

# Adjustment of diving behaviour with prey encounters and body condition in a deep diving predator: the Southern Elephant Seal

Joffrey Jouma'a\*, Yves Le Bras, Gaëtan Richard, Jade Vacquié-Garcia, Baptiste Picard, Nory El Ksabi and Christophe Guinet\*

CEBC, UMR 7372 ULR-CNRS, 79360 Villiers en Bois, France

## Summary

1. Optimal diving models have been developed to investigate how air-breathing predators should adjust their diving behaviour to optimize their foraging efficiency. Using time-depth recorders and 3D accelerometers, we addressed this question on six free-ranging Southern Elephant Seal (SES) females equipped on Kerguelen Island.

2. We hypothesize that seals would initially increase their foraging time with distance to the foraging patches before reducing it for physiological reasons, regardless of the prey encountered. We expect that SES spends more time at depths where more Prey Catch Attempts (PCA) occur, that is at the bottom. We also hypothesize that bottom time should be related to both the seal body density and the swimming effort dedicated to catching prey, as we expect seals to be more active when catching prey. Finally, because oxygen is acquired at the surface only, we expect that recovery times increase with the duration of the previous dives.

3. A total of 72.6% of PCA detected by accelerometer occurred at the bottom of the dive. At shallow depths (< 300 m), seals spent more time at the bottom in dives where PCA occurred compared to non-PCA dives. At deeper depths, SES had shorter bottom times in PCA dives due to higher swimming effort. When only dives associated with PCA were considered, the time spent at the bottom increased with the number of PCA. In addition, the closer the seal was to neutral buoyancy, the longer was the bottom duration. Body density, that is buoyancy, was found to be a critical factor in controlling variations in the dive duration through the swimming effort to access the prey at the bottom of the dive. Finally, post-dive surface intervals were related to the duration and swimming effort of the previous dive.

4. This study reveals how a marine top predator adjusts the time spent at the bottom depending on its body density, prey encounter rate and prey accessibility. It also highlights that using the duration of the foraging phase as a proxy of foraging success can be seriously misleading in SES. Finally, the need to use an energetic approach with bio-logging technology to study behavioural ecology is emphasized.

**Key-words:** bio-logging, buoyancy, foraging behaviour, marine mammal, optimal diving theory

## Introduction

Many animals are bound to a specific site which they have to return to, often for catching their prey or feeding their offspring, like seabirds returning to the colony to feed their chicks. They are thus limited to areas around this central place to find resources. This specificity leads to particular temporal and energetic constraints, due to energy expendi-

ture to travel to and from this central place and/or a limited time available for feeding before returning to the central place (Pyke 1984; Kacelnik, Houston & Schmid-Hempel 1986). In an aquatic environment, dives performed by air-breathing predators can be considered as a special case of the central place foraging theory (Houston & McNamara 1985). Because they are physiologically constrained to come up to the surface to renew their oxygen supply, it induces complex decisions rule in order to optimize resource acquisition.

\*Correspondence authors. E-mails: christophe.guinet@cebc.cnrs.fr; joffreyjoumaa@icloud.com

The number of encountered prey was generally assumed to be proportional to the time spent searching since there are few data on the quality of the patches encountered by animal. The first studies on optimal diving behaviours therefore examined strategies that maximize time spent at the foraging patch, and it was expected that the decision to end a dive was entirely based on oxygen reserves (Kramer 1988; Houston & Carbone 1992; Thompson, Hiby & Fedak 1993; Carbone & Houston 1994). The main prediction of this assumption is that breath-holding divers should stay at depth as long as their oxygen store allows it. The duration of most dives was therefore expected to approach the aerobic dive limit (Thompson & Fedak 2001), which is the dive duration at which all the usable oxygen stores have been used (Houston 2011). However, models based on this theory were unrealistic because many species end most of their dives before reaching this limit (Costa, Gales & Goebel 2001; Costa *et al.* 2004).

Although the diving performance of an air-breathing animal clearly depends on its physiological abilities, it was found that other factors play important roles in the decision to stay or leave a patch, such as predation risk (Heithaus & Frid 2003), distribution, abundance, depth and energy content of the prey (Ydenberg & Clark 1989; Thompson & Fedak 2001; Cornick & Horning 2003; Sparling *et al.* 2007). Thompson & Fedak's (2001) model examined how breath-holding predators adjust their dive time budget in relation to depth and patch quality, whilst taking into account the oxygen balance. They showed that there is a net benefit to ending dives early, without fully depleting their oxygen stores, if no prey is encountered. This benefit is higher in lower density patches and reduced in the deepest dives. Thompson, Hiby & Fedak (1993) showed that in deep dives, animals swim with the minimum cost of transport during the transit phase, suggesting that the costs associated with deepest dives can be minimized by behavioural mechanisms.

Animals can adjust their swimming effort finely through variations in stroke frequency and body angle (Sato *et al.* 2003; Fossette *et al.* 2010; Miller *et al.* 2012) to reduce oxygen consumption and maximize time at depth. However, they are also affected by intrinsic parameters such as buoyancy, which is determined by body composition, and more specifically, by the percentage of adipose tissue (Crocker, Le Boeuf & Costa 1997; Beck, Bowen & Iverson 2000; Sato *et al.* 2003). Several studies highlight the influence of buoyancy on different aspects of diving behaviour, such as rate of ascent and descent (Webb *et al.* 1998; Beck, Bowen & Iverson 2000; Sato *et al.* 2003; Adachi *et al.* 2014). In a recent study on southern elephant seal, *Mirounga leonina* (SES hereafter), Richard *et al.* (2014) showed that, in negatively buoyant SES, 1% variation in buoyancy resulted in a 20% variation of swimming effort, during the ascent phase. Therefore, taking into account buoyancy appears to be essential for the prediction of the optimal diving behaviour.

This result reflects the recent development of bio-logging. Today, mouth-opening and head movement can be detected

using Hall sensors (Wilson *et al.* 2002) or accelerometers (Okuyama *et al.* 2009; Suzuki *et al.* 2009; Naito *et al.* 2010, 2013; Viviant *et al.* 2010) to provide a set of new proxies for prey encounter rates. Furthermore, accelerometers can be also used to monitor swimming effort as well as animal posture such as pitch in water. Changes in Prey Catch Attempts (PCA hereafter) and swimming behaviour can then be monitored throughout the dive when pressure sensors are added. With these series of information (occurrence and number or history of PCA), we can indirectly assess the quality of the area visited by animals and investigate the fine-scale behavioural responses of diving predators in relation to the habitat quality.

As part of this study, we investigated how a free-ranging marine predator, the southern elephant seal, adjusts its diving behaviour to recent prey encounters, distance to prey patches (depth) and its buoyancy. Knowing that time spent at the bottom of a dive corresponds to the main foraging time of SES (Guinet *et al.* 2014) we make the following predictions:

1. Seals should first increase their foraging time with increasing distance, that is dive depth, to the foraging patch and then decrease it, whether they encounter prey or not (Houston & Carbone 1992).
2. In agreement with Thompson & Fedak's prediction (2001) for a given diving depth, seals should increase their bottom time when more PCA occur at the dive's bottom phase compared to when no PCA occur.
3. The amount of time the seal allocates to foraging at the bottom of their dive should be related to both its body density and to its swimming effort to catch prey as we expect that seals are more active when catching prey. Furthermore, individuals closer to neutral buoyancy should be able to allocate more time at the bottom of their dive because the round trip cost of transport is minimum at neutral buoyancy (Miller *et al.* 2012; Adachi *et al.* 2014), and as a consequence, the amount of energy spent by the individual and the amount of oxygen consumed are both reduced (Tucker 1975).
4. Because oxygen is acquired at the surface with diminishing returns, that is nonlinear (Butler & Jones 1997), recovery times increase with the duration of the preceding dive (Kooyman & Ponganis 1998). Thus, shallow dives yield a higher net rate of oxygen acquisition and deeper dives result in a higher proportion of time spent recuperating at the surface (Kramer 1988). To maximize the proportion of time spent in the food patch, we predict that surface time should increase with target depth (Houston & Carbone 1992).

