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Permalink

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Journal

Proceedings of the Royal Society B, 281(1797)

ISSN

0962-8452

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Publication Date

2014-12-22

DOI

10.1098/rspb.2014.2120

Peer reviewed

The foraging benefits of being fat in a highly migratory marine mammal

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Foraging theory predicts that breath-hold divers adjust the time spent foraging at depth relative to the energetic cost of swimming, which varies with buoyancy (body density). However, the buoyancy of diving animals varies as a function of their body condition, and the effects of these changes on swimming costs and foraging behaviour have been poorly examined. A novel animal-borne accelerometer was developed that recorded the number of flipper strokes, which allowed us to monitor the number of strokes per metre swam (hereafter, referred to as strokes-per-metre) by female northern elephant seals over their months-long, oceanic foraging migrations. As negatively buoyant seals increased their fat stores and buoyancy, the strokes-per-metre increased slightly in the buoyancy-aided direction (descending), but decreased significantly in the buoyancy-hindered direction (ascending), with associated changes in swim speed and gliding duration. Overall, the round-trip strokes-per-metre decreased and reached a minimum value when seals achieved neutral buoyancy. Consistent with foraging theory, seals stayed longer at foraging depths when their round-trip strokes-per-metre was less. Therefore, neutrally buoyant divers gained an energetic advantage via reduced swimming costs, which resulted in an increase in time spent foraging at depth, suggesting a foraging benefit of being fat.

1. Introduction

Efficient foraging is invaluable for an animal striving to maintain the positive energy balance that is required for survival and reproduction [1]. The energy balance of foraging animals is determined by the difference between energy intake from prey ingestion and energy expenditure associated with foraging activities. As animals often search for or transit to aggregations of prey over long distances, locomotor costs (i.e. energy costs expended in propulsive activities) are a major component of the energy expended while foraging [2]. This is especially the case for breath-hold divers, as they repeatedly dive to search for and feed on prey by way of energetically expensive swimming [3,4].

Foraging theory predicts that breath-hold divers adjust time spent foraging at depth depending on food abundance as well as the energetic cost of swimming [5–8]. Changes in swimming costs are likely to have strong influences on time spent foraging at depth, and thus foraging efficiency [6]. For example, a reduction in swimming costs may allow for longer foraging durations at depth by saving oxygen that would have been used for transit to and from foraging depths [9,10]. However, previous empirical studies have mostly focused on the effects of food abundance rather than the effect of changes in swimming costs on foraging strategies (but see [11,12]).

Buoyancy affects the swimming costs of aquatic animals via effects on swimming behaviour, such as stroking frequency, glide duration or pitch angle. The relationship between buoyancy and swimming strategy may apply across a range of aquatic animals, from fishes to whales (e.g. fish [13,14], diving mammals [15–17], birds [18–20] and sea turtles [21]), representing transitions from

continuous stroking, to stroking-and-gliding, to prolonged gliding as buoyancy aids in generating thrust force along the swimming path. Previous studies suggest that marine mammals may reduce swimming costs by employing prolonged gliding aided by negative buoyancy during the descent phase of dives [15,16,22]. This was confirmed by experimental modification of buoyancy in seals [17,23]. However, the apparent benefits of negative buoyancy to swimming costs are less clear when the round-trip cost to and from foraging depths is considered, because divers that are aided by negative buoyancy during descent need to increase swimming effort to overcome negative buoyancy during ascent [16,17,23,24]. A modelling study suggested that the round-trip cost of transit to the foraging depth should be minimal when divers are neutrally buoyant [25]. This prediction has not been fully tested under natural conditions owing to the technological difficulties of measuring the swimming costs of free-ranging animals in relation to significant changes in their buoyancy that can occur as fat stores increase while foraging at sea (e.g. [26,27]).

Measuring the energetic cost of swimming has been a major focus of bioenergetics studies on marine animals [28]. Previous studies estimated the energetic costs of swimming using measurements of heart rates or isotope dilution rates (see [28,29] for a review), but these approaches have some limitations in time resolution or in the requirement of surgical skills to implant loggers. An alternative approach is to quantify the behaviour of animals to estimate swimming costs. A key behavioural parameter is flipper stroking frequency because the number of strokes and the dynamic acceleration caused by stroking correlate linearly with oxygen consumption in a variety of species [30–34] (but see [35]). Accelerometry is an effective method to measure propulsive strokes, which are recorded as oscillating acceleration signals at high sampling rates (usually more than 10 Hz). However, recording at high sampling rates limits the recording period owing to limitations in logger memory or battery power [36]. Only one study, which used accelerometry, showed a change in stroking effort of southern elephant seals over their post-breeding foraging migrations (less than 80 days), but the study mainly focused on the validation of estimating seal density using stroking effort and swim speed [37]. The paucity of long-term acceleration data has hindered further understanding of the relationships among buoyancy, swimming costs and foraging behaviour in long distance migrants such as highly pelagic marine animals.

To overcome these limitations, we developed a novel instrument that summarizes the predetermined acceleration signals (i.e. flipper strokes) from high-frequency raw data to allow long recording durations (150 days at maximum). We used this new long-term accelerometry technique to: (i) continuously track the swimming costs of female northern elephant seals *Mirounga angustirostris* during their months-long oceanic foraging migrations, where seal buoyancy shifted from highly negative to neutral; (ii) evaluate how natural changes in seal buoyancy affect swimming costs; and (iii) test whether changes in swimming costs affect time spent foraging at depth.

2. Material and methods

(a) Device design and attachment

(i) Field experiments
We investigated the at-sea swimming behaviour of 14 female northern elephant seals during their months-long oceanic foraging migrations. Fieldwork was conducted at the Año Nuevo State Reserve, CA, USA (37°5′ N, 122°16′ W) during the seals' breeding season ($n = 7$, addressing the two-month post-breeding foraging migration (February–April), hereafter referred to as the short foraging migration) and moulting season ($n = 7$, addressing the seven-month post-moulting foraging migration (June–December), hereafter referred to as the long foraging migration), in 2011 and 2012. Each seal was immobilized with an intramuscular injection of Telazol (Tiletamine hydrochloride and Zolazepam hydrochloride, Fort Dodge Animal Health, Fort Dodge, IA, USA) to allow for the attachment of data loggers. Body mass and other morphometric measurements were obtained using standard protocols [38,39]. Upon return from their foraging migration, seals were immobilized for the recovery of the data loggers and collection of post-deployment measurements.

Each seal was equipped with a 'Stroke Logger' (see the next section), a 0.5 W ARGOS transmitter (Wildlife Computers, Redmond, WA, USA) and a VHF transmitter (ATS, Isanti, MN, USA). The data loggers were wrapped in rubber splicing tape and glued to the animal's back (Stroke Logger and VHF transmitter) and head (ARGOS transmitter) using 5 min epoxy with high-tension mesh netting and cable ties.

(ii) Instruments
Stroke Loggers (Little Leonardo Co., Tokyo, Japan; diameter 20.2 and 20.2 mm, length 73 and 96.8 mm, mass 48 and 68 g, for post-breeding and post-moulting deployments, respectively) are designed to detect stroking behaviour and pitch angles using measurements of acceleration at a high sampling rate (32 Hz) with an on-board data-processing algorithm. The use of the algorithm and storage of summary data every 5 s allowed for a long recording duration. Stroke Loggers have a depth sensor and a two-axis acceleration sensor (along the longitudinal and lateral body axes). Depth data were recorded every 5 s. Raw longitudinal accelerations (measured at 32 Hz) were averaged every 5 s to extract the gravity vector (i.e. posture; see [16]), and the resulting values (-1 to $+1g$) were converted into pitch angles by arcsin(longitudinal acceleration)*$180/\pi$ [16], assuming that the longitudinal axis of a seal matches that of the logger. Swim speed was calculated using a trigonometric function with depth and pitch angle data (i.e. $\triangle$ depth/$\sin\theta$). Lateral acceleration data were used to compute the number of strokes every 5 s. Lateral accelerations often contain low-frequency variations (i.e. static accelerations) that presumably relate to various turning and rolling movements (i.e. changes in posture) by seals [16]. High-pass filtering has been applied to separate the static accelerations from raw lateral accelerations to obtain dynamic accelerations associated with propulsive activities (i.e. flipper strokes) of seals (e.g. [16,17]). In this study, we developed a simple on-board data-processing algorithm by using moving averages to obtain dynamic accelerations, instead of high-pass filtering algorithm, to reduce the battery consumption of loggers (see the electronic supplementary material, figure S1, for more detail about the algorithm). The new algorithm gave us dynamic accelerations (electronic supplementary material, figure S1) and number of strokes (electronic supplementary material, figure S2) that closely matched those obtained by the high-pass filtering method [16,17]. The resulting number of strokes (i.e. a cycle of swaying hind flippers) were counted and recorded every 5 s.

(b) Data analysis
(i) Dive phase definition
Time at first dive was set as the start of the oceanic migration and each dive was defined using a minimum depth of 10 m. Descent, bottom and ascent phases of the dive were defined as follows (as per [23]): (i) descent phase was the period from the start of a dive to the first time when the rate of depth change was negative;

(ii) bottom phase was the period between the end of the descent phase and the beginning of the ascent phase; and (iii) ascent phase was the period from the last time when the rate of depth change was positive to the end of the dive. We considered the descent and the ascent phases as transit phases, and the bottom phase as the time spent at foraging depth [40].

(ii) Calculating number of strokes per metre swam and time spent in prolonged gliding during the transit phase

We calculated locomotor costs of swimming as the number of flipper strokes divided by the distance travelled during the transit phases of each dive (i.e. number of strokes per metre swam, hereafter referred to as strokes-per-metre), based on the idea that the number of flipper strokes correlates linearly with oxygen consumption [30,41]. The distance travelled was estimated with a trigonometric function using the rate of depth change and pitch angle ($\triangle$ depth/$\sin\theta$). Strokes-per-metre was calculated for the descent and the ascent phases of each dive, and the round-trip strokes-per-metre was defined as the sum of descent and ascent strokes-per-metre. Note that we calculated strokes-per-metre during the transit phases of each dive, not including the bottom phase, because our aim was to test whether the locomotor cost during transit affects time spent at foraging depth. For statistical analysis, the strokes-per-metre values for each dive were averaged to obtain a daily mean strokes-per-metre.

We calculated the proportion of time spent in prolonged gliding during the transit phases of each dive, because prolonged gliding is a key strategy to reduce swimming costs [15]. In this study, we defined prolonged gliding phases as any period during transit with no strokes for 5 s (the finest time resolution of the data from Stroke Loggers) or more. The total duration of prolonged gliding during the descent (or the ascent) phase was calculated for each dive, and then divided by the descent (or the ascent) duration to calculate the proportion of time spent in prolonged gliding during the transit phases of each dive. Then, those values were averaged daily for statistical analysis.

The total buoyancy of breath-hold divers changes with depth owing to residual air in the lungs, but this effect is reduced at greater depths because air volume decreases with depth following Boyle's law [27]. To minimize the effect of gases on buoyancy, we only used data from depths 100 m or more, as per Aoki et al. [23], because in this study we focused not on the effect of residual air but on the effect of body density on swimming costs.

(iii) Estimating seal buoyancy

We calculated drift rate (the vertical rate of passive descent or ascent while drifting through the water column, represented in $m\,s^{-1}$) during the so-called 'drift dives' [27] to estimate the buoyancy of the seal. The buoyancy of seals at depth is related to their relative amounts of adipose and lean tissue [42], making it possible to estimate changes in body density from their buoyancy, measured by drift rate [27]. Drift rate has strong positive correlations with body density obtained from isotope dilution analysis of body composition [23]. In this study, we constructed automated algorithms to select drift dives, detect drift phases and calculate drift rates by finding the inflection points in dive profiles. We modified the method described in Fedak et al. [43] by adding four criteria as follows: a drift phase should (i) have no depths less than 100 m (to minimize the effect of gases in the lungs on buoyancy as with calculating other swimming parameters), (ii) have no strokes (i.e. the seal is passively drifting through the water column), (iii) be longer than 20% of the total duration of the dive, and (iv) have little variance in depth change rate during the entire drift phase (i.e. mean-squared residual should be less than $5\,m^2$ as per Biuw et al. [27]). After running the automated algorithm, we excluded $5.3 \pm 5.8\%$ (mean $\pm$ s.d.) of drift rates as outliers by visual inspection of dive shape [44].

Then, $0.1\,m\,s^{-1}$ was added to all drift rate values of less than $-0.1\,m\,s^{-1}$, and $0.1\,m\,s^{-1}$ was subtracted from all drift rates values of more than $+0.1\,m\,s^{-1}$, to reduce the impact of abrupt transitions from -0.1 to $+0.1\,m\,s^{-1}$ (see [44] for a detailed discussion). Finally, we fitted a cubic spline to the drift rate data using a built-in function (interpolate2) in IGOR Pro v. 6.04 (WaveMetrics Inc., Lake Oswego, OR, USA) to estimate the daily drift rate (as per [44]). Finally, the daily estimates of drift rates were used for comparisons with daily-averaged values of other parameters.

(iv) Statistical analysis

Statistical analysis was carried out with R (v. 2.15.3, Foundation for Statistical Computing, Vienna, Austria). The lmer function in the lme4 package was used to fit generalized linear mixed models (GLMM). All GLMMs in this study included individual as a random effect. The mcmcsamp function in the coda package was used to calculate 95% confidence intervals (CI) for slopes. In GLMMs with multiple explanatory variables, Akaike's information criterion corrected for small sample size (AIC_c) was calculated to select the most parsimonious model having the lowest AIC_c value. Data are presented as means $\pm$ s.e. unless otherwise stated.

3. Results

Stroke Loggers tracked the swimming and diving behaviour of female northern elephant seals for the entire short, post-breeding foraging migration (78.1 ± 7.3 days, $n = 7$ seals) and for $61.4 \pm 3.5\%$ of the long, post-moulting foraging migration (139.9 ± 6.9 days, $n = 7$ seals) that lasted for 228.0 ± 5.9 days on average (mean $\pm$ s.d.). At the start of each migration, all 14 seals were negatively buoyant, as indicated by the negative drift rate values (figure 1; electronic supplementary material, figure S3). Seals gradually became more buoyant as they increased their fat stores while foraging over the course of the migration. All seals were still negatively buoyant at the end of the short foraging migration, but five of seven seals became neutrally buoyant by the end of the recording period during the long foraging migration, as indicated by the drift rates being zero (i.e. seals neither sink nor rise during the drift phase [27]) (figure 1; electronic supplementary material, figure S3).

The data from the Stroke Loggers allowed us to monitor the changes in the locomotor costs of swimming of the seals during their migrations. As the migration progressed, strokes-per-metre increased during the descent phase but decreased during the ascent phase (figure 1; electronic supplementary material, figure S3). Round-trip strokes-per-metre, calculated as the sum of descent and ascent strokes-per-metre, gradually decreased, because ascent strokes-per-metre decreased more than descent strokes-per-metre increased (figures 1 and 2; electronic supplementary material, figure S3). Round-trip strokes-per-metre was lowest (approx. 0.25 strokes m^{-1}) when neutral buoyancy was achieved (figure 3a), where strokes-per-metre during the descent and the ascent phases of the dive was equivalent (figure 2; electronic supplementary material, figure S4). Drift rates had a positive relationship with descent strokes-per-metre (GLMM, slope mean = 0.386 with 95% CI of 0.370–0.402), but had a negative relationship with ascent strokes-per-metre (GLMM, slope mean = -1.009 with 95% CI of -1.027 to -0.989). Overall, drift rates had a negative relationship with round-trip strokes-per-metre (GLMM, slope mean = -0.622 with 95% CI of -0.641 to -0.604).
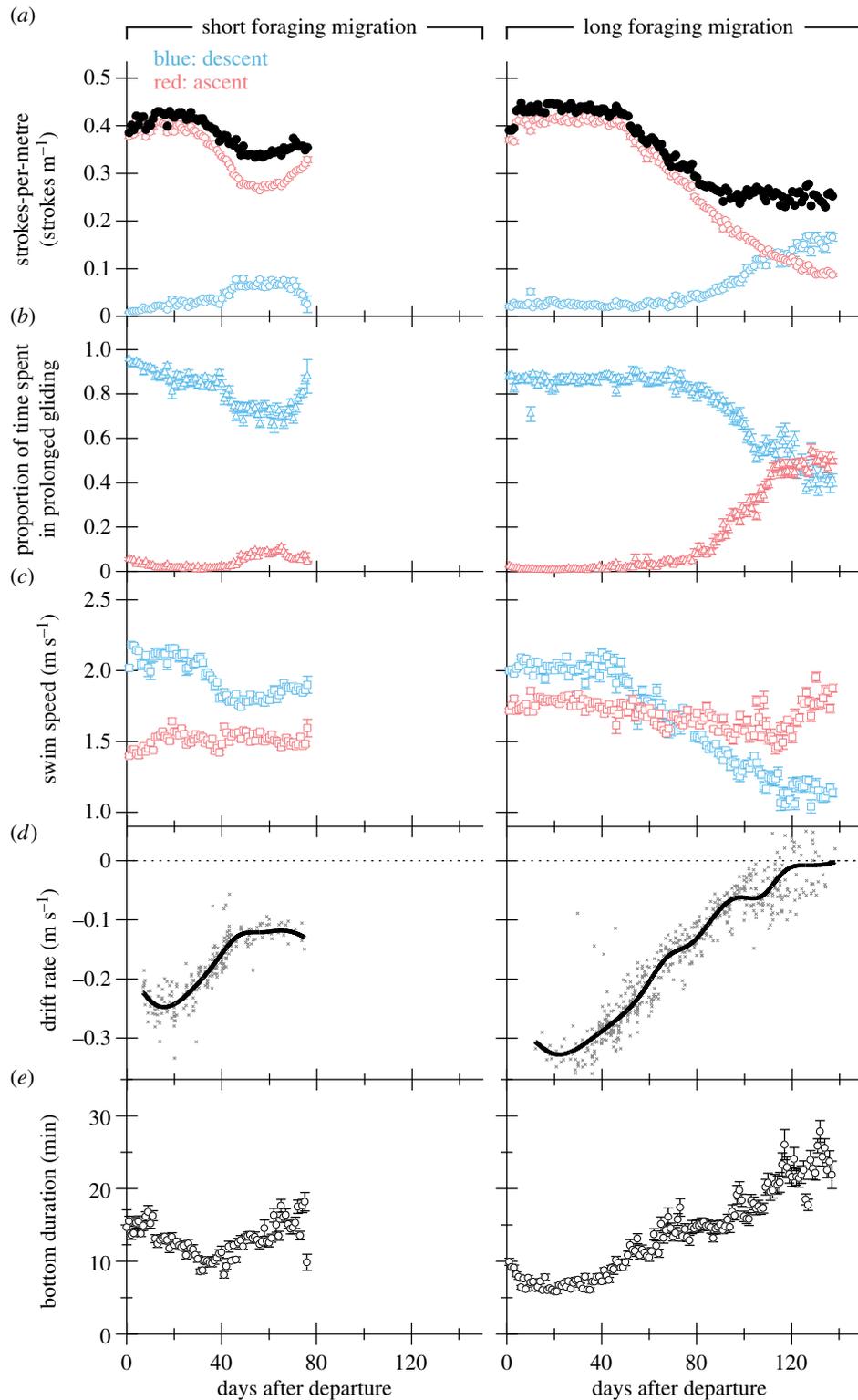
Figure 1. Examples of the time series for (*a*) strokes-per-metre (number of strokes per metre swam, represented in strokes m^{-1}), (*b*) the proportion of time spent in prolonged gliding, (*c*) swim speed, (*d*) drift rate and (*e*) bottom duration. Left and right panels each show one seal during the short (seal ID: T35) and long (seal ID: U754) foraging migration, respectively (all other 12 seals are shown in the electronic supplementary material, figure S3). In (*a*), open blue and red circles represent daily-averaged values of descent and ascent strokes-per-metre, respectively, with standard errors. Filled black circles represent round-trip strokes-per-metre, which is calculated as the sum of descent and ascent strokes-per-metre. In (*b*), open blue and red triangles represent daily-averaged values of the proportion of time spent in prolonged gliding during the descent and the ascent phases, respectively, with standard errors. In (*c*), open blue and red squares represent daily-averaged values of descent and ascent swim speed, respectively, with standard errors. In (*d*), grey cross marks represent drift rates calculated from each drift dive. Thick black lines represent interpolated values of drift rate. Grey dotted lines indicate neutral buoyancy (i.e. drift rate = 0). In (*e*), open black circles represent daily-averaged values of bottom duration with standard errors.

The proportion of time spent in prolonged gliding during the transit phases of each dive exhibited the opposite trend as did strokes-per-metre in response to changes in drift rates

(figures 1 and 2; electronic supplementary material, figure S3). As the migrations progressed, the proportion of time spent in prolonged gliding gradually decreased during the descent
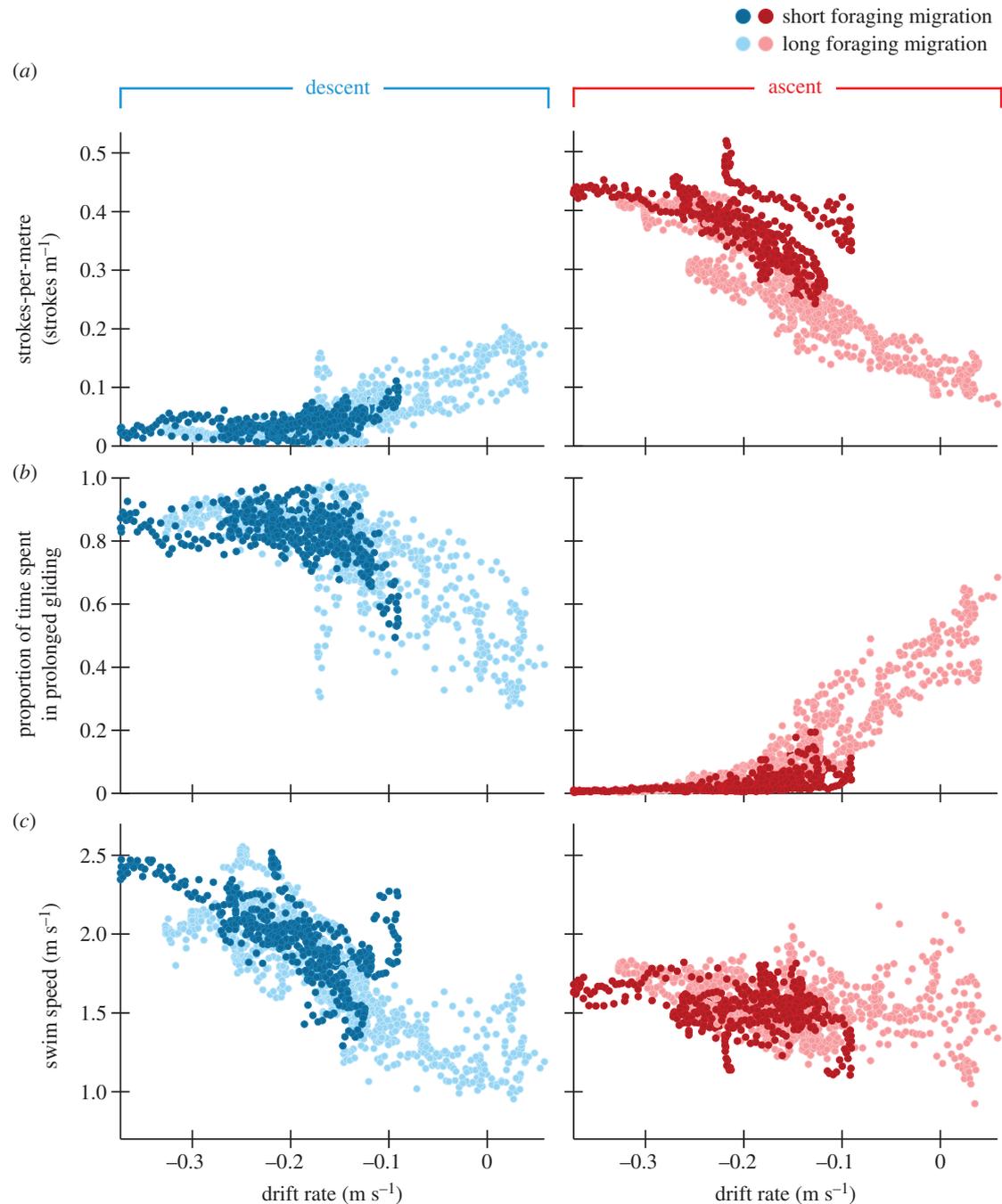
Figure 2. (*a*) Strokes-per-metre, (*b*) proportion of time spent in prolonged gliding, and (*c*) swim speed plotted against drift rates for all 14 individuals. Left and right panels show daily values of each parameter during the descent (blue colours) and the ascent (red colours) phases, respectively. Filled dark and light blue (or red) circles represent daily values for seals during short and long foraging migration, respectively.

phase, but gradually increased during the ascent phase (figure 1; electronic supplementary material, figure S3). Then, those values were equivalent at approximately 0.4 when neutral buoyancy was achieved (i.e. drift rate was 0) (figure 2). Drift rates had a negative relationship with the proportion of time spent in prolonged gliding during descent phase (GLMM, slope mean = −1.214 with 95% CI of −1.269 to −1.153) but had a positive relationship with that during ascent phase (GLMM, slope mean = 1.463 with 95% CI of 1.388–1.486).

Swim speed during the descent phase decreased largely from approximately 2.5 to 1.0 m s^{-1} as seals became more buoyant, but swim speed during the ascent phase remained around 1.5 m s^{-1} throughout the migrations (figures 1 and 2; electronic supplementary material, figures S3 and S4). Both descent and ascent swim speeds were affected by drift rates, but

descent swim speed was much more sensitive to changes in drift rates (GLMM, descent swim speed: slope mean = −3.27 with 95% CI of −3.36 to −3.19; ascent swim speed: slope mean = −0.55 with 95% CI of −0.62 to −0.47).

Pitch angle during the descent phase became steeper as drift rate increased (electronic supplementary material, figure S5; GLMM, slope mean = −74.2 with 95% CI of −80.2 to −68.1). However, pitch angle during the ascent phase was not significantly affected by drift rates (electronic supplementary material, figure S5; slope mean = −1.6 with 95% CI of −8.2 to 5.1), although pitch angles varied widely over the range of drift rates for both descent and ascent phases (electronic supplementary material, figure S5).

Transit duration during both descent and ascent phases slightly increased as seals became more buoyant (electronic
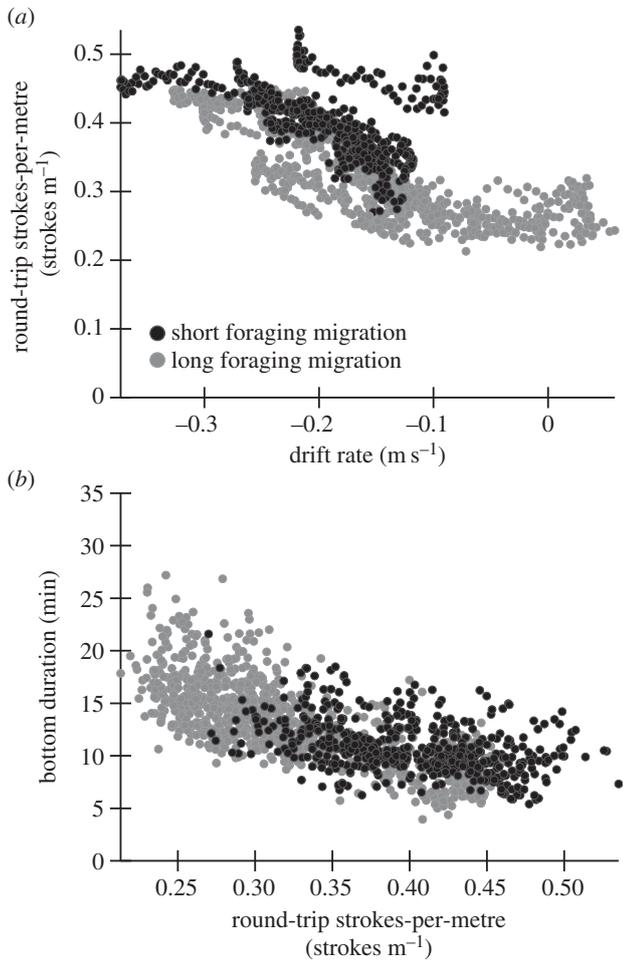
Figure 3. The relationships among drift rates, round-trip strokes-per-metre and bottom duration for all 14 individuals. (a) Round-trip strokes-per-metre, plotted against drift rates. (b) Bottom duration, plotted against round-trip strokes-per-metre. In both panels, filled black and grey circles represent daily values for seals during short and long foraging migration, respectively.

supplementary material, figure S6; GLMM, descent transit duration: slope mean of drift rate = 5.29 with 95% CI of 4.79–5.79; ascent transit duration: slope mean of drift rate = 5.30 with 95% CI of 4.88–5.73). Transit duration also increased with dive depth (electronic supplementary material, figure S6; GLMM, descent transit duration: slope mean of dive depth = 0.003 with 95% CI of 0.002–0.003; ascent transit duration: slope mean of dive depth = 0.003 with 95% CI of 0.002–0.003).

Seals spent more time at the bottom phases of dives (bottom duration) when seals approached neutral buoyancy (figure 1; electronic supplementary material, figures S3 and S7; GLMM, slope mean of drift rate = 35.9 with 95% CI of 34.5–37.3) and their round-trip strokes-per-metre decreased (figure 3b; GLMM, slope mean of round-trip strokes-per-metre = −48.9 with 95% CI of −50.9 to −46.8). Statistical analysis using AIC$_c$ showed that the most parsimonious model explaining bottom duration included round-trip strokes-per-metre but not dive depth (electronic supplementary material, table S1a). Also, dive efficiency (i.e. bottom duration per dive cycle, which is composed of transit time, bottom time and post-surface time) increased as round-trip strokes-per-metre decreased (electronic supplementary material, figure S8), although dive depth also had a slight effect on dive efficiency (electronic supplementary material, table S1b).

4. Discussion

(a) Buoyancy determines locomotor costs of swimming

Using long-term accelerometry, we demonstrated that the round-trip locomotor cost of swimming (round-trip strokes-per-metre) decreased as female northern elephant seals approached neutral buoyancy during their oceanic foraging migrations. The reduction of round-trip locomotor costs (figure 3a) was caused by the small increase in descent strokes-per-metre (buoyancy-aided direction) relative to the large decrease in ascent strokes-per-metre (buoyancy-hindered direction) (figure 2), which means that buoyancy changes affect strokes-per-metre in opposite ways and with different magnitudes according to the vertical direction of the swimming path.

The different trends in descent and ascent strokes-per-metre could be explained by changes in stroking effort and time spent in prolonged gliding in relation to buoyancy changes. During descent, the proportion of time spent in prolonged gliding remained high when seals were negatively buoyant (range = 0.4–0.9; figure 2). This indicates that seals largely relied on negative buoyancy as the thrust force for gliding, which kept their stroking effort low [15,17]. In addition, descent pitch angles were steeper when seals were more buoyant (electronic supplementary material, figure S5), which might allow seals to descend with less stroking activity because a steeper pitch angle would bring the vector of forward motion closer to that of the force of gravity [16]. For these reasons, descent strokes-per-metre stayed low, compared with ascent strokes-per-metre, over a range of negative buoyancy values (figure 2). During ascent, negatively buoyant seals employed prolonged gliding less than during descent (figure 2). This is probably because seals had to generate thrust force by actively stroking to overcome negative buoyancy. In fact, strokes-per-metre at negative buoyancy was higher during ascent than during descent (figure 2). As buoyancy increased, seals were able to ascend with less thrust force from active stroking. Hence, ascent strokes-per-metre decreased largely as seals approached neutral buoyancy (figure 2). Overall, round-trip strokes-per-metre decreased as seals approached neutral buoyancy (figure 3a).

The changes in strokes-per-metre and time spent in prolonged gliding were reflected in changes in swim speed. During descent, negatively buoyant seals largely relied on gliding (figure 2). Gliding speed is expected to decrease as seals approach neutral buoyancy [17,25]. In accordance with this prediction, descent swim speed decreased as seals approached neutral buoyancy (figure 2; electronic supplementary material, figure S4). By contrast, during ascent, negatively buoyant seals employed active stroking (high ascent strokes-per-metre) more than prolonged gliding (figure 2). Seals appeared to adjust stroking effort depending on buoyancy changes to maintain a narrow range of ascent swim speeds (figure 2; electronic supplementary material, figure S4), which might reflect a swim speed that minimizes swimming costs in the buoyancy-hindered direction [25,45,46].

Here, we present the close relationships among locomotor costs of swimming (strokes-per-metre), time spent in prolonged gliding and swim speed (figure 2). These results show a remarkable agreement with a biomechanical model by Miller et al. [25] that predicted increased round-trip swimming costs as body density deviates from neutral buoyancy. Miller et al. [25] also predicted that round-trip swimming costs would not change largely around neutral buoyancy,

which is again supported by our results (figure 3*a*). Seals around neutral buoyancy displayed similar swimming behaviours during descent and ascent, including similar values for proportion of time spent in prolonged gliding and swim speed (figure 2), suggesting the effects of buoyancy changes on strokes-per-metre are similar for both descent and ascent swimming directions around neutral buoyancy.

(b) Locomotor costs of swimming affect foraging time

Bottom duration increased significantly (from approx. 10 to 20 min) with decreasing round-trip locomotor costs of swimming during transit (from approx. 0.5 to 0.25 strokes m^{-1}), as seals' buoyancy changed from highly negative to neutral (figure 3). The results suggest that reduced oxygen consumption for locomotor movements during transit might contribute to prolong bottom duration [37,47,48]. Prolonged bottom duration (figure 3*b*) will probably allow seals to increase the energy gained during foraging, as northern elephant seals forage primarily at the bottom of their dives [40]. In addition, increased dive efficiency (i.e. increased bottom duration per dive cycle, shown in the electronic supplementary material, figure S8) suggests that seals gained a foraging benefit from achieving neutral buoyancy by being fat. A similar foraging benefit has also been suggested in a study [37] that assessed the relationship among stroking effort and dive duration in southern elephant seals, a species that undergoes similarly significant changes in their body density (buoyancy) during oceanic migrations [27].

Other, not mutually exclusive, factors may partly explain why bottom duration increased as seals approached neutral buoyancy and decreased round-trip strokes-per-metre. First, the quality of a prey patch at foraging depth may affect bottom duration. For example, seals may prolong bottom duration to increase foraging effort in richer feeding grounds, an idea supported by theoretical and empirical studies on the diving behaviour of some seal species [7,49]. Second, changes in body size may affect bottom duration, because large body mass increases oxygen-carrying capacity while simultaneously reducing the rate of oxygen use, allowing seals to stay underwater longer [50,51]. Third, seasonal hypometabolism (i.e. decreased field metabolic rate) may also contribute to increased time spent at foraging depth [52,53]. Fourth, using flipper-beat frequency alone may miss a substantial part of kinematic variation (i.e. stroke amplitude) and hence energy expenditure during transit (e.g. [23]), possibly leading to the changes in bottom duration. Finally, bottom duration could increase owing to decreasing locomotor costs of swimming during bottom phase. The bottom phase of dives contains a series of vertical excursions (i.e. swim up and down; e.g. [40]), and the swimming costs during bottom phase may decrease as seals approach neutral buoyancy in the same manner to the transit phase. However, alternative hypotheses might explain the effect of prey patch quality or increased body size on bottom duration of dives. For example, higher prey patch quality may lead to decreased bottom duration depending on timescales [54,55], suggesting diving animals should stay longer at foraging depth as the patch quality declines [56,57]. In addition, increased body size may lead to decreased bottom duration by increasing swimming costs owing to increased drag force (i.e. because of increased cross-sectional area) [42]. Thus, these other factors may affect bottom duration of dives, but the magnitude of those effects

is still unclear, raising the need for further investigations about the factors determining the increased bottom duration with decreased round-trip locomotor costs (figure 3*b*).

One weakness in energetic estimates from accelerometry is that accelerometers do not provide information on changes in resting metabolic rates (i.e. maintenance cost) [34]. For a short-term study, one may be able to assume the same resting metabolic rates over the study period to estimate the total cost of transport (maintenance cost + locomotor cost) (e.g. [30]). However, for a long-term study such as ours, the resting metabolic rate of seals is likely to change largely owing to changes in body mass, state of pregnancy or seasonal hypometabolism (e.g. [52,58]), precluding us from quantitatively estimating the maintenance cost during dives (see the electronic supplementary material, figure S9, for our attempt to calculate round-trip gross energetic cost, which highlights the need for accurate measurement of maintenance cost in the field). In this study, more buoyant seals increased transit (descent and ascent) duration slightly (electronic supplementary material, figure S6), indicating that seals expended more energy for maintenance costs during transit to a foraging depth, which should somewhat counteract the energetic benefits gained from prolonging bottom duration. But in fact, bottom duration increased disproportionally larger with drift rates compared to transit durations (electronic supplementary material, figures S6 and S7), suggesting a significant effect of decreased locomotor costs on bottom duration (figure 3*b*). Nevertheless, quantitative energetic estimates of maintenance costs are needed to understand fully how seals allocate available oxygen to locomotion and foraging activities.

In summary, we successfully tracked changes in the locomotor cost of swimming in ocean-migrating seals by using long-term records of flipper strokes. Our results indicate the close associations among seal buoyancy, swimming costs and foraging behaviour; seal buoyancy appeared to affect not only locomotor costs via reductions in propulsive activities, but also foraging gains via increased time spent at foraging depth, suggesting a foraging benefit of achieving neutral buoyancy by being fat. We have shown that long-term accelerometry studies are a potentially powerful tool to study the locomotory and foraging strategies of a variety of free-ranging marine animals. While our study examined the effect of buoyancy changes in elephant seals, our results are relevant to other marine animals whose body composition varies with the increase and decrease in fat stores over their long foraging migrations. For example, grey seals and New Zealand fur seals like elephant seals are aided by negative buoyancy during the descent phase [26,59], suggesting that they passively glide on descent and stroke on ascent. However, right whales and deep-diving sperm whales are positively buoyant and stroke on descent and passively glide on ascent [60,61]. Given that the parameters which govern the costs of locomotion are the same, we would expect that these species also would have an increased cost of locomotion as they deviate from neutral buoyancy. Finally, a recent study shows that white sharks like elephant seals exhibit drift dives that reflect changes in their body composition and thus buoyancy over their long migrations [62]. Thus, deviations from neutral buoyancy may have locomotor effects in other large marine vertebrates as well. The locomotor costs of deviating from neutral buoyancy have an important implication on storing optimal amount of fat against food shortage or reproduction, especially in capital

breeding species in which fat storage during reproduction has clear fitness advantages [63].

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