

## RESEARCH ARTICLE

# Variation in body condition during the post-moult foraging trip of southern elephant seals and its consequences on diving behaviour

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**ABSTRACT**

Mature female southern elephant seals (*Mirounga leonina*) come ashore only in October to breed and in January to moult, spending the rest of the year foraging at sea. Mature females may lose as much as 50% of their body mass, mostly in lipid stores, during the breeding season due to fasting and lactation. When departing to sea, post-breeding females are negatively buoyant, and the relative change in body condition (i.e. density) during the foraging trip has previously been assessed by monitoring the descent rate during drift dives. However, relatively few drift dives are performed, resulting in low resolution of the temporal reconstruction of body condition change. In this study, six post-breeding females were equipped with time–depth recorders and accelerometers to investigate whether changes in active swimming effort and speed could be used as an alternative method of monitoring density variations throughout the foraging trip. In addition, we assessed the consequences of density change on the swimming efforts of individuals while diving and investigated the effects on dive duration. Both descent swimming speed and ascent swimming effort were found to be strongly correlated to descent rate during drift dives, enabling the fine-scale monitoring of seal density change over the whole trip. Negatively buoyant seals minimized swimming effort during descents, gliding down at slower speeds, and reduced their ascent swimming effort to maintain a nearly constant swimming speed as their buoyancy increased. One per cent of seal density variation over time was found to induce a 20% variation in swimming effort during dives with direct consequences on dive duration.

**KEY WORDS:** Body condition, Buoyancy, Speed, Swimming effort, *Mirounga leonina*

**INTRODUCTION**

The investigation of the temporal change in foraging success of top predators provides essential information on their ecology, as well as on the distribution of their prey. Such information is inherently difficult to obtain in marine ecosystems because of logistical constraints. However, since the development of the first time–depth recorders (TDRs) (Kooyman, 1965), a broad range of bio-logging

tools has become available to researchers. These instruments have enabled our understanding of foraging behaviour and its relationships to environmental and physiological variables to be refined in an increasing number of seabird and marine mammal species (Kooyman, 1965; Wilson, 1992; P  tz and Bost, 1994; Handrich et al., 1997; P  tz et al., 1998).

Recently, head-mounted accelerometers have been shown to provide reliable information on the occurrence of prey capture events in seals during extended foraging trips (Naito et al., 2010; Suzuki et al., 2009; Viviant et al., 2010; Gallon et al., 2013). This approach, however, does not provide information on the size and energy content (i.e. quality) of either the prey or the associated foraging costs, such that the energy gain by the individual cannot be assessed. In addition to the number of prey-catch events, data on energy expenditure, as well as the related change in body condition, are required to assess the type and quality of prey consumed. Indeed, the change in body condition reflects the ability of the animal to allocate excess assimilated food resources towards lipid stores when maintenance and foraging costs have been covered. Therefore, to assess prey quality, there is a need to estimate fine temporal changes in the condition of the seal, as well as the foraging costs.

In deep-diving phocid seals, such as the elephant seals (*Mirounga* spp.), the buoyancy of an individual is determined primarily by its body composition, in particular, by the ratio of lipid to lean tissue (Crocker et al., 1997; Webb et al., 1998). Lean tissue is denser than seawater, whereas adipose tissue is less dense and, therefore, animals with a large proportion of lipid will be more buoyant (Beck et al., 2000; Lovvorn and Jones, 1991a; Lovvorn and Jones, 1991b; Nowacek et al., 2001; Webb et al., 1998). Elephant seals regularly perform dives during which they spend a large proportion of time descending passively through the water column ('drift dives'). Monitoring of the descent rate during these dives has already been used to track density (i.e. lipid content) changes in elephant seals during their foraging trips (Crocker et al., 1997; Biuw et al., 2003). The vertical speed of elephant seals when descending passively is directly related to buoyancy, with more buoyant seals (i.e. with a higher lipid proportion) sinking at a slower rate, or even becoming positively buoyant, compared with leaner ones (Crocker et al., 1997; Biuw et al., 2003; Miller et al., 2012). However, such 'drift rate' data obtained from TDRs can only provide a general temporal trend in body composition change as few drift dives are detected daily (Dragon et al., 2012).

As the buoyancy of a seal is directly related to its density ( $\rho_{\text{animal}}$ ), variations in speed and effort during active swimming must be related to variation in its lipid and muscle proportions (Miller et al., 2012). Miller et al. (Miller et al., 2004) and Watanabe et al. (Watanabe et al., 2006) working on sperm whales (*Physeter macrocephalus*) and Baikal seals (*Phoca sibirica*), respectively,

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**List of symbols and abbreviations**

$a$	acceleration
$A$	frontal or surface area
$C_D$	drag coefficient
COT	cost of transport
Effort <sub>ascent</sub>	ascent swimming effort
$F_B$	buoyancy force
$F_D$	drag force
$g$	gravitational gravity ( $9.8 \text{ m s}^{-2}$ )
$G$	girth
$L$	length or size
$P_b$	proportion of total amount of the bones to body mass
$P_{bw}$	proportion of total amount of the body water to body mass
$P_l$	proportion of total amount of the lipid to body mass
$P_p$	proportion of total amount of the protein to body mass
$R$	radius
$S$	surface area
SES(s)	southern elephant seal(s)
TDR	time depth recorder
$U$	speed
$U_{\text{phase}}$	speed during the phase
$U_{\text{abs}}$	absolute speed
$U_{\text{hor}}$	horizontal speed
$U_{\text{vert}}$	vertical speed
$V$	volume
$\theta$	pitch
$\rho_{\text{animal}}$	density of the animal
$\rho_b$	density of the bone
$\rho_{bw}$	density of the body water
$\rho_{\text{drift}}$	density of the seal calculated by drift rates
$\rho_l$	density of the lipid
$\rho_p$	density of the protein
$\rho_{\text{seal}}$	density of the seal
$\rho_{sw}$	density of the sea water

showed that the variation of deceleration during glides and terminal speed during prolonged glides was a consequence of the variation in body condition as the buoyancy of animals changes with their density. Correspondingly, Watanabe et al. (Watanabe et al., 2006) demonstrated that body density can be estimated by speed and pitch during prolonged glides. Subsequently, in controlled experiments on northern elephant seals (*Mirounga angustirostris*), Aoki et al. (Aoki et al., 2011) have documented that individuals adjust their stroke patterns in relation to buoyancy, increasing their stroke rate during descents and decreasing it during ascents as they become more buoyant. This suggests that seals adjust propulsive force in relation to their density to maintain swim speed by increasing or decreasing their stroke cycle frequency and stroke intensity (lateral acceleration amplitude). Furthermore, Miller et al. (Miller et al., 2012) predict that cost of transport (i.e. the amount of energy consumed per unit of mass and distance covered) should increase when deviating from neutral buoyancy, they also predict that cost of transport should increase in animals which have been artificially manipulated; negatively buoyant northern elephant seals were found to glide down during the descent phase and to stroke actively during the ascent, whereas the opposite results were obtained for positively buoyant seals. These observations suggest that keeping track of the hydrodynamic gliding performance of freely diving animals should provide a powerful approach to track changes in body condition. Therefore, the monitoring of these parameters while animals are at sea can provide new tools to investigate at a fine temporal scale their change in body condition in relation to environmental parameters (Miller et al., 2012). This might be particularly useful for the vast majority of seal species that do not perform ‘drift dives’.

Capital breeding phocid seals lose a large proportion of their body mass while fasting during the lactation period (Arnbom et al., 1997). For example, southern elephant seal (SES) (*Mirounga leonina*, Linnaeus 1758) females lose 25–50% of their initial weight over the breeding season, mostly in lipid stores that are mobilised for milk production and maintenance of metabolism (McCann et al., 1989). Hence, when leaving the colony after the breeding season, female SESs have depleted a large proportion of their lipid stores, resulting in a higher body density and, therefore, more negative buoyancy. During the post-breeding foraging trip, female seals start replenishing their energy stores, resulting in an increase in buoyancy. Consequently, these animals provide an opportunity to test, in free-ranging individuals, the predictions by Watanabe et al. (Watanabe et al., 2006) and Aoki et al. (Aoki et al., 2011) that changes in swimming speed during the gliding phase, and stroking pattern during the descent or ascent of a dive, should be tightly related to changes in seal density.

The aims of this study, therefore, were to use such changes in swimming behaviour to monitor at a fine temporal scale the recovery in body condition in post-breeding SESs over the complete foraging trip. Furthermore, Miller et al. (Miller et al., 2012) predict that change in buoyancy should have direct consequences on swimming effort, and we wanted to assess whether changes in the mean dive duration observed through the whole foraging trip were related to changes in seal buoyancy.

**RESULTS****Data**

The accelerometers recorded data for between 54 and 81 days for a mean ( $\pm$ s.d.) number of dives of  $3866 \pm 400$  dives recorded per seals. The number of drifts selected varied from 50 to 125 (i.e.  $2.1 \pm 1.1\%$  of the dives), and we selected  $48 \pm 15\%$  of the descents and  $55 \pm 10\%$  of the ascents (see Materials and methods and Table 1).

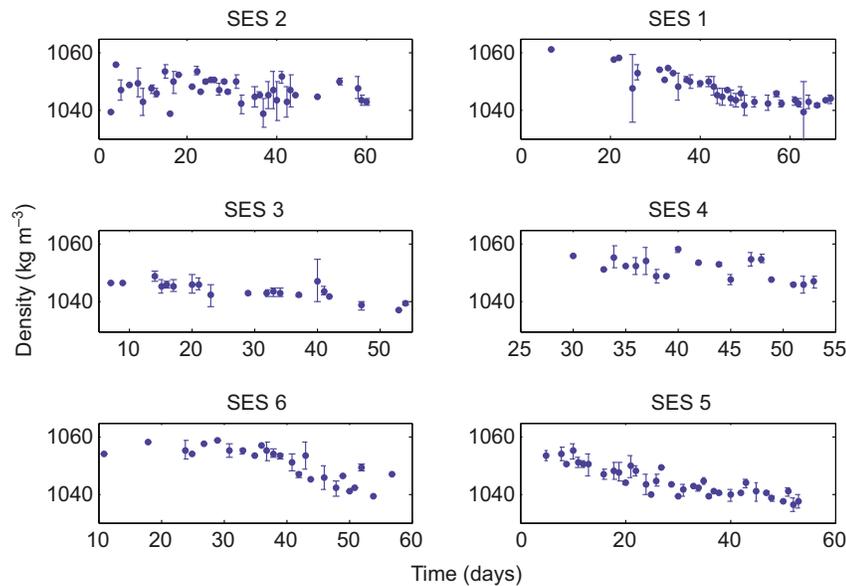
**Drift dive model**

Drift dives allowed us to estimate the body density of seals (see Eqn 8) for each drift dive identified. When several drift dives occurred on the same day, the corresponding mean density ( $\pm$ s.d.) was calculated (Fig. 1). On average, the six seals performed  $1.3 \pm 0.6$  drift dives per day and  $82.8 \pm 35.2$  drift dives over the recording period (Table 1). Interestingly, all drift dives detected from TDR-only data were confirmed to be truly drifting dives when adding the accelerometer information. Indeed, no differences could be detected in the daily drift rate calculated from TDR-only data versus TDR–accelerometer data (paired Wilcoxon test,  $P=0.94$ ), indicating that drift rates were precisely estimated from TDR-only data. However, the variance in drift rates calculated for a given day estimated from TDR-only data was marginally greater compared with that of TDR–accelerometers (paired Wilcoxon test,  $P=0.08$ ).

**Table 1. Comparison of duration of the trip and numbers of dives used and selected for the study**

Individual	Total dives	Drift dive	Descents selected	Ascents selected
1	4515	90	1481	1880
2	3361	125	2190	2256
3	4123	50	1091	1866
4	3768	48	2246	2455
5	3707	123	1670	1857
6	3727	61	2094	2256

See also Materials and methods.



**Fig. 1. Density of the six elephant seals, calculated by the mean drift rates per day.** The charts in the left column represent seals that had the accelerometer fixed onto the head, those in the right column represent seals that had accelerometers on the back. Means  $\pm$  s.d. are shown.

The six seals exhibited the same general trend: a decreasing density over the foraging trip, corresponding to decreasing drift rates (i.e. an increase in the proportion of lipids). Interestingly, very few drift dives were observed during the initial part of the foraging trip. After approximately 10 to 15 days, few drift dives were detected daily, and when several drift dives did occur on the same day, it is worth noting the large standard error (s.d.) associated with the mean value.

#### Speed versus swimming effort during ascent and descent

For each seal, both absolute speed and swimming effort during ascents and descents were calculated (see Materials and methods). All seals exhibited the same general swimming behaviour while diving.

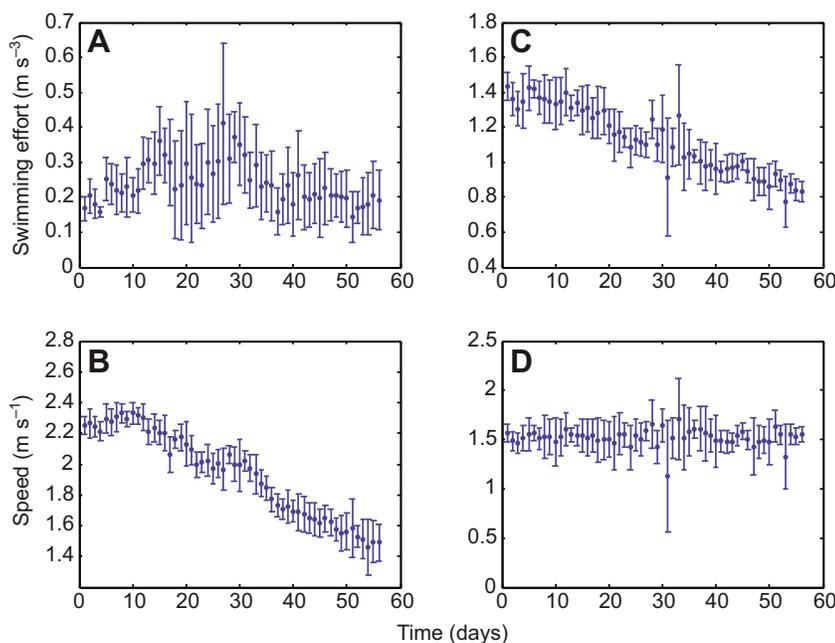
For the descent phase, despite some day-to-day variation, no trends in swimming effort could be detected over the length of the recording period (Fig. 2A). Descent swimming effort values were very low (approximately  $0.2 \text{ m s}^{-3}$ ). However, absolute descent

speed showed a decreasing trend, with the noticeable exception of the first 10 to 15 days at sea, when absolute speed remained unchanged, or even increased (Fig. 2B).

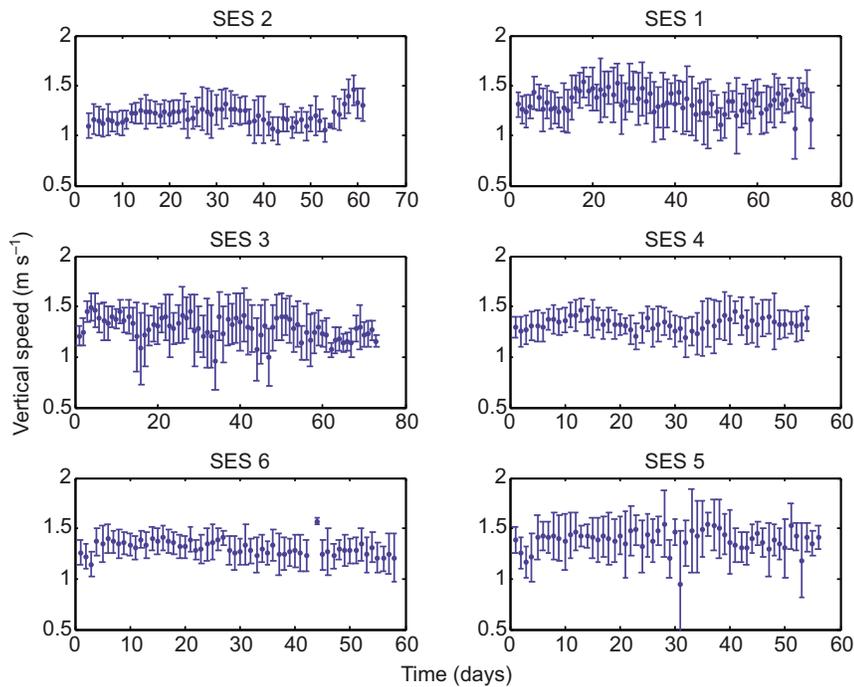
For the ascent phase, after approximately the first 10–20 days where swimming effort increased, seals progressively decreased their swimming effort while heading to the surface (Fig. 2C). This allowed them to maintain nearly constant vertical and absolute ascent swimming speeds over the whole foraging trip (Fig. 2D). Indeed, for all individuals combined, we obtained a mean vertical speed ( $\pm$ s.d.) of  $1.31 \pm 0.06 \text{ m s}^{-1}$  (Fig. 3), a mean absolute ascent swimming speed of  $1.55 \text{ m s}^{-1}$  and a standard deviation of  $0.08 \text{ m s}^{-1}$  for a mean ascent pitch of  $56.7 \pm 14.2 \text{ deg}$ .

#### Estimation of density using the two models

Changes in seal density estimated from the drift rate,  $\rho_{\text{drift}}$  ( $\text{kg m}^{-3}$ ), were related to the changes in absolute descent speed or ascent swimming effort through linear regressions. The first model related the mean seal density estimated from drift dives,  $\rho_{\text{drift}}$ , to the



**Fig. 2. Comparison of swimming effort and absolute speed between ascent and descent.** Example of swimming effort during descent (A) and ascent (C), and absolute speeds during descent (B) and ascent (D) of seal 5 during the trip. Mean  $\pm$  s.d. is shown.



**Fig. 3. Mean vertical speed per day over the trip for the six seals.** Conventions are as Fig. 1. Means  $\pm$  s.d. are shown.

corresponding mean absolute descent speed,  $U_{\text{descent}}$  ( $\text{m s}^{-1}$ ), for a given day (Eqn 1). The second model related  $\rho_{\text{drift}}$  to the mean ascent swimming effort,  $\text{Effort}_{\text{ascent}}$  ( $\text{m s}^{-3}$ ), for a given day (Eqn 2). The correlation coefficients for both models are shown in Table 2:

$$\rho_{\text{drift}} = a \times U_{\text{descent}} + b, \quad (1)$$

$$\rho_{\text{drift}} = a \times \text{Effort}_{\text{ascent}} + b. \quad (2)$$

For the linear regressions, we used values of mean absolute speed and mean swimming effort from days that values of drift rate were available.

Descent speed was positively correlated to ascent swimming effort for all seals (Table 3).

High to very high correlations were found between variations in density that were estimated from drift rates and descent speeds, and to a lesser extent, with ascent swimming effort (cf.  $r^2$ ; Table 2). Higher correlations tended to be found for seals 1, 4 and 5 (back-mounted loggers) compared with seals 2, 3 and 6 (head-mounted loggers). However, among the seals with head-mounted accelerometers, very little variation in density was detected from the drift dives for seals 2 and 3. This indicates that they did poorly while foraging at sea. Indeed, correlation coefficients were significantly related to the absolute variation of the  $\rho_{\text{drift}}$  over the recording period ( $P < 0.01$ ). Therefore, the lower correlations found in some individuals might also be explained by their small density variations.

Using the relationships found, variation in seal density over the whole foraging trip was reconstructed from the descent absolute speed (Fig. 4).

#### Changes in diving behaviour and swimming effort in relation to seal density

Using linear mixed-effect models, we assessed how dive duration varied over time (measured in days after departure from Kerguelen Island), the corresponding estimated seal density, as well as the mean bottom depth of the dive. Time, density and mean bottom depth were fixed factors, and individuals were the random factor. Dive duration varied negatively with seal density ( $t = -3.77$ ,  $P < 0.01$ ) and positively with the mean bottom depth of the dive ( $t = 33.91$ ,  $P < 0.001$ ), whereas time tended to have a positive but not significant effect ( $t = 1.67$ ,  $P = 0.096$ ).

The next step was to assess, when controlling for the mean bottom depth of the dive, which part of the dive (descent, bottom or ascent durations) varied most with increasing dive duration. For a given bottom depth of the dive, descent and bottom durations decreased, whereas ascent durations increased with increasing seal density with bottom duration variations explaining most of the variation in the complete dive duration (Table 4).

The variation of ascent swimming effort expressed as a percentage was found to be significantly related to the variation in seal density ( $t = 1.9$ ,  $P = 0.05$ ) but unrelated to the initial seal density ( $P = 0.85$ ).

**Table 2. Results of the linear regression between density (obtained by drift rates) and absolute speed of descents (Eqn 1) and swimming effort of ascents (Eqn 2)**

Individual and location of accelerometers	$\rho_{\text{drift}} = a \times U_{\text{descent}} + b$	$r^2$	$\rho_{\text{drift}} = a \times \text{Effort}_{\text{ascent}} + b$	$r^2$
1 back	$\rho_{\text{drift}} = 24.62 U_{\text{descent}} + 991.8$	0.85	$\rho_{\text{drift}} = 61.02 \text{Effort}_{\text{ascent}} + 1011$	0.64
2 head	$\rho_{\text{drift}} = 8.65 U_{\text{descent}} + 1029$	0.13	$\rho_{\text{drift}} = 13.13 \text{Effort}_{\text{ascent}} + 1031$	0.11
3 head	$\rho_{\text{drift}} = 9.02 U_{\text{descent}} + 1021$	0.4	$\rho_{\text{drift}} = 19.62 \text{Effort}_{\text{ascent}} + 1027$	0.66
4 back	$\rho_{\text{drift}} = 22.13 U_{\text{descent}} + 1005$	0.85	$\rho_{\text{drift}} = 22.04 \text{Effort}_{\text{ascent}} + 1022$	0.24
5 back	$\rho_{\text{drift}} = 17.17 U_{\text{descent}} + 1011$	0.73	$\rho_{\text{drift}} = 25.64 \text{Effort}_{\text{ascent}} + 1016$	0.96
6 head	$\rho_{\text{drift}} = 23.39 U_{\text{descent}} + 1002$	0.45	$\rho_{\text{drift}} = 43.21 \text{Effort}_{\text{ascent}} + 1006$	0.44

**Table 3. Results of the linear regression between mean absolute descent speed and mean ascent swimming effort per day for each seal with the linear regression equation and the correlation coefficient**

Individual and location of accelerometers	Effort <sub>ascent</sub> = $a \times U_{\text{descent}} + b$	$r^2$
1 back	Effort <sub>ascent</sub> = $0.54U_{\text{descent}} - 0.40$	0.88
2 head	Effort <sub>ascent</sub> = $0.30U_{\text{descent}} + 0.62$	0.94
3 head	Effort <sub>ascent</sub> = $0.38U_{\text{descent}} - 0.09$	0.63
4 back	Effort <sub>ascent</sub> = $1.02U_{\text{descent}} - 0.82$	0.87
5 back	Effort <sub>ascent</sub> = $0.64U_{\text{descent}} - 0.12$	0.97
6 head	Effort <sub>ascent</sub> = $0.41U_{\text{descent}} + 0.24$	0.93

## DISCUSSION

The results of the present study clearly demonstrate that monitoring descent swimming speed and ascent swimming effort using accelerometers combined with TDRs can provide information on changes in body density (i.e. body condition) in female SESs during their post-breeding foraging trip. Furthermore, as predicted by Miller et al. (Miller et al., 2012), this study reveals that limited changes in body density may have major consequences on an individual's swimming effort.

### Drift dive model

The drift dive model was found to provide a good estimation of seal density in juvenile elephant seals (see Aoki et al., 2011). In our study, and despite inter-individual variation, the six seals exhibited a decrease of density over the foraging trip, indicating that the SES females increased their lipid proportion (i.e. body reserve).

All TDR-detected drift dives were retained from data analyses after checking the corresponding accelerometer data. This indicates that drift dives can be isolated with high accuracy from TDR data only. Furthermore, no differences in drift rates estimated from TDR-only data versus TDR–accelerometer data were found, but the variance of drift rate values for a given day was marginally larger in TDR-only data compared with that of TDR–accelerometers. The

**Table 4. Results of the linear mixed-effect models explaining dive duration in relation to other dive factors with individuals as the random factor**

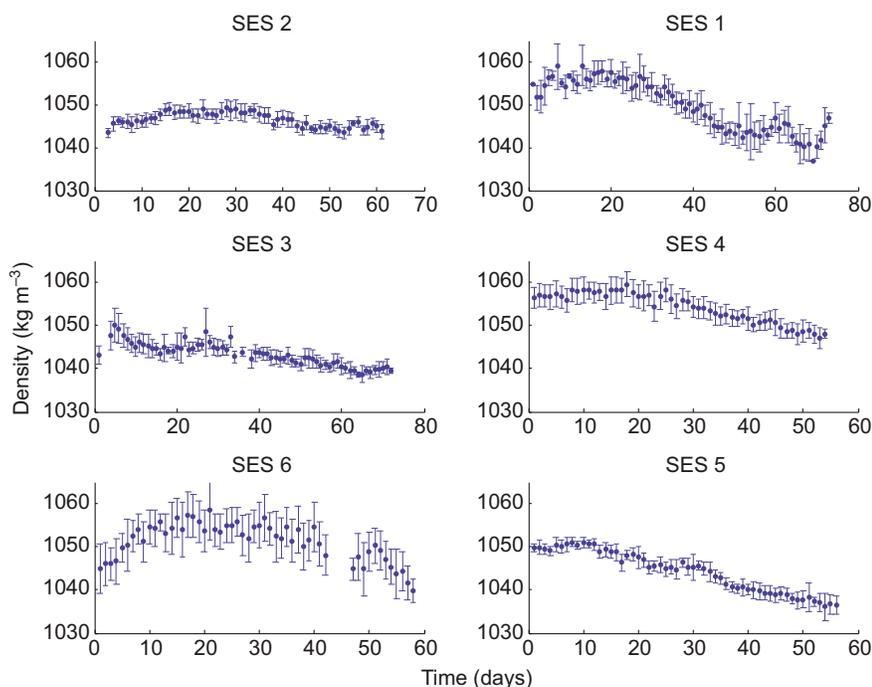
Fixed factors	Value	<i>t</i> -value	<i>P</i> -value
Descent duration	166.7	281.2	<0.01
Bottom duration	295.3	873.9	<0.01
Ascent duration	125.7	245.6	<0.01
Mean bottom depth	21.9	29.7	<0.01

main limitation of using drift dives for the monitoring of body condition is the fact that they occur so rarely at certain times. This is particularly true for the initial part of the foraging trip (up to the first 20 days). Another limitation of this approach is the relatively large standard error associated with the mean daily drift rate, questioning the finer temporal scale accuracy. Furthermore, this approach can only be used for the few species that are known to perform drift dives.

### Drift rate bias

Drift rate is a consequence of seal buoyancy directly related to body density, which is a function of body composition (proportion of total body fat). At greater deviation from neutral buoyancy, drag has a non-linear increasing effect to slow the absolute increase in drift rate (Miller et al., 2012).

In terms of a seal drifting passively through water, the terminal velocity will be influenced by external characteristics. These include the density of the seawater itself, which varies with salinity. Therefore, when seals cross water masses with contrasting densities, the estimation of seal density will also be affected. As the Splash10 tags have no salinity sensor, we were unable to assess sea water density and, therefore, account for these variations. However, this could be addressed in future work. Furthermore, according to previous work conducted on Kerguelen SESs equipped with tags measuring temperature and salinity, seawater densities that are likely to be encountered in these waters range from 1.027 to 1.030 g cm<sup>-3</sup> (Charrassin et al., 2008; Bailleul et al., 2010). According to Biuw et



**Fig. 4. Estimation of density using the linear regression equation 1. Means  $\pm$  s.d. for the six seals are shown (see Table 2).**

al. (Biuw et al., 2003), such seawater density variations could explain approximately 2.5% of the variation seal density estimation. Therefore, the effect of sea water density on the estimation of seal density was considered marginal within the scope of this study.

Drift rate can also be influenced by physiological and behavioural changes, such as residual air in the lungs and the orientation of the seal's body in the water. In this study, calculations were only performed for dives deeper than 200 m. During diving, the increase in pressure from the surrounding water causes the lungs to collapse in seals, and complete lung collapse is supposed to occur between 150 and 200 m (Kooyman and Sinnett, 1982; Falke et al., 1985; McDonald and Ponganis, 2012). Interestingly, nearly identical results were obtained when performing the analyses and calculating descent speed and ascent swimming effort from, and up to, the surface, suggesting that the lung compression effect had a limited effect in the calculation of these parameters (supplementary material Fig. S1).

### Speed versus swimming effort during ascent and descent

Both descent swimming speed and ascent swimming effort exhibited significant and concomitant changes over the foraging trips. According to the findings of Aoki et al. (Aoki et al., 2011), in a controlled experiment, such changes were most probably directly related to the variation of seal density. It is worth noting that negatively buoyant seals performed prolonged descent glides, regardless of their initial density. Inversely, all seals maintained a nearly constant swimming speed while ascending but, to do so, their density varied and modifications of swimming effort would be required. Our results suggest that seals try to reach the bottom part of their dive by passively gliding as long as they are denser than the surrounding sea water, which is likely to reduce their cost of transport. However, the descent gliding speed is highly sensitive to the buoyancy of the seal as it decreases with increasing buoyancy. During the ascent phase, the nearly constant swimming speed with very low intra-individual variance is likely to be related to the dive eco-physiological process in order to reduce the risk of decompression sickness, an acute phenomenon associated with gas uptake at pressure (for a review, see Hooker et al., 2012). Furthermore, lowering the swimming effort saves up their energy as buoyancy improves.

Both absolute descent speed and ascent swimming effort were correlated to seal density, indicating that a change in seal density has direct consequences on diving behaviour. We observed that SESs performed extended glides to descend. However, as their density decreased, so did their absolute descent speed, resulting in longer descent duration to reach a given depth for a given swimming angle. By contrast, as predicted by Miller et al. (Miller et al., 2012), as body condition improves, seals were able to decrease their swimming effort to maintain an identical absolute ascent speed, resulting in an overall decrease of swimming effort as their density decreased progressively over time. In recent studies, Miller et al. (Miller et al., 2012) and Sato et al. (Sato et al., 2013) have demonstrated theoretically and experimentally that the cost of transport in diving seals is reaching minimum value at neutral buoyancy. Through their post-breeding foraging trip, female density decreases toward neutral buoyancy and, as a consequence, the cost of transport should diminish.

### Estimation of density using the two models

Absolute descent speed and ascent swimming effort were correlated to drift dive estimated seal density. According to this result, we suggest that the simultaneous monitoring of drift rate and the

relative change of descent swimming speed or ascent swimming effort for negatively buoyant seals allows a high-temporal resolution indirect monitoring of seal density over the foraging trip. Indeed, the monitoring of drift rate provides an easy way to calculate the absolute value of seal density, whereas the monitoring of descent speed and ascent swimming effort variations provides a good relative variation at a fine temporal scale.

Nearly all seals exhibited an increase of their density during the first part (10 to 20 days) of their trip. This may be because, after one month fasting and lactating, post-breeding females may allocate most of their food resources to protein stores (muscle), resulting in an increase in body density. Alternatively, decreased density may indicate that female SESs are not foraging very successfully when leaving the colony, or may be focused on travelling to the detriment of foraging. Recent works on the monitoring of prey-catch events using head-mounted accelerometers on SESs (Gallon et al., 2013; Guinet et al., 2014) reveal that, in general, SESs exhibit a lower prey-catch rate per unit of time and travel greater distances when leaving and coming back to the colony. This suggests that they may, indeed, favour travelling over foraging (C.G., unpublished data).

Thereafter, all seals exhibited, to a different extent, a decrease in body density, indicative of a progressive increase of their lipid proportion, concomitant with an increasing mass. Indeed, on average, SES females were found to gain ~0.9 kg per day spent at sea (Guinet et al., 2014). Generally, the decrease in body density slowed towards the end of the foraging trip when the seals start to head back to the colony, again, when they are likely to favour travelling over foraging.

### Back- or head-mounted accelerometers

Lower regression coefficients were found with head-mounted accelerometers compared with those that were back-mounted. This suggests that back-mounted accelerometers allow for a more precise assessment of swimming effort and may, therefore, return more accurate results. The main purpose of head-mounted accelerometers was to detect prey-catch events, whereas those that were back-mounted were deployed mostly to assess swimming effort. However, results suggest that this could be an artefact caused by confounding factors. Indeed, for two out of the three seals with head-mounted accelerometers, limited changes in body density over time was observed, preventing the detection of strong relationships with descent absolute speed and ascent swimming effort. Interestingly, accelerometers deployed simultaneously on the head and on the back (number 1) provided nearly identical results. Therefore, the exact influence of head- versus back-mounted accelerometers to monitor changes in seal density should be investigated in greater detail in the future.

### Swimming effort

As body condition improves, absolute descent speed decreases and, as discussed earlier, as long as the seal remains negatively buoyant, the descent duration to reach a given depth will increase. Although large dive-to-dive variation in descent angle was observed, no trends in diving angle could be detected for the duration of the foraging trip. Seals do not appear to compensate their lower absolute descent speed by performing steeper dives. Changes in descent diving angle are more likely to be related to local variations of foraging success and are more likely to occur when seals are favouring horizontal displacements. Many diving predators, including SESs, king penguins and fur seals, dive at a steeper angle after a successful foraging event (Hanuise et al., 2013; Viviant et al., 2014). This

resulted in a significant increase of transit time to reach a given depth as body condition improves and body density decreases, but no direct increase of the swimming effort is detected for the descent phase (but the overall expenditure related to the basal metabolic rate will increase with increasing descent duration). As predicted by Miller et al. (Miller et al., 2012), negatively buoyant SESs were found to minimize their swimming effort and, consequently, are likely to minimize their energy expenditure by performing extended glides for most of the descent, rather than minimizing their descent transit time.

During the ascent, seals are able to decrease their swimming effort as density decreased to maintain a nearly constant absolute ascent swimming speed. As a result and as long as the seal remains negatively buoyant, the overall swimming effort during the descent and ascent transit phases decreases with decreasing body density. One important finding of our study was that, regardless of the initial body density, a 1% variation in seal density (i.e. approximately  $10.5 \text{ kg m}^{-3}$ ) resulted in a 15% variation in ascent swimming effort (Fig. 5), indicating that leaner seals exhibit a greater swimming effort than fatter ones, which are closer to neutral buoyancy, concurring with the prediction of Miller et al. (Miller et al., 2012). As seal density over the post-breeding foraging trip may vary by as much as  $20 \text{ kg m}^{-3}$ , this may represent a nearly 40% decrease in ascent swimming effort between the highest and lowest seal densities. This should result in a significant decrease in energy expenditure, which remains to be estimated. During the bottom phase of the dive, with the exception of few very active swimming chase phases, seals tend to, most of the time, alternate between active ascent phases and gliding descent phases (C.G., unpublished data). Variation in ascent swimming effort is, therefore, likely to be extrapolated over most of the dive. This important result is consistent with the findings of Beck et al. (Beck et al., 2000) on grey seals and of Thums et al. (Thums et al., 2013), who found that lipid content strongly influences the dive behaviour of seals, with fatter individuals having longer dive

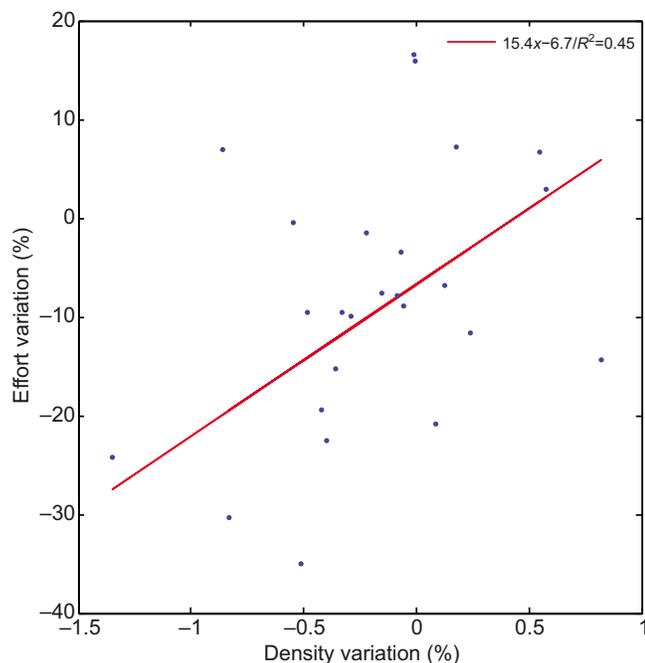


Fig. 5. Regression between percentages of ascent swimming effort variation and percentages of density variation for the six seals.

durations than leaner ones. This suggests that lipid content is likely to influence seal diving behaviour. However, as no accelerometers were deployed, those authors were not in a position to relate their findings to the variation of swimming effort with lipid content.

Furthermore, our results suggest that increased dive duration over the foraging trip could be explained by the number of days that had elapsed since departure. This suggests that the eco-physiological training, resulting in greater diving skills, of the seal improves, as has been suggested for northern elephant seals (Hassrick et al., 2010). Interestingly, however, the variation in dive duration when controlling for diving depth was, in fact, found to vary mostly with seal density. This result suggests that in negatively buoyant seals, swimming effort decreases with decreasing seal density, allowing the seal to perform longer dives. Therefore, according to Miller et al., 2012, we should expect that the cost of transport, and consequently the amount of energy a seal should produce to cover a given distance (i.e. the swimming effort), is minimal when seals are reaching neutral buoyancy and that the cost increases when they depart from it.

When controlling for the mean bottom depth, increased overall dive duration with decreasing density, in these negatively buoyant seals, was partly explained by a longer descent phase to reach a given depth and a longer ascent duration to swim back to the surface. However, the increase of bottom dive duration had the largest contribution to explaining the overall increase of dive duration. This result has strong ecological implications as it indicates that by improving their body condition (i.e. decrease their density towards neutral buoyancy), seals are able to decrease their swimming effort (locomotion costs) and, therefore, reduce the amount of oxygen that is allocated to swimming. As a consequence, they are able to spend more time underwater and, in particular, they can spend more time actively foraging at depth. As SES females forage mainly at the bottom of their dive [75% of prey-catch events take place at bottom phases (Guinet et al., 2014)], this result has strong implications on their foraging efficiency (i.e. seals reaching neutral buoyancy are more efficient than leaner seals). Indeed, variation of the swimming effort per unit of time spent diving both at the dive and at the multi-dive level were found to be related to seal density and to decrease with decreasing density.

We acknowledge that swimming effort provides only an indirect indication of energy expenditure during locomotion. However, numerous studies have highlighted strong and linear relationships between locomotion effort and oxygen consumption for a broad range of taxa (see Schmidt-Nielsen, 1972; Mayhew, 1977; Booth 2009). Furthermore, in a recent study on post-breeding SES females, Genin et al. (A.G., G.R., J.J., B.P., N. El Skabi, J.V.-G. and C.G., unpublished) found that surface interval duration, related to the number of breaths taken, was highly correlated to the dive duration and the overall swimming effort of the previous dive. According to the findings of Miller et al. (Miller et al., 2012), we predict that positively buoyant seals at the end of their long (i.e. 8 month) foraging trips should exhibit a decrease in their dive duration and an increase in body condition and, therefore, their foraging efficiency should decrease.

### Perspectives

Accelerometers provide detailed insights into the change in seal density, as well as swimming strategy according to density. Our study suggests that in poor years, the foraging efficiency of elephant seals decreases owing to a lower prey-catch rate per unit of time, as well as an increase in foraging costs from decreasing body condition. This effect would ordinarily not be accounted for.

In the current study, accelerometers were used to assess the pitch of the seals and their swimming effort. Other studies (Viviant et al., 2010; Gallon et al., 2013; Guinet et al., 2014) underline the use of accelerometers for assessing prey-catch events during dives throughout the entire foraging trips of pinnipeds. As a result, future work should assess whether the variation in seal density along the foraging track can be related to the foraging success on one hand and swimming effort on the other hand. Furthermore, investigation of the variation of dive duration in relation to swimming effort should provide a new way to assess the respective contributions of basal metabolic rate and locomotion cost in the overall metabolic rate of free-ranging seals.

## MATERIALS AND METHODS

### Field site and study animals

Six post-breeding female SESs (mean mass=309±68 kg; mean length=247±17 cm; ±s.d.; Table 5) from Kerguelen Island (49°20'S, 70°20'E) were anaesthetized using a 1:1 combination of tiletamine and zolazepam (Zoletil 100), which was injected intravenously (McMahon et al., 2000), and equipped with an Argos-GPS satellite tag (Splash10-F, Wildlife Computer, USA) combined with a TDR-accelerometer (TDR-MK10-X, Wildlife Computer, USA). Splash10-F devices were set to transmit Argos locations daily and collect GPS location data. Sampling intervals of GPS locations was set to a minimum of 20 minutes, i.e. slightly shorter than the mean dive duration of the species (Hindell et al., 1991), pressure and temperature were sampled at 1 Hz. MK10-X was also set to collect and archive pressure and temperature levels every second. Three-axis accelerations (sway, surge and heave) that measure both dynamic acceleration (such as propulsive activities) and static acceleration (such as gravity or pitch) were sampled at 16 Hz. The six Splash10-F tags were glued onto the heads of seals. In 2010, three of the accelerometers were glued onto the back of the head, and one seal (number 1) was simultaneously equipped with an accelerometer glued onto its back (MK10-D, Wildlife Computer). In 2011, two accelerometers were deployed on the back of the seals and one was deployed on the head (Table 5).

Data loggers were glued onto the heads and the backs of the seals using quick-setting epoxy (Araldite AW 2101) after cleaning the fur with acetone. The loggers were recovered when SES females returned to shore to moult (i.e. January–February following deployments). Once ashore, seals were located using their Argos locations.

### Data analysis

Data processing and analyses were conducted using MATLAB (The MathWorks, Natick, MA, USA). First, pressure data were used to identify surface intervals and dives. Dives were split into three phases: descent, bottom and ascent, and then classified into four categories based on diving behaviour, namely: drift dives, exploratory dives, shallow active dives and deep active dives (Dragon et al., 2012). The mean bottom depth corresponded to the mean value of the depth readings during the bottom phase of a dive. The passive drift phase of the drift dive was isolated to estimate the density of a seal according to Biuw et al. (Biuw et al., 2003).

Seal density was estimated from the drift dive model, which provides a simplified situation to estimate body density because balance of force is simpler when the animal is only sinking passively (Crocker et al., 1997; Biuw et al., 2003). However, because so few passive drift dives are performed daily (Dragon et al., 2012), body condition variation becomes

difficult to assess at a fine temporal scale. In contrast, speed and swimming effort, calculated during the descent and ascent of each dive, provide a high-frequency time series with SESs performing ~60 to 70 dives daily (Boyd and Arnborn, 1991; Dragon et al., 2012). Although seal density can be estimated from descent or ascent glides (Watanabe et al., 2006), the correct calculation of seal density to take into account all forces is more complex. Therefore, our approach was to calculate seal density only from the drift dives, which is simpler. Swimming speed and swimming effort were used to obtain a high-resolution time series. When both pieces of information were available, we investigated the relationship between drift dive estimated seal density and the corresponding swimming speed and effort data on a daily basis.

### Descent swimming speed

Information on the body angle (from the acceleration sensor) and vertical speed (as determined from the depth recorder) provided us with an estimate of the actual swimming speed during the long ascent and descent phase (Sato et al., 2003). However, this method is only reliable for steeper body angles.

Acceleration data were processed according to Sato et al. (Sato et al., 2003), Watanabe et al. (Watanabe et al., 2006) and Aoki et al. (Aoki et al., 2011). Different filters applied on the three axes were used to characterize the different components of seal movement. The gravity component of the movement was obtained by applying a low-pass filter at 0.2 Hz on the three axes. We used the lower-frequency gravity-based accelerations of the three axes to calculate the pitch,  $\theta$  (Eqn 3), of the seal using the three axis acceleration data (Tuck, 2007) that was sampled at 16 Hz using:

$$\theta = \arctan\left(\frac{x}{\sqrt{y^2 + z^2}}\right), \quad (3)$$

where  $x$ ,  $y$  and  $z$  are the filtered acceleration values for the longitudinal, lateral and vertical axis (Sato et al., 2003; Watanabe et al., 2006; Aoki et al., 2011). The comparison of the data obtained simultaneously from the head and back accelerometer (seal 1) revealed a difference between the mean pitches obtained by both of the accelerometers. Furthermore, the mean pitch calculated by both accelerometers when the seal was breathing at the surface between two dives revealed that the pitch obtained by the head accelerometer exhibited an offset compared with the back accelerometer. Consequently, we calculated a mean pitch difference between the three head and back accelerometers of 13.9 deg, and we used this mean value to inter-calibrate the accelerometers between seals. So head accelerometers were corrected accordingly to provide comparable data with those deployed on the back.

Swaying accelerations often contained low frequency variations that were assumed to be the result of various turning and rolling movements by the seals. These were separated using a high-pass filter in order to extract the information on flipper stroking activity. To select an appropriate filter band, the power spectral density of each swaying acceleration record was calculated using a fast Fourier Transformation. Lateral axis was processed with a 0.6 Hz-wide band-pass filter to assess the result of the swimming movement. The remaining peaks and troughs with absolute intensities greater than a set threshold of 0.2 m s<sup>-2</sup> were considered to represent individual strokes (Sato et al., 2003). Stroking rate and the intensity of the hind-flipper movement allowed the calculation of a swimming effort index (Eqn 4):

$$\text{Swimming effort} = \frac{\sum |\text{peaks}|}{\Delta t}. \quad (4)$$

**Table 5. Loggers deployed on the six elephant seals**

Individual	Mass (kg)	Size (cm)	Accelerometer	Position	Date of departure	Days recorded
1	377	266	MK10-D/ MK10-X	Back and head	11/21/2010	74
2	331	266	MK10-X	Head	10/28/2010	61
3	395	252	MK10-X	Head	11/01/2010	81
4	245	225	MK10-X	Back	10/29/2011	54
5	249	240	MK10-X	Back	10/31/2011	56
6	255	232	MK10-X	Head	10/31/2011	58

Similar to Aoki et al. (Aoki et al., 2011), swimming effort ( $\text{m s}^{-3}$ ) was the sum of the absolute value of lateral acceleration peaks,  $\Sigma|\text{peaks}|$  ( $\text{m s}^{-2}$ ), during the duration of the phase studied,  $\Delta t$  (s). The peaks correspond to the intensity of hind-flipper movements, and so the index reflects the intensity per second. It should be pointed out that the swimming effort calculated by us was strongly related to overall dynamic body acceleration (ODBA) (Wilson et al., 2006) with a mean correlation coefficient ( $\pm$ s.d.) of  $0.77 \pm 0.15$  between the two methods at the dive scale. Moreover, we compared swimming efforts calculated using the lateral axis and those calculated using the three axes during descents, bottoms and ascents over time for seal 1. We observed a good correlation between lateral axis and the three axes with mean coefficients of correlation of 0.95 for descents, 0.89 for bottoms and 0.83 for ascents (supplementary material Fig. S2). As a result, using the three axes to calculate the swimming effort index provides no additional information and adds noise as we worked on relative variation and not on absolute values (supplementary material Fig. S3). Furthermore, recent studies on fur seal have found that flipper stroke is a better predictor of energy expenditure, whereas no relationships are found with ODBA (J. du Dot, unpublished data). Therefore, this index of swimming effort was preferred to ODBA as it focused on lateral acceleration, which is a direct measurement of the propulsive activities, whereas ODBA provides an integrated index of all acceleration sources, some of them being unrelated to the propulsive effort. Only the lateral axis accelerations were used because phocid seals mostly use lateral movements of the hind-flippers for propulsion. In addition, the power spectral density of the longitudinal and the vertical axes obtained by a fast Fourier Transformation did not show high frequencies that corresponded to any swimming hind-flipper movement.

### Forces and body composition

When swimming, seals are subjected to external forces. The balance of these forces affects the energetic cost of movement (Tucker, 1975). In marine mammals, the primary forces are hydrodynamic drag and buoyancy (Schmidt-Nielsen, 1972). The drag of the seal during drifts and glides depends on their speed (Watanabe et al., 2006; Aoki et al., 2011):

$$F_D = 0.5C_D\rho_{\text{sw}}AU^2, \quad (5)$$

where  $F_D$  is drag force (N),  $C_D$  is the drag coefficient,  $\rho_{\text{sw}}$  ( $\text{kg m}^{-3}$ ) is the density of the seawater,  $A$  is the frontal or surface area of the seal ( $\text{m}^2$ ) and  $U$  is swim speed ( $\text{m s}^{-1}$ ). Drag force always opposes the direction of

movement and increases with speed. Buoyancy is defined as the sum of the weight force and the Archimedes's force (Lovvorn et al., 1991; Beck et al., 2000):

$$F_B = (\rho_{\text{sw}} - \rho_{\text{animal}})Vg, \quad (6)$$

where  $F_B$  is buoyant force (N),  $\rho_{\text{animal}}$  is the density of the animal ( $\text{kg m}^{-3}$ ),  $V$  is the volume of the animal ( $\text{m}^3$ ) and  $g$  is the acceleration of the gravity ( $=9.81 \text{ m s}^{-2}$ ). If  $\rho_{\text{animal}}$  is higher than  $\rho_{\text{sw}}$ , buoyancy will be negative and the animal will sink passively. Conversely, extra energy will have to be expended when the animal returns to the surface. In marine mammals,  $\rho_{\text{animal}}$  is mainly determined by the relative amount of lipid and lean tissue:

$$\rho_{\text{animal}} = \rho_l \times P_l = \rho_p \times P_p + \rho_b \times P_b + \rho_{\text{bw}} \times P_{\text{bw}}, \quad (7)$$

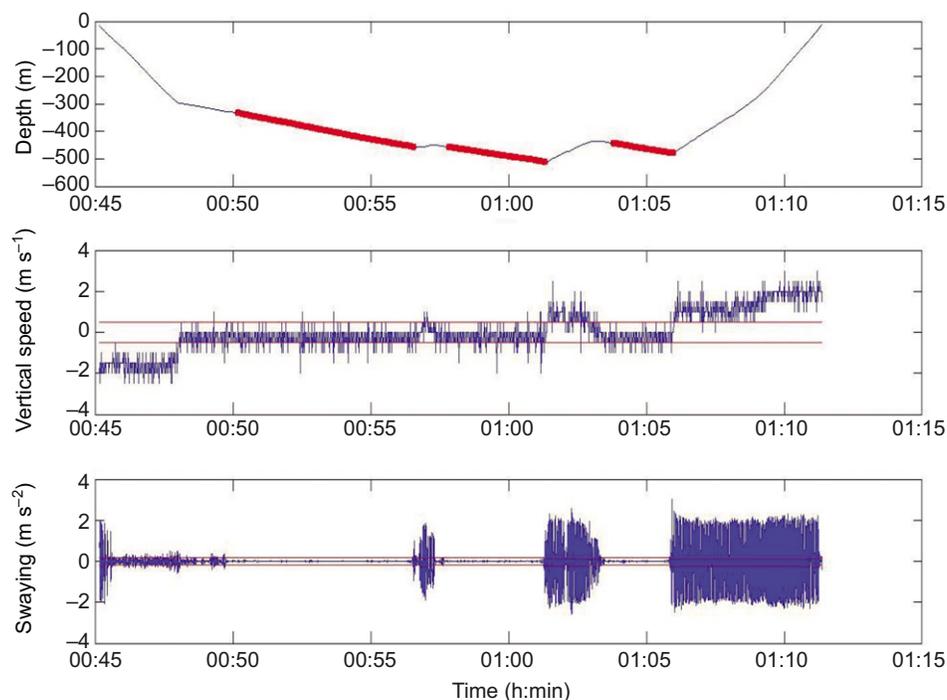
where  $\rho$  is the density of the component,  $P$  is the proportion of the component, and subscripts l, p, b and bw refer to lipid, protein, bone mineral (ash) and body water (Biuw et al., 2003; Aoki et al., 2011). To gain an idea of the density values, we can refer to human values:  $\rho_l=900.7$ ,  $\rho_p=1340$ ,  $\rho_a=2300$  and  $\rho_{\text{bw}}=994 \text{ kg m}^{-3}$  (Moore et al., 1963). We assume in the following models that female SESs on their post-breeding trip have a high proportion of lean tissue and that they will increase their proportion of lipid during their foraging trip. Consequently, the variation in density would mainly be due to the variation of lipid proportion. Bone and ash contribution to variation of density are assumed to be negligible.

We used a median ( $\pm$ s.d.) seawater density for the Southern Ocean of  $1027.5 \pm 2 \text{ kg m}^{-3}$ .

### Drift dives model

Drift dive identification (Fig. 6) was processed in two steps: we used first the complete TDR allowing us to (i) identify drift dives and (ii) isolate the passive drift phase during those dives (see Dragon et al., 2012). For each drift dive, a drift rate was determined as the slope coefficient of a linear regression between depth and time (Biuw et al., 2003; Bailleul et al., 2007; Mitani et al., 2010). In a second step, we used accelerometer data to exclude phases of active swimming during drift phases assessed by the TDR-only data. Active swimming was considered to take place when lateral acceleration exceeded the  $-0.2$  to  $0.2 \text{ m s}^{-2}$  range. Subsequently, we only analysed truly passive drift phases to estimate seal density.

During passive drift phases, SESs are only subject to drag force and buoyancy. Thus, during ascending drift phases  $F_B=F_D$ , and during descending drift phases  $F_B=-F_D$  (Biuw et al., 2003; Aoki et al., 2011). Given



**Fig. 6. Drift dive identification.** Example of a drift dive depth profile (A) with the associated vertical speed profile (B) and the lateral axis of accelerometers representing the movement profile of the hind flipper (C). We consider the passive drifts during bottom (red on the depth profile) when vertical speed is bounded between  $-0.4$  and  $0.4 \text{ m s}^{-1}$  and the lateral acceleration between  $-0.2$  and  $0.2 \text{ m s}^{-2}$ .

Eqns 5 and 6, we obtain the mean seal density for descending drift phases (Eqn 8).

$$\rho_{\text{seal}} = \rho_{\text{sw}} + \frac{U_{\text{drift}}^2 \cdot C_D \cdot \rho_{\text{sw}} \cdot S_{\text{seal}}}{2g \cdot V_{\text{seal}}}, \quad (8)$$

where  $U_{\text{drift}}$  is the speed ( $\text{m s}^{-1}$ ) of the seal during the passive drift phase, i.e. the drift rate.  $C_D$  is the drag coefficient based on the total surface area ( $S_{\text{seal}}$ ) and fixed to 0.69 (Biuw et al., 2003; Aoki et al., 2011). Animal volume is considered to be equivalent to two opposing cones with a common base that corresponds to total girth (Bell et al., 1997; Biuw et al., 2003; Aoki et al., 2011):

$$S_{\text{seal}} / V_{\text{seal}} = \frac{\sqrt{1 + \frac{L^2}{3R^2}} + \sqrt{1 + \frac{2L^2}{3R^2}}}{L}. \quad (9)$$

$L$  is the mean size of the seal between the sizes measured at the beginning and the end of the trip at sea, and  $R$  is the radius of the cones common base (unmeasured in the field). To obtain  $R$ , we used the empirical relationship described by Castellini and Calkins (Castellini and Calkins, 1993) between  $m$  the mass (kg),  $L$  the size (m) and  $G$  the girth ( $\text{m}^2$ ):  $m=45.7LG$ . As  $G=2\pi R$ , we obtain:

$$R^2 = \frac{m}{4\pi^2 \times 45.7L}, \quad (10)$$

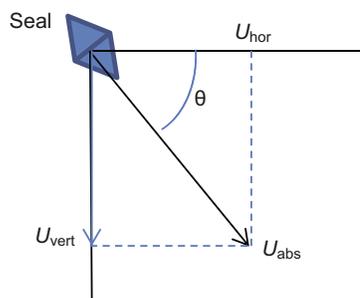
where  $m$  is the mean mass of the seal between the masses measured at the beginning and the end of the pelagic trip.

### Speed versus swimming effort during ascent and descent

Previous experimental studies on seals have shown that stroking effort is tightly related to seal density (Aoki et al., 2011; Miller et al., 2012). However, the precise calculation of body density when the seal is actively swimming is complicated owing to the complex balance of forces. For this reason, we investigated the direct relationship between the body density estimated from drift dives and the swimming speed stroking effort during descent and ascent phases of the dive. Indeed, positively buoyant seals stroke actively during the descent phase of the dive. Negatively buoyant seals, however, stroke actively during their ascent (Watanabe et al., 2006; Aoki et al., 2011; Miller et al., 2012). Therefore, change in swimming effort and speed during the ascent and the descent phase of the dive were monitored through the whole foraging trip, assuming that a change in seal density should influence either one of these two parameters. During the ascent and descent, the swimming speed can be calculated by combining information on the vertical speed and the seal pitch (Fig. 7) using the following relationship:

$$U_{\text{abs}} = \frac{U_{\text{vert}}}{\sin \theta}. \quad (11)$$

Swimming speed calculated by Eqn 11 (see Miller et al., 2004) was considered reliable when the absolute body pitch was over 30 deg. As a result, we use this proxy for deep descents and ascents, i.e. ending and starting below 400 m deep, respectively, and with an absolute pitch over 30 deg (Watanabe et al., 2006).



**Fig. 7. Geometry of movement of a descending elephant seal.** The absolute speed vector ( $U_{\text{abs}}$ ) is the sum of the horizontal speed vector ( $U_{\text{hor}}$ ) and the vertical speed vector ( $U_{\text{vert}}$ ). The vertical speed is the depth covered by the seal per second.

Seals were considered as fully compressed for depths greater than 200 m [to exclude variation of density, which might be caused by lung collapse under pressure (see Biuw et al., 2003)].

During descents and ascents, seals are always subject to buoyancy and drag force but, as they are gliding, the balance of forces incorporates the acceleration of the seal. However, the derivation of speed incorporates error as the speed is already an estimate. Therefore, we used the variation of speed and the variation of stroking effort during ascents and descents over the trip to describe the variation of body condition over time.

Change in dive parameters – descent, ascent, dive and bottom time durations – along the foraging trip were assessed using a generalized linear model using diving depth, as well as pitch angle for the descent and ascent and body density as covariables. The individual was included as a random effect.

### Change in swimming effort in relation to seal density

During their foraging trip, seals exhibited periods during which they increased or decreased their density. The minimum and maximum densities at the beginning and the end of each of these periods were assessed and density variation, expressed as a proportion (%) of the initial density for each of these periods, was calculated. For the corresponding periods, the variations in seal swimming effort were also calculated. As post-breeding females always remain negatively buoyant, most of their descents are characterized by prolonged glides, and therefore most of the swimming effort takes place during the ascent phase of the dive. The variations of ascent swimming effort were expressed as a percentage (%) of the initial swimming effort at the beginning of each of the corresponding density variation periods. Because accelerometers had not been inter-calibrated before deployment, we used the variation in percentage, rather than the absolute swimming effort. A calculation of absolute swimming effort, comparable between seals, would have required such absolute calibration, whereas the calculation of a relative variation did not.

### Linear mixed-effect model

We used a linear mixed-effect model in the statistical platform R (R Development Core Team, 2012) to explain the variation of a dive factor by other dive explanatory variables (i.e. fixed factors) with individuals as the random factor. In order to compare the effects of the fixed factors, the fixed factors were standardized. The value of each coefficient is therefore indicative of its relative contribution to the explained factor. Several explanatory variables were found to be inter-correlated, and therefore multicollinearity could occur. As a consequence, only variables exhibiting a correlation coefficient lower than 0.75 were kept in the model. When higher correlation coefficients were found, the models were run with only one of the two inter-correlated variables.

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### Competing interests

The authors declare no competing financial interests.

### Author contributions

G.R. designed the global model with the participation of C.G. G.R., J.V.G., J.J., B.P. and A.G. performed the data and statistical analyses. All authors participated in the discussion and interpretation of results. The manuscript was primarily edited by G.R., J.A., F.B. and C.G.

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## Supplementary material

Supplementary material available online at <http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.088542/-DC1>

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