## Materials and methods

### ETHICS STATEMENTS

The Ethics Committee of the French Polar Institute (IPEV) validated all scientific procedures applied on elephant seals. All

animals in this study were handled and cared for in total accordance with its guidelines and recommendations.

#### DEPLOYMENT OF DEVICES AND DATA COLLECTION

We used data from six post-breeding females SES (mean mass = 309 ± 68 kg; mean length = 247 ± 17 cm, Table 1) equipped on the Kerguelen Islands (49°20'S, 70°20'E) with an Argos-GPS satellite tag (Splash 10-F; Wildlife Computers, Redmond, WA, USA) combined with a time-depth recorder–accelerometer (TDR-MK10-X; Wildlife Computers). The six Splash-10-F tags were glued to the fur on the seals' heads. In 2010, three time-depth recorder–accelerometers were also glued on the head of three different seals, with another time-depth recorder–accelerometer (MK10-X; Wildlife Computers) on the back of one of them. The following year, two MK10-X were deployed on the animals' backs and one on the head, again on three different seals. Pressure was sampled at 1 Hz by TDR, ± 1% of reading. Data loggers were set to collect and archive pressure every second, while triaxial acceleration was sampled at 16 Hz.

The seals were captured with a canvas head-bag and anaesthetized using a 1:1 combination of Tiletamine and Zolazepam (Zoletil 100) injected intravenously (McMahon *et al.* 2000; Field *et al.* 2002). Data loggers were glued using a quick-setting epoxy glue (Araldite AW 2101), after the fur was cleaned with acetone. The loggers were then recovered when females SES returned to shore to moult (i.e. January–February following deployments). Seals ashore were located using their Argos locations.

All scripts used thereafter for data treatment and analysis are available upon request.

#### DIVE CYCLE STATISTICS

A dive cycle is defined as a dive (descent, bottom and ascent phases) followed by a period of time spent at the surface. Because there is drift over time in pressure transducers in TDR, due to different factors during a dive, a zero offset correction of depth was applied to our data set using a custom script performed with a commercial software package (MATLAB 8.1; The MathWorks, Natick, MA, USA). Only dives deeper than 15 m were kept for analysis, otherwise seals were considered to be at the surface. This threshold was chosen to avoid subsurface movements to be identified as dives. Each dive was then divided into three different phases: descent, bottom and ascent phases by using a vertical speed criterion chosen after a sensitivity analyses. Descent and ascent phases were characterized as a period when the vertical speed from or towards the surface, fitted to a polynomial of degree 4, was >0.75 m s<sup>-1</sup>. This is similar to the approach of Luque (2007) in its R package *diveMove*, but differs from most studies which determine the bottom time from the moment when a certain percentage of the maximum dive depth is achieved (Lesage, Hammill & Kovacs 1999; Inasley *et al.* 2008). Here, the bottom phase refers to a period between the descent and ascent phase where the fitted curve of the vertical speed was lower than

0.75 m s<sup>-1</sup>, in absolute terms. Time spent at the surface is the time lapse between two dives. This definition of the surface time results in a conservative definition of a dive, which avoids considering small subsurface excursions as dives. However, it also introduces consistent overestimation of time spent loading oxygen at the surface, as it includes the periods of descent and ascent above 15 m. Diving variables were calculated for each dive with MATLAB, using custom dive-analysis scripts. The selected diving variables were maximum depth (m), dive duration (s), time spent during descent, bottom and ascent phases (s). Data from the accelerometers were used to estimate stroke rate (Sato *et al.* 2003) and the intensity of the hind flipper movement, and subsequently used to calculate a swimming effort index (eqn 1), by using a 0.6 Hz-wide band pass centred on the second peak identified from the power spectral density.

$$\text{Swimming effort} = \frac{\sum |\text{peaks}|}{\Delta t} \quad \text{eqn 1}$$

The swimming effort (m s<sup>-3</sup>) was defined as the summed value of absolute acceleration peaks,  $\sum |\text{peaks}|$  (m s<sup>-2</sup>), over the relevant periods  $\Delta t$  (s) (Richard *et al.* 2014). Hereafter, the total swimming effort is defined as the sum of the absolute lateral acceleration (m s<sup>-2</sup>) only, that is without considering effort duration. Dive angles, defined as angles from the horizontal plane, were then calculated according to Tuck (2007) by using static acceleration obtained with a low-pass filtering (cut-off frequency of 0.2 Hz) applied to the three axes (eqn 2).

$$\text{Pitch} = \arctan \left( \frac{x}{\sqrt{(y^2 + z^2)}} \right) \quad \text{eqn 2}$$

#### BODY DENSITY

Body density variation over time was estimated according to methodology outlined by Richard *et al.* (2014). For each drift dive, a drift rate was determined by calculating the slope between depth and time using linear regression (Biuw *et al.* 2003; Bailleul *et al.* 2007; Mitani *et al.* 2010). If there were several drift dives, the drift rate was averaged by day. A model was then built to monitor these daily drift rate variations with changes in daily average swimming speed during the descent phase (Richard *et al.* 2014). Using this relationship, variations in daily drift rate were then calculated for every daily average descent swimming speed calculated from others dives. Finally, based on the drift dives model developed by Biuw *et al.* (2003), we then used the change in drift rate to assess body density variations. This method provided us daily estimates of body density for each animal.

#### PATCH QUALITY

The patch quality was assessed by considering the number of PCA per unit of time spent in the bottom phase of the dive (as detected

**Table 1.** Descriptive information about the six post-breeding females SESs

Seal ID	Body mass (kg)	Size (cm)	Departure date	Days recorded	Number of dives	Number of drift dives
10A5015	377	266	11/21/2010	74	4515	90
10A5017	245	225	10/29/2011	54	3768	48
10A5019	249	240	10/31/2011	56	3707	123
10A5022	255	232	10/31/2011	58	3727	61
78524	331	266	10/28/2010	61	3361	125
78525	395	252	11/01/2010	81	4118	49

by acceleration). PCA rate was considered to be a good proxy for prey encounter rate; we assume prey encounter rate is positively correlated with improved patch quality. Dynamic accelerations resulting from strokes and rapid head movements were extracted from the three axes with an order 3 high-pass digital Butterworth filter with a normalized cut-off frequency of 0.33 Hz (performed with `butter` function). For each axis, a fixed window of one-s was used to calculate the standard deviation every second. Signals reduced in this way were smoothed using a moving standard deviation with a window size of 5 s. Finally, a 2-mean clustering was performed for each signal. 1 was associated with data from the higher cluster and 0 to the others. Possible PCAs occur when a 1 was found in the three axes. A continuous succession of 1 was identified as a single PCA.

#### DATA ANALYSIS

All statistical analyses were conducted using R (R Development Core Team 2014). Linear mixed-effects models were fit with the `nlme` package (Pinheiro *et al.* 2013). Individuals were included as random factors, and we accounted for the temporal correlation in our data using an autoregressive variance-covariance matrix (`corAR1`). Drift dives were identified using Dragon *et al.*'s (2012) method. These dives which are not thought to be foraging dives, but rather recovery dives (Crocker, Le Boeuf & Costa 1997), were excluded from our analyses.

A basic model including all diving variables was constructed to explain bottom time variations in order to test the effect of the number of PCA and the depth on bottom time. Basic models investigated the bottom time duration in relation to dive duration, dive angle, diving depth and swimming effort. The animal's body density was also included to our models due to its important influence on diving behaviour. Following our preliminary analysis, three analyses were conducted: dives with PCA, dives without PCA and all dives. For each analysis, multi-model inference was used to select the best basic model according to Akaike Information Criterion (AIC), using  `dredge` function from the `MuMIn` R-package (Barton 2013).

To explore the relationship between bottom times and patch quality, the number of PCA was added to the basic model chosen. Similarly, a quadratic depth term was set as a co-variable, representing an increase, followed by a decrease of bottom time with depth, as predicted in the Houston & Carbone model (1992). We assessed the significance of both parameters by comparing the basic model with the addition of one variable to the basic model, using an ANOVA test. To investigate the variations of bottom time with the availability and the vertical accessibility of prey according to energy spent, a model based only on swimming effort during the bottom phase was built. This parameter was examined in relation to depth, bottom duration, body density and number of PCA.

To identify a possible change in the influence of PCA (occurrence and number of events) and body density on bottom duration and swimming behaviour according to diving depth, simple linear mixed-effects models including the variable considered and the depth were fitted for every 50 m depth class, from 50 to 1050 m. The effects of PCA and body density were assessed by the associated estimate and confidence interval (see Table S4), which were represented on all figures by ribbon graphs.

Finally, we investigated post-dive intervals in relation to the effort expended by SESs in the previous dive, in terms of time, total swimming effort and patch quality explored. Post-dive surface intervals were found to be directly related to the number of breaths taken by SES (Génin *et al.* 2015). All models were evaluated for surface intervals ranging between upper and lower fences ( $Q3 + 1.5IQR$  and  $Q1 - 1.5IQR$ ) where  $Q1$  is the lower 25% quantile,  $Q3$  is the upper 25%

quantile and  $IQR = Q3 - Q1$ , to remove outliers. Less than 3.4% ( $n = 782$ ) of the surface interval data ( $n = 23196$ ) were excluded from the analyses at the dive scale. We focused on recovery periods likely to be related directly to the previous dive. Extended surface intervals may represent other surface behaviours, such as socializing or extended recovery periods at a multi-dive scale.

## Results

#### OVERALL DIVING BEHAVIOUR

A total of 23 196 dives were recorded from the six post-breeding females SESs: 2.1% were drift dives; the other 97.9% were processed to extract the number of PCA, dive angles and swimming effort. Mean dive duration was  $20.7 \pm 4.8$  min, and the maximum dive duration was 56.0 min (Table 2). The overall mean dive depth was  $542 \pm 226$  m reaching up to 1318 m. PCA were detected in 89.0% of non-drift dives. Within those dives, 14.8% of PCA occurred during the descent phase, 12.6% during the ascent and 72.6% during the bottom phase (Table 2).

#### BASIC MODELS

Although three different analyses were considered, that is situations considering all dives, dives with PCA and dives without, the global model, that is including all variables, was the most parsimonious in each situation ( $wAIC = 0.94$ ,  $wAIC = 0.99$  and  $wAIC = 0.62$  respectively; see Supporting Information, Table S1). We found a positive relationship between bottom time and dive duration, dive angles and swimming effort. Conversely, we found a negative relationship between bottom time and depth, swimming effort during descent phase and animal's body density (Table 3).

#### BOTTOM TIME VS. DEPTH RELATED TO PREY AVAILABILITY AND BODY DENSITY

The quadratic depth term emerged as a significant parameter in dives with and without PCA ( $P$ -value = 0.004 and  $P$ -value < 0.001, respectively; Table 4). However, even if the negative parameter tended to be in agreement with Houston & Carbone (1992) when considering all dives together, this variable was not significant ( $P$ -value = 0.302). In PCA dive, bottom time did not change with diving depth up to 550 m and decreased with greater diving depth. In non-PCA, bottom time increased with diving depth up to 550 m and then decreased with increasing diving depth (Fig. 1). For both dives with and without PCA, we therefore observed a break in bottom time, followed by a decrease around 550 m depth (Fig. 1).

Bottom time was significantly shorter when PCA were present (Table 4) compared to dives without PCA in the model that considered all dives. However, when considering diving depth, SESs exhibited longer bottom durations in the presence of PCA until 350 m (Fig. 1). Between

**Table 2.** Main dive characteristics obtained for the six post-breeding females SESs, drift dives excluded. Mean values are given with  $\pm$  SD

Seal ID	10A5015	10A5017	10A5019	10A5022	78524	78525
<i>n</i> Dives	4425	3768	3707	3727	3361	4118
Dive time (s)	1269.16 $\pm$ 307.76	1070.61 $\pm$ 198.45	1157.36 $\pm$ 281.87	1190.12 $\pm$ 212.46	1376.75 $\pm$ 286.89	1350.54 $\pm$ 271.27
Max dive time (s)	3027	3004	2968	3114	2801	3362
Bottom time (s)	758.35 $\pm$ 243.52	458.75 $\pm$ 216.37	571.55 $\pm$ 239.39	502.10 $\pm$ 270.14	573.78 $\pm$ 346.98	792.19 $\pm$ 329.49
Descent swimming effort (m s <sup>-3</sup> )	0.25 $\pm$ 0.09	0.33 $\pm$ 0.09	0.25 $\pm$ 0.14	0.23 $\pm$ 0.10	0.20 $\pm$ 0.14	0.20 $\pm$ 0.12
Bottom swimming effort (m s <sup>-3</sup> )	0.55 $\pm$ 0.14	0.85 $\pm$ 0.23	0.73 $\pm$ 0.21	0.70 $\pm$ 0.20	0.69 $\pm$ 0.23	0.53 $\pm$ 0.16
Ascent swimming effort (m s <sup>-3</sup> )	0.78 $\pm$ 0.17	1.52 $\pm$ 0.21	1.16 $\pm$ 0.20	1.32 $\pm$ 0.27	1.35 $\pm$ 0.20	0.89 $\pm$ 0.15
Descent angle (°)	-42.72 $\pm$ 11.23	-51.78 $\pm$ 11.39	-54.70 $\pm$ 12.71	-43.92 $\pm$ 10.50	-43.88 $\pm$ 9.62	-34.39 $\pm$ 9.51
Ascent angle (°)	52.62 $\pm$ 14.64	71.54 $\pm$ 7.08	69.01 $\pm$ 9.06	63.37 $\pm$ 11.20	46.52 $\pm$ 14.58	53.40 $\pm$ 13.93
Dive depth (m)	469 $\pm$ 230	563 $\pm$ 186	532 $\pm$ 215	583 $\pm$ 231	643 $\pm$ 221	508 $\pm$ 234
Max diving depth (m)	1318	1271	1183	1300	1188	1260
<i>n</i> PCA in descent phase	0.79 $\pm$ 1.54	1.76 $\pm$ 1.95	0.91 $\pm$ 1.47	2.28 $\pm$ 2.65	0.88 $\pm$ 1.47	1.31 $\pm$ 2.38
<i>n</i> PCA in bottom phase	8.88 $\pm$ 7.33	5.66 $\pm$ 4.65	6.62 $\pm$ 5.22	8.10 $\pm$ 7.98	4.43 $\pm$ 5.12	4.53 $\pm$ 6.05
<i>n</i> PCA in ascent phase	1.08 $\pm$ 1.78	1.29 $\pm$ 1.67	0.95 $\pm$ 1.39	1.66 $\pm$ 1.97	0.91 $\pm$ 1.55	1.05 $\pm$ 1.86
Surface time (s)	129.39 $\pm$ 129.52	143.26 $\pm$ 73.26	128.63 $\pm$ 72.17	138.85 $\pm$ 89.41	172.55 $\pm$ 159.48	143.43 $\pm$ 51.51

350 and 750 m dives with PCA had a shorter bottom duration compared to dives without. Beyond this depth, the difference is more tenuous, that is PCA estimate closer to 0, but seals spent more time at the bottom in PCA dives (Fig. 1). When only dives with PCA were taken into account, bottom duration was found to be negatively correlated ( $P$ -value  $< 0.001$ ) to PCA occurring in the transit phases but positively ( $P$ -value  $< 0.001$ ) to those occurring at the bottom of the dive (Table 4). The latter pattern is significant for depths ranging between 250 and 950 m (Fig. 2). Outside this depth range, the number of PCA does not significantly influence the time spent at the bottom.

All seals remained negatively buoyant during the time of this study, with seal density ranging from 1036 to 1059 kg m<sup>-3</sup>. The negative relationship found in basic models between bottom duration and body density occurred at almost all depth ranges (Fig. 3). Apart from 50 to 250 m and between 550 and 600 m, the closer to neutral buoyancy the SES was, the longer the dive bottom duration was.

#### SWIMMING EFFORT VS. BODY DENSITY

The total swimming effort increased almost linearly with depth (Fig. 4). However, a shift was observed at 300 m according to seal density. At shallower depth, body density does not influence significantly the total swimming effort. At greater diving depth, seals closer to neutral buoyancy exhibit a smaller swimming effort compared to denser ones (Fig. 4).

The distribution of bottom swimming effort according to depth ranges showed clear differences between dives with and without PCA (Fig. 5; Table 5). Generally, swimming effort at the bottom of the dive increased when PCA were present. However, from 150 m in the absence of PCA, seals clearly decreased their swimming effort at the bottom of their dive. We also found a positive relationship of the bottom swimming effort with maximum depth and body density, and a negative relationship with the bottom time (Table 5).

The model that considers only dives with PCA provides support for an increase of bottom swimming effort with the number of PCA, mediated by seal density (Table 5). In these dives, the seals swimming effort in the bottom phase was also found to increase with their body density.

A shift of the ratio of the total swimming effort at the bottom to the total swimming effort during transit phases, that is descent and ascent phases, is observed for diving depth close to 550 m (see Fig. S1). At this depth, the total bottom swimming effort becomes greater than the total transiting swimming effort. This ratio is also depending on the animal's body density (Table 6), which means the depth limit from which this ratio drops below 1, that is total transiting swimming effort  $>$  total bottom swimming effort, is reached sooner for denser (550 m for a seal den-

**Table 3.** Relationships between bottom time (bottomTime) and its predictors from best model chosen with parsimony (see Table S1) in each situation and associated *P*-value. Co-variables were dive duration (diveTime), maximum depth (maxDepth), ascent and descent angles (ascentAngle, descentAngle), ascent and descent swimming effort (ascentEffort, descentEffort) and body density (bodyDensity)

Models	Parameters	All dives ( <i>N</i> = 22 700)		Dives with captures ( <i>N</i> = 18 770)		Dives without captures ( <i>N</i> = 3930)	
		Estimate	<i>P</i> -value	Estimate	<i>P</i> -value	Estimate	<i>P</i> -value
bottomTime ~	diveTime	266.83 ± 0.91	<0.01	262.08 ± 0.95	<0.01	278.34 ± 2.14	<0.01
	maxDepth	-275.11 ± 0.95	<0.01	-273.84 ± 0.95	<0.01	-288.99 ± 4.48	<0.01
	descentAngle	-24.25 ± 0.70	<0.01	-24.50 ± 0.80	<0.01	-31.15 ± 2.08	<0.01
	ascentAngle	25.48 ± 0.74	<0.01	22.15 ± 0.76	<0.01	49.14 ± 2.93	<0.01
	descentEffort	-5.55 ± 0.64	<0.01	-5.57 ± 0.66	<0.01	-1.69 ± 2.79	0.55
	ascentEffort	15.81 ± 0.81	<0.01	13.91 ± 0.84	<0.01	23.95 ± 2.73	<0.01
	bodyDensity	-3.52 ± 1.10	<0.01	-3.15 ± 1.06	<0.01	-1.42 ± 4.67	0.76

**Table 4.** Results from ANOVAS between basic models and basic models with a quadratic term of maximum depth (maxDepth<sup>2</sup>), the number of PCA (PCA count) or the presence of PCA (PCA<sub>presence</sub>) added. For each models, the Akaike's information criterion (AIC) and the Bayesian information criterion (BIC) were calculated. For each co-variable added, the value and the standard deviation associated were calculated (Estimate) as well as the log-likelihood ratio (L.ratio) and associated *P*-value for each ANOVAS performed

Models	Parameters	AIC	BIC	Estimate	L.ratio	<i>P</i> -value
bottomTime ~ (All dives)	Basic model	258515.7	258603.8			
	Term added: maxDepth <sup>2</sup>	258516.7	258612.7	-0.128 ± 0.67	1.07	0.302
	PCA <sub>presence</sub>	258489.2	258585.3	-11.55 ± 2.31	28.49	<0.001
bottomTime ~ (Dives with PCA)	Basic model	229518.5	229605.4			
	Term added: maxDepth <sup>2</sup>	229512.1	229606.9	1.85 ± 0.68	8.41	0.004
	<i>n</i> PCA in bottom phase	229486.5	229581.3	4.33 ± 0.75	34.03	<0.001
	<i>n</i> PCA in transit phase	229503.7	229598.5	-2.79 ± 0.71	16.77	<0.001
bottomTime ~ (Dives without PCA)	Basic model	27693.1	27755.8			
	Term added: maxDepth <sup>2</sup>	27683.9	27752.4	-7.46 ± 2.75	11.17	<0.001

sity ranging between 1036 and 1045 kg m<sup>-3</sup>, see Fig. S1) than lighter animals (600 m for a seal density ranging between 1051 and 1059 kg m<sup>-3</sup>, see Fig. S1).

#### SURFACE TIME VS. EFFORT MADE

The selected model that surface intervals were best explained and positively related to the total swimming effort and dive duration (Table 7; wAIC = 0.73, see Table S3). Adding PCA did not improve the model (wAIC = 0.27, see Table S3).

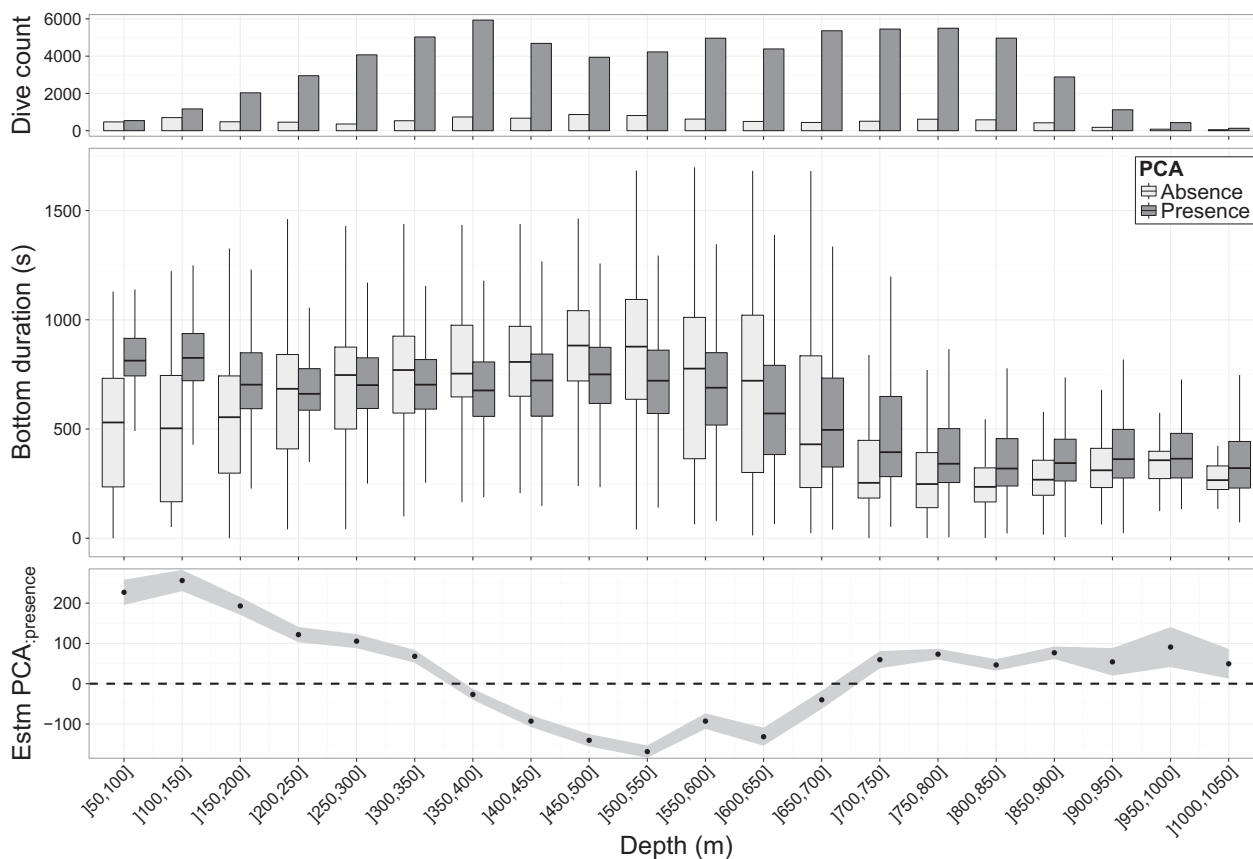
## Discussion

Although neither the exact quantity of prey ingested, nor their quality can be assessed, the accelerometer provides a quantitative index of the number of PCA. It allows us to investigate the changes in foraging behaviour of SES females in relation to their dive patterns. This method provides an estimate of where, when and how often foraging events occurred within a dive in these free-ranging marine predators. An increasing body of evidence

suggests that diving predators remain within their aerobic dive limit while diving (Costa, Gales & Goebel 2001; Costa *et al.* 2004) as the incurred costs of anaerobic dives are too high to forage efficiently (Kooyman *et al.* 1980, 1983). Only aerobic metabolism allows frequent, repetitive dives as elephant seals do. The current study suggests that to remain within their aerobic limit, SESs optimize their diving behaviour and duration according to a number of parameters including foraging success and buoyancy.

#### BOTTOM TIME AND DEPTH

Regardless of the prey encounter events, bottom time was found to decrease linearly with depth. However, this relationship was not significant according to the quadratic polynomial relationship as predicted by Houston & Carbone's (1992), which assumes that the foraging time correspond to the bottom duration. When distinguishing dives with and without PCA, the bottom duration was found to vary according to a quadratic polynomial for non-PCA (unsuccessful) dives. Bottom time first increased then



**Fig. 1.** Bottom duration related to depth and prey availability. The histogram represents the number of dives per boxplots. Between 350 and 700 m, bottom duration is less important when animals catch prey (estimate  $PCA_{:presence} < 0$ , see Table S4), whereas it is the opposite deeper (estimate  $PCA_{:presence} > 0$ , see Table S4).

decreased with depth in non-PCA dives. In successful dives, model outcome suggests the opposite: a decrease then an increase (Table 4). This result must be taken with caution due to the weakness of the quadratic depth term (estimate =  $1.85 \pm 0.68 \text{ m}^2$ ;  $P$ -value = 0.004). Bottom time remained fairly constant until the seals reached 550 m, whereupon bottom time was negatively related to increasing diving depth (Fig. 1). The patterns found for PCA dives were therefore consistent with studies examining behaviour of diving birds (Carbone & Houston 1994; Cook *et al.* 2008), where a nonlinear relationship of bottom time with depth are also found. At shallow depths, birds maintain low oxygen reserves in order to experience higher rates of oxygen intake. As dive depth increases, birds increase the size of their oxygen stores to allow more foraging time. When approaching the maximum dive duration, they decrease their foraging time at the bottom to compensate for increasing travel time with increasing diving depth (Carbone & Houston 1994). Our results are consistent with such a trade-off between foraging time and travel time. Beyond 550 m dive depth, depending on the seal's body density, the overall transiting swimming effort and therefore the cost to access the prey were found to exceed the swimming effort spent by the seal at the bottom of the dive (Fig. S1). This depth corresponds to the point

at which bottom time starts decreasing with increasing dive depth (Fig. 1).

#### BOTTOM TIME AND PCA

Our results indicate that SES has shorter bottom times in dives when PCA occurred compared to non-PCA dives. This is true between 350 and 700 m, but not for shallower depths where bottom time was longer in the presence of PCA. For dives deeper than 700 m, there was almost no difference in bottom time between dives with and without PCA. Therefore, at shallow and greater depths our results were consistent with Thompson & Fedak's predictions (2001). They suggest that there is a benefit to ending dives earlier when no PCA occur at shallow depths. Regardless of foraging success, seals should also maximize the bottom time for very deep dives to compensate for transit time between the surface and the dive bottom. Other empirical studies agree with these results, such as Sparling *et al.* (2007) on grey seals (*Halichoerus grypus*) and Mori *et al.* (2002) on Brünnich's guillemots, (*Uria lomvia*).

However, between 350 and 700 m, our results differ from predictions. SESs were found to perform longer bottom durations when no PCA occurred. They did it by

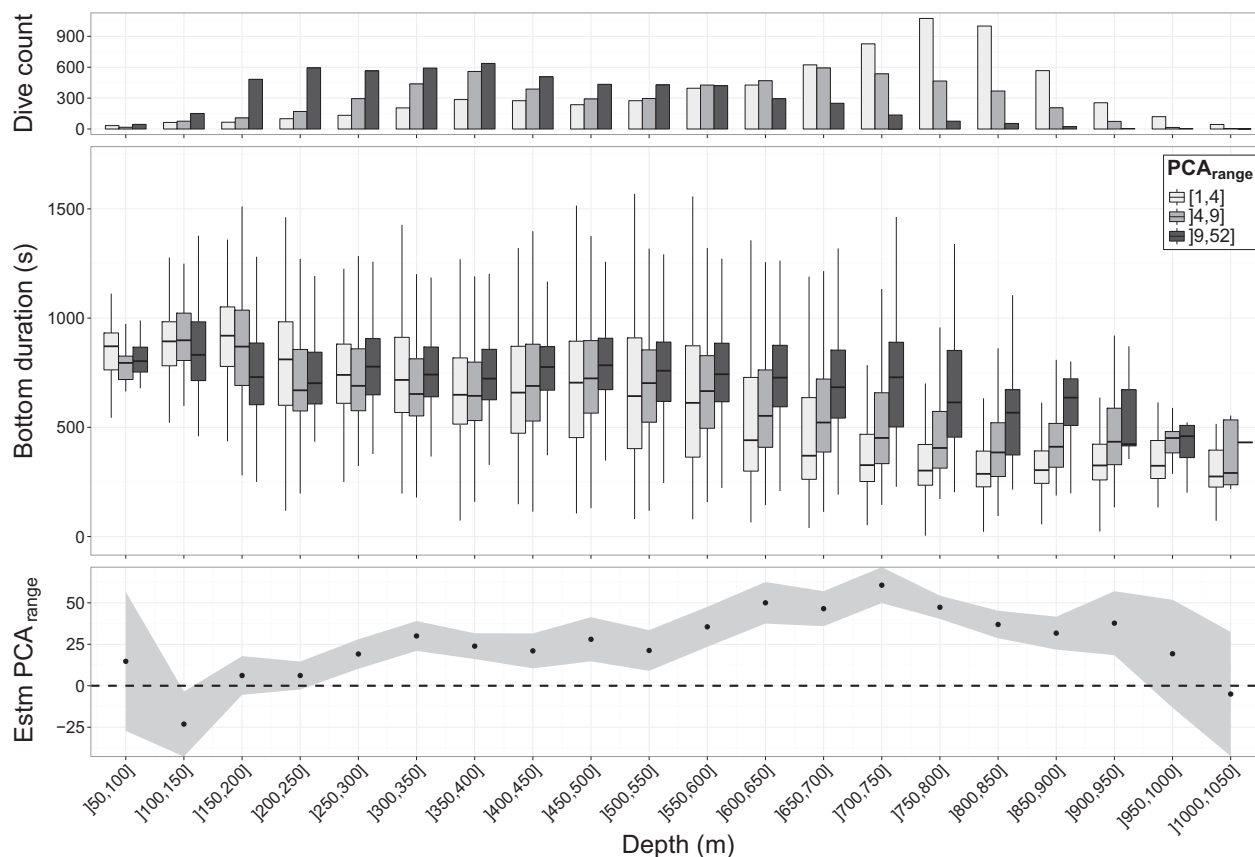


Fig. 2. Bottom duration related to depth and number of PCA at the bottom phase. The histogram represents the number of dives per box-plots. Below 250 m depth, bottom duration increases significantly with the number of PCA (estimate  $PCA_{Range} > 0$ , see Table S4).

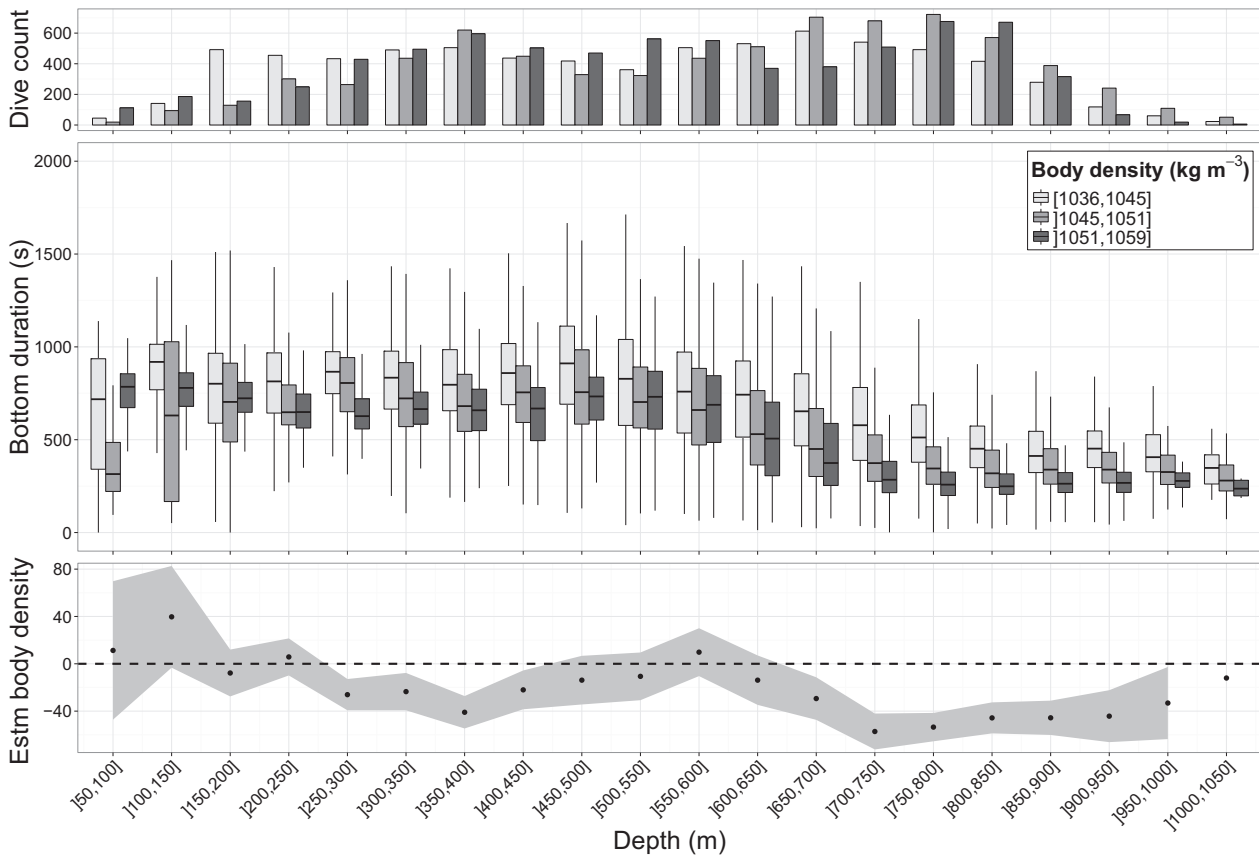
reducing their swimming effort during the bottom phase. It is unclear at this stage whether the reduction in the swimming effort is either related to a searching strategy where the seal ceases to actively swim to investigate their environment using visual or auditory cues, or to a general slow descending behaviour (mainly gliding) as long as they do not encounter prey. Preliminary investigation suggests that negatively buoyant post-breeding seals rely on their negative buoyancy to glide down at a low negative pitch while searching for their prey during the bottom phase of the dive. On average, the end of the bottom phase was  $61 \pm 109$  m deeper than the beginning of the bottom phase in non-PCA dives, while no trends were found in PCA dives. The reduction in energy and oxygen consumption could then allow them to stay at the bottom for longer periods (Boyd 1997; Cornick & Horning 2003). It also provides support for the inclusion of the energetic approach to study optimal foraging in free-ranging animals. This point should be investigated further: if our interpretation is correct, we expect to observe the opposite trend in positively buoyant seals with a decreasing depth between the beginning and the end of the bottom phase in non-PCA dives.

When considering dives where at least one PCA occurred, the more PCA performed by seals at any given bottom depth, the longer the bottom time was. This result

is consistent with what Cornick & Horning (2003) found in captive Steller sea lion, *Eumetopias jubatus*. This finding provides further support for the assumption that bottom time is positively related to patch quality. When SESs perform at least one PCA during the bottom phase, bottom time increases significantly with PCA, which is also consistent with Thompson & Fedak's prediction (2001). However, when only dive data are available, it is not possible to distinguish between non-PCA and PCA dives. Consequently, using the duration of the bottom foraging phase according to diving depth as a proxy of foraging success (Boyd, Reid & Bevan 1995; Fedak, Lovell & Grant 2001; Watwood *et al.* 2006) can be seriously misleading in SES. Non-PCA dives will be detected as the most successful dives over a broad range of diving depth. While positive residuals at shallow depths (up to 350 m) are likely to be indicative of higher foraging success, higher bottom duration residuals than expected at depths ranging from 300 to 700 m are likely to be indicative of a poor foraging success. This latter pattern is consistent with what Thums *et al.* (2013) found on adult female southern elephant seals at Macquarie Island.

When PCA occurred in descent and ascent phases, SESs significantly reduced the time they spent at the bottom with increasing numbers of PCA during these transit phases. This suggests that energy expenditure increases





**Fig. 3.** Bottom duration related to depth and animal's body density. The histogram represents the number of dives per boxplots. Except until 250 m depth and between 450 and 650 m, the fatter a SES, the more it can spend time at the bottom (estimate Body Density < 0, see Table S4).

when the seal is catching prey. This is expected to have direct consequences on the amount of time SESs are able to allocate to stay at the bottom of their dive (McConnell, Chambers & Fedak 1992).

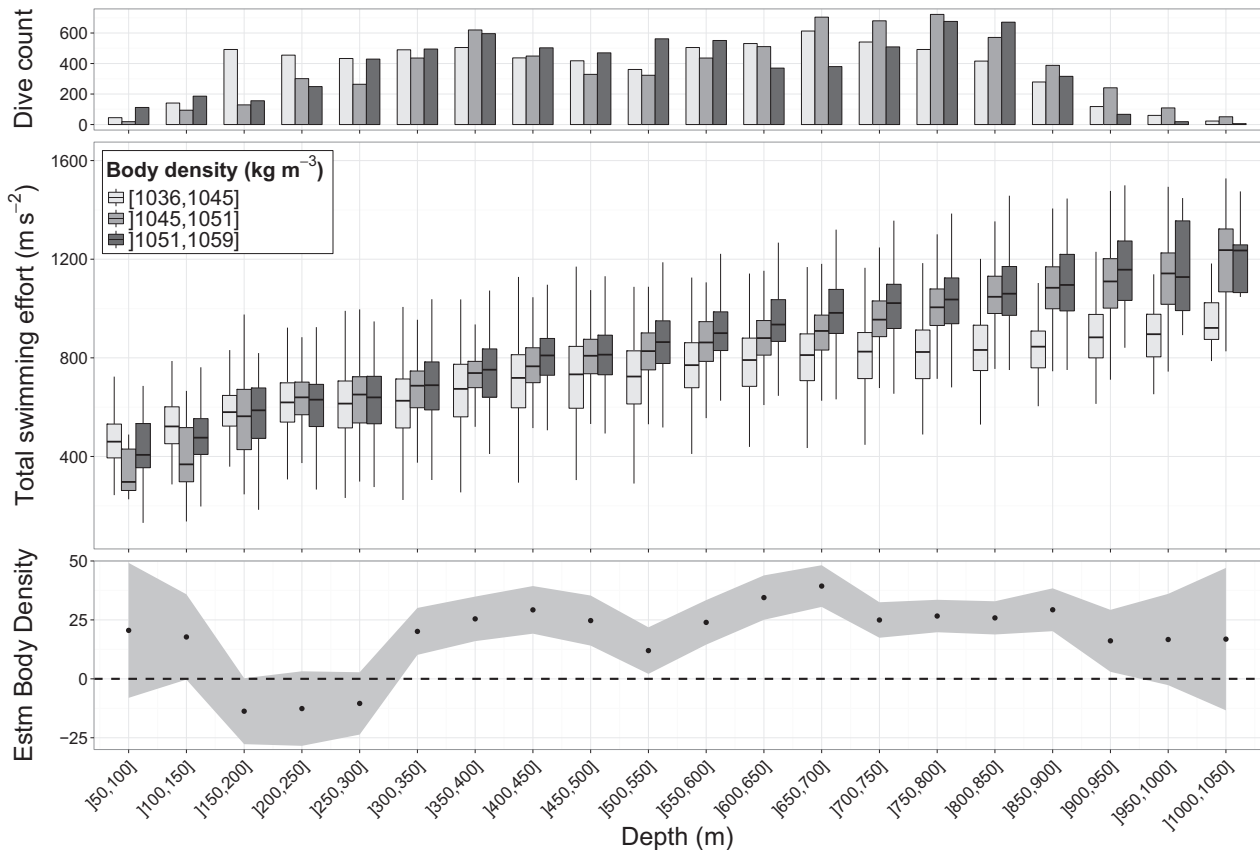
#### BOTTOM TIME, BODY DENSITY AND SWIMMING EFFORT

The animal's body density, or buoyancy, was an important parameter in controlling the duration of the dive bottom phase. The three basic models (Table 3) provide support for a negative relationship between bottom time and body density, that is the more negatively buoyant the seals, the shorter the bottom duration. This finding is consistent with results found by Beck, Bowen & Iverson (2000) that showed denser grey seals displayed shorter bottom duration compared to fatter seals. Our results are also in accordance with several other studies which show buoyancy as an important variable of diving behaviour (Webb *et al.* 1998; Beck, Bowen & Iverson 2000; Miller *et al.* 2004; Adachi *et al.* 2014; Richard *et al.* 2014) and that the round trip cost of transport is lowest at neutral buoyancy (Miller *et al.* 2012; Sato *et al.* 2013). Negatively buoyant animals are assisted during descent phase by their higher density, but must swim harder during the ascent (Richard *et al.*

2014). Williams *et al.* (2000) showed that several marine mammals used their buoyancy to adopt this energy-conserving strategy.

Seals are subjected to body compression during the whole dive, but particularly at the beginning which may explain inversions of slope for the first depth ranges (Fig. 4). Complete lung collapse is supposed to occur at these depths (Kooymann & Sinnett 1982; Falke *et al.* 1985; McDonald & Ponganis 2012). When their lungs are not completely collapsed, seals which are negatively buoyant but close to neutral buoyancy remain positively buoyant and should provide an overall greater total swimming effort to remain at those depths, compared to more negatively buoyant seals. The opposite relationship is found at greater diving depths, where buoyancy is almost exclusively related to body composition, that is lipid proportion: seals tending to provide higher total swimming effort when they are further from neutral buoyancy.

We found a positive relationship between the swimming effort at the bottom and the number of PCA occurring during the bottom of a dive. In other words, SESs are swimming more actively when catching prey. Seals closer to neutral buoyancy spend more time at the bottom of their dive compared to denser animals which were



**Fig. 4.** Total swimming effort related to depth and animal's body density. The histogram represents the number of dives per boxplots. A shift is observed around 300 metres depth; denser animals must provide a higher effort below that depth (estimate Body Density > 0, see Table S4).

**Table 5.** Relationship for the top-ranked model of the bottom swimming effort (bottomEffort) with bottom time (bottomTime), maximum depth (maxDepth), body density (bodyDensity), presence of PCA ( $PCA_{:presence}$ ) or number of capture attempts ( $n$  PCA), depending on the situation (all dives or dives with PCA), and associated  $P$ -value

Models	Parameters	Estimate	$P$ -value
bottomEffort (All dives)	bottomTime	$-0.11 \pm 0.001$	<0.001
	maxDepth	$0.05 \pm 0.001$	<0.001
	bodyDensity	$0.02 \pm 0.002$	<0.001
bottomEffort (Dives with PCA)	$PCA_{:presence}$	$0.05 \pm 0.004$	<0.001
	bottomTime	$-0.12 \pm 0.001$	<0.001
	maxDepth	$0.02 \pm 0.001$	<0.001
	bodyDensity	$0.02 \pm 0.001$	<0.001
	$n$ PCA	$0.05 \pm 0.001$	<0.001

observed to make a greater swimming effort during the bottom phase to maintain themselves at their preferred foraging depth.

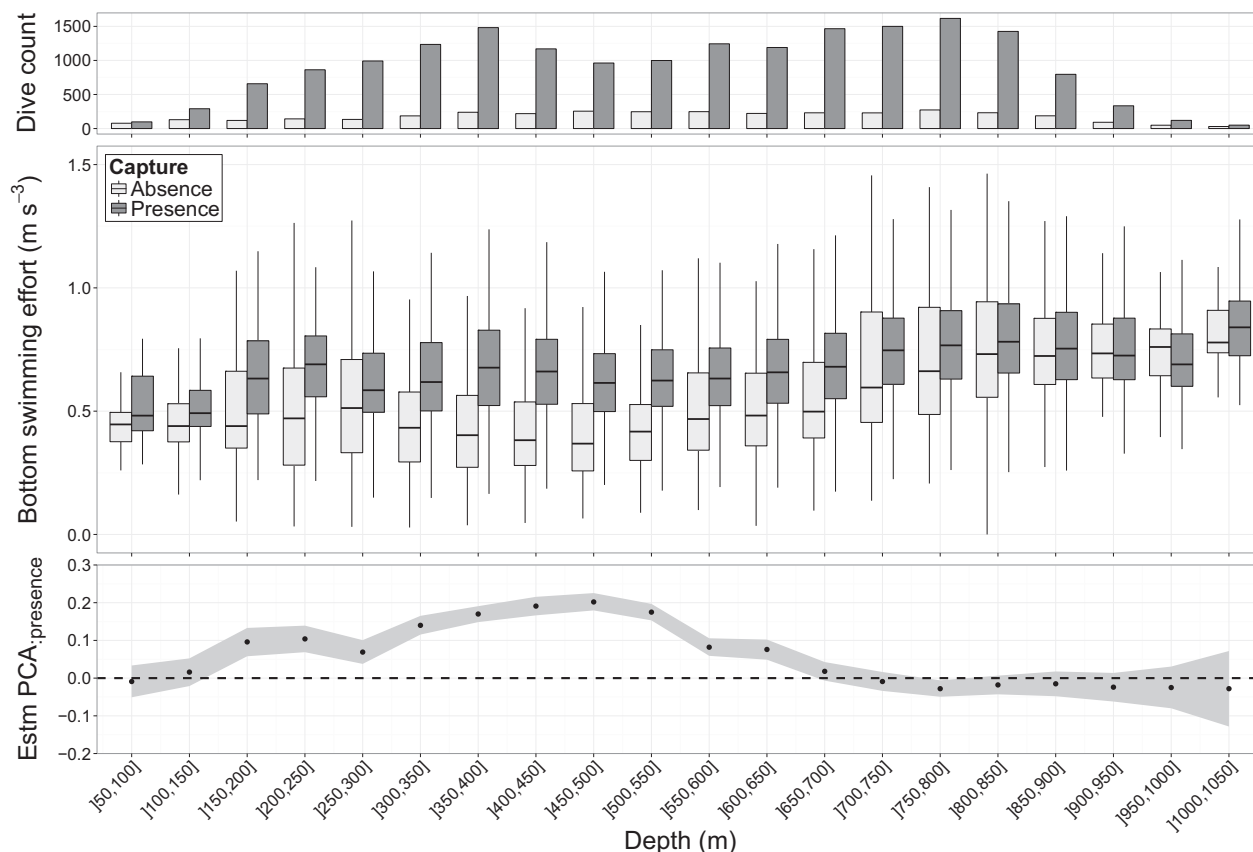
#### SURFACE TIME AND DIVING BEHAVIOURS

Surface time is expected to vary with increasing dive duration and foraging effort in diving predators. Kramer (1988) claimed that post-dive interval should

increase with depth due to the shape of the oxygen uptake function. We found that the time spent at surface replenishing the oxygen stores was positively related to dive duration and total swimming effort exerted during the previous dive. Le Boeuf *et al.* (2000) also found a strong effect of dive duration on surface time, but this was highly variable and depended on the seal studied. That variability observed could be due to the variation of the total swimming effort measured in the current study. Because dive duration and total swimming effort are both positively related to diving depth, the maximum depth reached was also found to positively influence the duration of the surface interval. Despite the fact that the swimming effort at the bottom of the dive was positively related to the number of PCA, the number of PCA itself was not found to be a significant parameter in this model. Similarly, the swimming effort is likely to be related to the seal's buoyancy and was found to contribute significantly to the bottom duration in our study.

#### Conclusions

This study highlights the importance of using a correct metrics of foraging success to accurately reflect true for-



**Fig. 5.** Bottom swimming effort related to depth and prey availability. The histogram represents the number of dives per boxplots. Below 150 m depth, bottom swimming effort is more important for dives with prey catch attempts (estimate  $PCA_{\text{presence}} > 0$ , see Table S4). This difference disappears beyond 550 m depth.

**Table 6.** Relationship for the ratio of total bottom swimming effort to total transit swimming effort ( $\frac{TOT_{\text{bottomEffort}}}{TOT_{\text{transitEffort}}}$ ) with depth (maxDepth) and body density (bodyDensity), and associated  $P$ -value

Model	Parameters	Estimate	$P$ -value
$\frac{TOT_{\text{bottomEffort}}}{TOT_{\text{transitEffort}}} \sim$	maxDepth	$-0.09 \pm 0.01$	$<0.001$
	bodyDensity	$-0.07 \pm 0.02$	0.015

**Table 7.** Relationship for the top-ranked model of the surface time (surfaceTime) with total swimming effort (diveEffort), dive time (diveTime) of the previous dive, and associated  $P$ -value

Model	Parameters	Estimate	$P$ -value
surfaceTime $\sim$	diveEffort	$3.68 \pm 0.08$	$<0.001$
	diveTime	$2.90 \pm 0.13$	$<0.001$

aging success. This is essential to investigate further the relationship between time spent at the bottom and prey acquisition, which is assumed by most of the optimal foraging models developed (Kramer 1988; Houston & Carbone 1992; Thompson, Hiby & Fedak 1993; Carbone & Houston 1996). Finally, this study demonstrates the

usefulness of accelerometers to understand diving behaviour. Data from these highlight for the first time the combined effects of buoyancy, prey encounters and diving depth, on variations in swimming effort in a free-ranging marine predator, and consequently, in the control at very fine scale of the diving behaviours in a marine mammal.

## Acknowledgements

The authors would like to thank all the persons involved in the tagging and controls of elephant seals on Kerguelen Island and the French Polar Institute (Institut Paul Emile Victor, IPEV), for providing logistic and financial support. This work was carried out in the framework of the ANR Blanc MYCTO-3D-MAP, ANR VMC IPSOS-SEAL programs and CNES-TOSCA program ('Éléphants de mer océanographes'). This study is part of a IPEV program no. 109, (P.I. H. Weimerskirch) and the observatory Mammifères Explorateurs du Milieu Océanique, (MEMO SOERE CTD 02). The authors also thank the Total Foundation for financial support as well as Malcolm O'Toole and Tiphaine Jeanniard du Dot for correcting the English. They would particularly like to thank Patrick Duncan for his writing assistance and his informed proofreading. J.J. was supported by «Direction Générale de l'Armement».

## Data accessibility

Data deposited in the Figshare repository: <http://dx.doi.org/10.6084/m9.-figshare.1452900> (Jouma'a et al. 2015).

## References

- Adachi, T., Maresh, J.L., Robinson, P.W., Peterson, S.H., Costa, D.P., Naito, Y. *et al.* (2014) The foraging benefits of being fat in a highly migratory marine mammal. *Proceedings of the Royal Society of London B: Biological Sciences*, **281**, 20142120.
- Bailleul, F., Charrassin, J.-B., Monestiez, P., Roquet, F., Biuw, M. & Guinet, C. (2007) Successful foraging zones of southern elephant seals from the Kerguelen Islands in relation to oceanographic conditions. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **362**, 2169–2181.
- Barton, K. (2013) MuMIn: Multi-model inference. R package version 1.9.13.
- Beck, C.A., Bowen, W.D. & Iverson, S.J. (2000) Seasonal changes in buoyancy and diving behaviour of adult grey seals. *The Journal of Experimental Biology*, **203**, 2323–2330.
- Biuw, M., McConnell, B., Bradshaw, C.J.A., Burton, H. & Fedak, M. (2003) Blubber and buoyancy: monitoring the body condition of free-ranging seals using simple dive characteristics. *The Journal of Experimental Biology*, **206**, 3405–3423.
- Boyd, I.L. (1997) The behavioural and physiological ecology of diving. *Trends in Ecology & Evolution*, **12**, 213–217.
- Boyd, I.L., