implies similar changes in actual transit speed, i.e. that pitch changes do not correlate with changes in body condition and density. This assumption will be important to evaluate once longer-term data records including accelerometry become available; in addition, it will be important to assess whether variation in body density also correlates with changes in pitch angle. For example, it might be predicted that animals in poorer, denser, body condition should make steeper dives in order to reduce overall transit costs to depth and spend a higher percentage of time foraging. Alternatively, poor condition animals may be more likely to transit horizontally, resulting in overall shallower pitch dives (Sato et al., 2003). Some initial records of pitch angle over entire feeding migrations of elephant seals indicate that pitch may not be strongly correlated with body density (T. Adachi, unpublished data).

Models based upon physics can be useful to describe the physical constraints under which animals evolve, and to make predictions of animal behaviour and physiology based upon those constraints (Houston et al., 2007). In this paper, we used simple forms of two different models to make predictions about $U_{\text{COT,min}}$, and the minimum COT itself, of a theoretical diver over a range of buoyancy conditions. It is assumed that evolution will favour swimming speed strategies that achieve the minimum COT (Watanabe et al., 2011), but speed of individuals may also be influenced by other motivational factors (Gallon et al., 2007). In order to simplify the models to evaluate the influence of buoyancy alone, we held basal metabolic rates, body mass and shape, and swimming efficiency variables constant. Of course, those conditions might not apply to animals in the real world. Leaner animals likely also have reduced mass and surface area than fat animals, which might somewhat alter the drag they experience (Vogel, 1994). Efficiency of muscle activity might also change over the extremes of force and speed conditions covered by the models. However, locomotory systems in divers seemed to be designed to cope with a wide range of variations in speed and force, and likely respond to maintain efficiency in the face of these variations (Rome, 1994; Rome, 1998). Actuator-disc theory estimates power based upon the thrust and induced speed across the disc, so a larger area disc will require a lower induced speed and therefore lower induced power. More research is needed to estimate the appropriate values for an actuator disc with the thrusting organs used by buoyant divers. Further analysis of the periodicity, shape and wake structure of thrusting in buoyant divers could examine how to more accurately apply actuator-disc theory to estimate swimming costs for these taxa (Ellington, 1984).

The active-to-passive drag ratio (λ) was set to 1.0 in all simulations, and no parameter for changes in profile drag from the oscillating thrust organ was included in the model. Though there is no consensus about a correct value for λ (see Aoki et al., 2011), it is plausible that total drag experienced by a swimmer could be greater during thrusting than gliding due to the oscillatory motion of the flippers and that this component of total drag could increase

as thrusting effort increases (Fish et al., 1988). If λ were much greater than 1.0, there may be a region of non-neutral buoyancy where COT is strongly reduced in the aided direction due to the benefit of prolonged gliding at lower drag forces than are experienced during thrusting. However, increased drag forces in the hindered direction as a consequence of profile drag during intense thrusting should lead to higher COT in the hindered direction than modelled here. Both models assumed constant speed throughout each transit, which may not be realistic in all conditions. Animals are thought to make use of stroke-and-glide swimming, during which speed oscillates around an apparent preferred speed (Aoki et al., 2011), when buoyancy aids swimming but not enough for prolonged gliding. It would be interesting to develop dynamic energetic models to consider whether and how such changes in swim speed might influence COT. In such a model, considerations of muscle efficiency and the active to passive drag ratio (λ) may be important.

Gliding at a shallow pitch angle effectively reduces the influence of buoyancy on the direction of movement as a function of $\sin(\theta)$. A shallower pitch angle naturally leads to more horizontal transit as function of $\cos(\theta)$. Production of lift to maintain a non-vertical gliding angle may be a means to convert gravitational potential energy into horizontal transit (Gleiss et al., 2011), but it cannot make vertical transit more efficient. Shallow pitch-angle gliding in the aided direction *via* production of lift necessarily increases induced drag, which would reduce gliding speeds in the aided direction with no corresponding benefit in the hindered transit direction.

Both models predict that extremes of body density away from neutral buoyancy should increase round-trip COT. Gliding at terminal velocity in the aided direction is the lowest COT strategy at extremes of body density away from neutral buoyancy, but the cost paid in the other direction will exceed those savings. It is likely to be very difficult to measure the influence of buoyancy on metabolic rate directly, given the difficulty of controlling the host of other factors that influence diving metabolic rates. Fahlman et al. (Fahlman et al., 2008) did not find evidence that experimental manipulation of body density away from neutral buoyancy caused diving metabolic rates to increase, and indeed proposed that Steller sea lions might adjust their diving lung volumes to compensate for experimental changes in their body density. Beck et al. (Beck et al., 2000) reported that dive duration and time spent in the bottom phase of dives was greater when animals were closer to neutral buoyancy, with no corresponding increase in surface intervals. Although dive duration may be influenced by many factors, such as prey availability (Lovvorn et al., 1991; Thompson and Fedak, 2001), the fact that surface interval duration did not increase with dive duration in Beck et al.'s (Beck et al., 2000) study suggests that transit to and from depth was more efficient when animals were closer to neutral buoyancy. If so, there may be a locomotion cost associated with extreme variations in energy reserves, when those variations cause total body density to deviate strongly from neutral buoyancy.

APPENDIX

Sensitivity analyses for active-passive drag ratios and pitch angle

If active drag is greater than passive drag ($\lambda > 1$; supplementary material Fig. S1, left, and Fig. S2, left), then the cost of thrusting necessarily increases as drag forces are greater. This also means that the minimum COT speed decreases. In this case, the cost of thrusting in the hindered direction increases even more than when $\lambda = 1$, with no benefit in the aided direction, as gliding at terminal speed is still the best option. Indeed, any additional thrusting is even

more costly, so the COT curve increases very steeply away from the minimum COT point. Thus, when $\lambda > 1.0$, the increase in round-trip COT with deviations in body density away from neutral buoyancy is still apparent.

When $\lambda < 1$ (supplementary material Fig. S1, right, and Fig. S2, right), the costs of stroking in both directions decreases. This causes the predicted minimum COT speed in both directions to increase as drag forces are essentially lower. Also, the increase in COT away from the minimum COT point becomes less steep as there is less additional cost to thrusting to a greater speed than that achieved by gliding. However, the same result exists that the savings in the aided direction are not equal to those in the hindered direction once prolonged gliding does start. Of course, if $\lambda \ll 1$, then we might expect gliding to never occur as thrusting would always be very efficient.

As expected, a non-vertical pitch angle has a higher COT to depth than a vertical pitch angle (supplementary material Figs S3 and S4), but the influence of buoyancy on the round-trip costs is unchanged.

From this we can conclude that the influence of non-neutral buoyancy on round-trip COT or the behaviour patterns predicted by the model is not highly sensitive to the active-passive drag ratio or the diving pitch angle.

LIST OF SYMBOLS AND ABBREVIATIONS

a	basal metabolic rate
A	area of the actuator disc
A_{body}	reference surface area of the body
C_d	drag coefficient
C_L	locomotor cost
COT	cost-of-transport
F_b	buoyancy force or buoyant force
F_d	drag force
g	gravitational acceleration (9.8 m s^{-2})
GMR	gross metabolic rate
LME	linear mixed effects
P_{ind}	Induced power
R	flipper length
SRDL	satellite relay data logger
T	thrust
u	swim speed
$U_{\text{COT,min}}$	minimum cost-of-transport speed
V_{animal}	volume of the animal body
v_i	induced velocity across actuator disc
ε_{pA}	product of propeller and chemical efficiencies
λ	active-to-passive drag ratio
ρ_{animal}	density of the animal body
ρ_{sw}	density of the surrounding seawater
ρ_w	density of the surrounding fluid
Φ	stroke amplitude in radians
θ	pitch angle

ACKNOWLEDGEMENTS

We would like to thank the many collaborators under the SeaOS project, including the Hindell and Costa laboratories, under which the elephant seal tagging work was carried out. Thanks to Mark Johnson and Robert Dudley for insightful comments and to Taiki Adachi for sharing unpublished data on the pitch angles of diving elephant seals.

FUNDING

Funding support was provided by a grant from the National Environment Research Council (NERC NE/c00311X/1).

REFERENCES

- Aoki, K., Watanabe, Y. Y., Crocker, D. E., Robinson, P. W., Biuw, M., Costa, D. P., Miyazaki, N., Fedak, M. A. and Miller, P. J. O. (2011). Northern elephant seals adjust gliding and stroking patterns with changes in buoyancy: validation of at-sea metrics of body density. *J. Exp. Biol.* **214**, 2973–2987.

- Beck, C. A., Bowen, W. D. and Iverson, S. J. (2000). Seasonal changes in buoyancy and diving behaviour of adult grey seals. *J. Exp. Biol.* **203**, 2323-2330.
- Biuw, M., McConnell, B., Bradshaw, C. J. A., Burton, H. and Fedak, M. (2003). Blubber and buoyancy: monitoring the body condition of free-ranging seals using simple dive characteristics. *J. Exp. Biol.* **206**, 3405-3423.
- Breiman, L. (2001). Random forests. *Mach. Learn.* **45**, 5-32.
- Cook, T. R., Kato, A., Tanaka, H., Ropert-Coudert, Y. and Bost, C.-A. (2010). Buoyancy under control: underwater locomotor performance in a deep diving seabird suggests respiratory strategies for reducing foraging effort. *PLoS ONE* **5**, e9839.
- Davis, R. W. and Weihs, D. (2007). Locomotion in diving elephant seals: physical and physiological constraints. *Philos. Trans. R. Soc. Lond. B* **362**, 2141-2150.
- Ellington, C. P. (1984). The aerodynamics of hovering insect flight. V. A vortex theory. *Philos. Trans. R. Soc. Lond. B* **305**, 115-144.
- Fahlman, A., Hastie, G. D., Rose, D. A. S., Naito, Y. and Trites, A. W. (2008). Buoyancy does not affect diving metabolism during shallow dives in Steller sea lions *Eumetopias jubatus*. *Aquat. Biol.* **3**, 147-154.
- Falke, K. J., Hill, R. D., Qvist, J., Schneider, R. C., Guppy, M., Liggins, G. C., Hochachka, P. W., Elliott, R. E. and Zapol, W. M. (1985). Seal lungs collapse during free diving: evidence from arterial nitrogen tensions. *Science* **229**, 556-558.
- Fedak, M. A., Anderson, S. S. and Curry, M. G. (1983). Attachment of a radio tag to the fur of seals. *J. Zool.* **200**, 298-300.
- Fedak, M. A., Lovell, P. and Grant, S. M. (2001). Two approaches to compressing and interpreting time-depth information as collected by time-depth recorders and satellite linked data loggers. *Mar. Mamm. Sci.* **17**, 94-110.
- Fedak, M., Lovell, P., McConnell, B. and Hunter, C. (2002). Overcoming the constraints of long range radio telemetry from animals: getting more useful data from smaller packages. *Integr. Comp. Biol.* **42**, 3-10.
- Feldkamp, S. D. (1987). Swimming in the California sea lion: morphometrics, drag and energetics. *J. Exp. Biol.* **131**, 117-135.
- Fish, F. E., Innes, S. and Ronald, K. (1988). Kinematics and estimated thrust production of swimming harp and ringed seals. *J. Exp. Biol.* **137**, 157-173.
- Gallon, S. L., Sparling, C. E., Georges, J.-Y., Fedak, M. A., Biuw, M. and Thompson, D. (2007). How fast does a seal swim? Variations in swimming behaviour under differing foraging conditions. *J. Exp. Biol.* **210**, 3285-3294.
- Gleiss, A. C., Norman, B. and Wilson, R. O. (2011). Moved by that sinking feeling: variable diving geometry underlies movement strategies in whale sharks. *Funct. Ecol.* **25**, 595-607.
- Gosler, A. G., Greenwood, J. J. D. and Perrins, C. (1995). Predation risk and the cost of being fat. *Nature* **377**, 621-623.
- Hansen, E. S. and Ricklefs, R. E. (2004). Foraging by deep-diving birds is not constrained by an aerobic diving limit: a model of avian depth-dependent diving metabolic rate. *Am. Nat.* **163**, 358-374.
- Hays, G., Marshall, G. J. and Seminoff, J. A. (2007). Flipper beat frequency and amplitude changes in diving green turtles, *Chelonia mydas*. *Mar. Biol.* **150**, 1003-1009.
- Hooker, S. K., Miller, P. J. O., Johnson, M. P., Cox, O. P. and Boyd, I. L. (2005). Ascent exhalations of Antarctic fur seals: a behavioural adaptation for breath-hold diving? *Proc. R. Soc. Lond. B* **272**, 355-363.
- Houston, I. H., Stephens, P. A., Boyd, I. L., Harding, K. C. and McNamara, J. M. (2007). Capital or income breeding? A theoretical model of female reproductive strategies. *Behav. Ecol.* **18**, 241-250.
- Johnson, W. (1994). *Helicopter Theory*. New York: Courier Dover Publications.
- Kooyman, G. L. (1989). *Diverse Divers: Physiology and Behaviour*. Berlin: Springer-Verlag.
- Lovvorn, J. R. and Jones, D. R. (1991). Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks (*Aythya* spp.). *Can. J. Zool.* **69**, 2879-2887.
- Lovvorn, J. R., Jones, D. R. and Blake, R. W. (1991). Mechanics of underwater locomotion in diving ducks: drag, buoyancy, and acceleration in a size gradient of species. *J. Exp. Biol.* **159**, 89-105.
- Lovvorn, J. R., Watanuki, Y., Kato, A., Naito, Y. and Liggins, G. A. (2004). Stroke patterns and regulation of swim speed and energy cost in free-ranging Brünnich's guillemots. *J. Exp. Biol.* **207**, 4679-4695.
- McMahon, C. R., Burton, H., McLean, S., Slip, D. and Bester, M. (2000). Field immobilisation of southern elephant seals with intravenous tiletamine and zolazepam. *Vet. Rec.* **146**, 251-254.
- Miller, P. J. O., Johnson, M. P., Tyack, P. L. and Terray, E. A. (2004). Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *J. Exp. Biol.* **207**, 1953-1967.
- Ng, P. and Maechler, M. (2007). A fast and efficient implementation of qualitatively constrained quantile smoothing splines. *Stat. Model.* **7**, 315-328.
- Pinheiro, J. C. and Bates, D. M. (2000). *Mixed-Effects Models in S and S-PLUS*. New York: Springer.
- Ribak, G., Weihs, D. and Arad, Z. (2005). Submerged swimming of the great cormorant *Phalacrocorax carbo sinensis* is a variant of the burst-and-glide gait. *J. Exp. Biol.* **208**, 3835-3849.
- Rome, L. C. (1994). The mechanical design of the muscular system. *Adv. Vet. Sci. Comp. Med.* **38A**, 125-179.
- Rome, L. C. (1998). Some advances in integrative muscle physiology. *Comp. Biochem. Physiol.* **120B**, 51-72.
- Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B. and Naito, Y. (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *J. Exp. Biol.* **206**, 1461-1470.
- Sato, K., Watanuki, Y. and Naito, Y. (2006). The minimum air volume kept in diving Adélie penguins: evidence for regulation of air volume in the respiratory system. *Coastal Mar. Sci.* **30**, 439-442.
- Sato, K., Shiomi, K., Watanabe, Y., Watanuki, Y., Takahashi, A. and Ponganis, P. J. (2010). Scaling of swim speed and stroke frequency in geometrically similar penguins: they swim optimally to minimize cost of transport. *Proc. R. Soc. Lond. B* **277**, 707-714.
- Sato, K., Shiomi, K., Marshall, G., Kooyman, G. L. and Ponganis, P. J. (2011). Stroke rates and diving air volumes of emperor penguins: implications for dive performance. *J. Exp. Biol.* **214**, 2854-2863.
- Skrovan, R. C., Williams, T. M., Berry, P. S., Moore, P. W. and Davis, R. W. (1999). The diving physiology of bottlenose dolphins (*Tursiops truncatus*). II. Biomechanics and changes in buoyancy at depth. *J. Exp. Biol.* **202**, 2749-2761.
- Sumich, J. L. (1983). Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, *Eschrichtius robustus*. *Can. J. Zool.* **61**, 647-652.
- Thompson, D. and Fedak, M. A. (2001). How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Anim. Behav.* **61**, 287-296.
- Thompson, D., Hiby, A. R. and Fedak, M. A. (1993). How fast should I swim? Behavioural implications of diving physiology. *Symp. Zool. Soc. Lond.* **66**, 349-368.
- Tucker, V. A. (1975). The energetic cost of moving about. *Am. Sci.* **63**, 413-419.
- Tyack, P. L., Johnson, M., Soto, N. A., Sturlese, A. and Madsen, P. T. (2006). Extreme diving of beaked whales. *J. Exp. Biol.* **209**, 4238-4253.
- Videler, J. J. and Nolet, B. A. (1990). Costs of swimming measured at optimum speed: scale effects, differences between swimming styles, taxonomic groups and submerged and surface swimming. *Comp. Biochem. Physiol.* **97A**, 91-99.
- Vogel, S. (1994). *Life in Moving Fluids: the Physical Biology of Flow*. Princeton, NJ: Princeton University Press.
- Wakeling, J. M. and Ellington, C. P. (1997). Dragonfly flight. III. Lift and power requirements. *J. Exp. Biol.* **200**, 583-600.
- Watanabe, Y., Baranov, E. A., Sato, K., Naito, Y. and Miyazaki, N. (2006). Body density affects stroke patterns in Baikal seals. *J. Exp. Biol.* **209**, 3269-3280.
- Watanabe, Y. Y., Sato, K., Watanuki, Y., Takahashi, A., Mitani, Y., Amano, M., Aoki, K., Narazaki, T., Iwata, T., Minamikawa, S. et al. (2011). Scaling of swim speed in breath-hold divers. *J. Anim. Ecol.* **80**, 57-68.
- Webb, P. M., Crocker, D. E., Blackwell, S. B., Costa, D. P. and Boeuf, B. J. (1998). Effects of buoyancy on the diving behavior of northern elephant seals. *J. Exp. Biol.* **201**, 2349-2358.
- Weis-Fogh, T. (1972). Energetics of hovering flight in hummingbirds and in *Drosophila*. *J. Exp. Biol.* **56**, 79-104.
- Williams, T. M., Kooyman, G. L. and Croll, D. A. (1991). The effect of submergence on heart rate and oxygen consumption of swimming seals and sea lions. *J. Comp. Physiol. B* **160**, 637-644.
- Williams, T. M., Davis, R. W., Fuiman, L. A., Francis, J., Le Boeuf, B. J., Horning, M., Calambokidis, J. and Croll, D. A. (2000). Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* **288**, 133-136.
- Williams, T. M., Fuiman, L. A., Horning, M. and Davis, R. W. (2004). The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the stroke. *J. Exp. Biol.* **207**, 973-982.

Fig. S1. Results for active-passive drag ratios of 2.0 (left) and 0.5 (right) for the standard model.

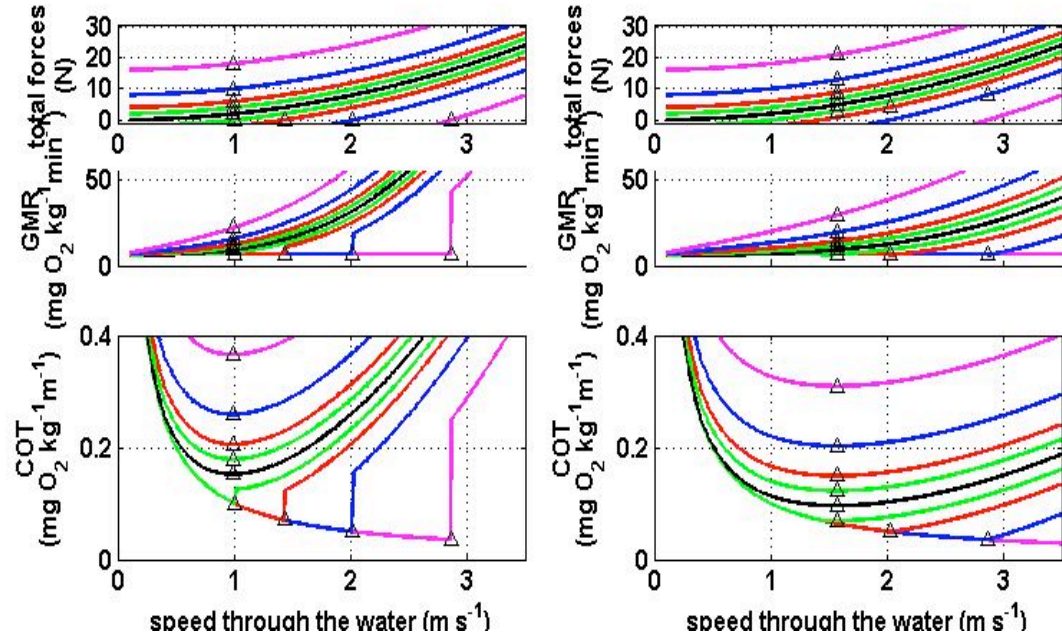


Fig. S2. Summary results for the external work model for active-passive drag ratios of 2.0 (left) and 0.5 (right).

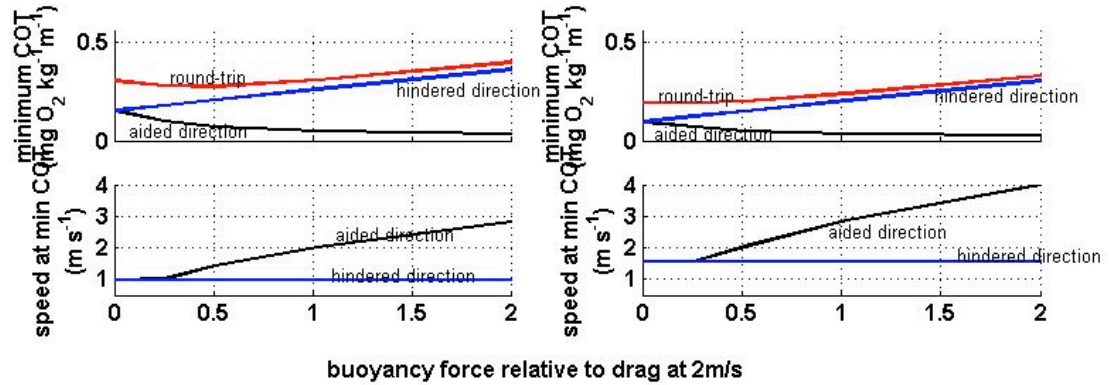


Fig. S3. Results for the external work model at 30 deg pitch. Model run with the same input parameters as Fig. 2, right in the main paper. Note that the total forces achieved (top) are less than in Fig. 2 because the buoyancy forces are smaller by $\sin(30 \text{ deg})$, or 50%. Note, however, that the other patterns in the model are the same.

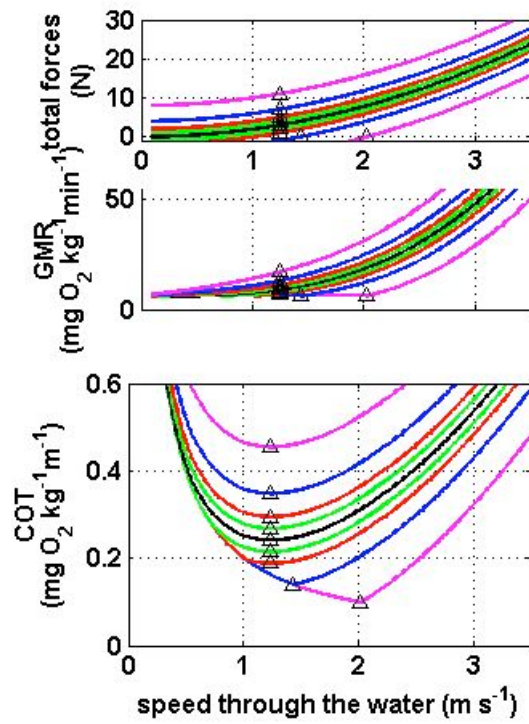


Fig. S4. Summary of external work model with pitch angle set to 30 deg. As in Fig. S3, total buoyancy forces are smaller by $\cos(30 \text{ deg})$, or 50%. Note also that round-trip COT at the most extreme buoyancy (top, red line) is $0.74 \text{ mg O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ at 30 deg, double that at 90 deg pitch.

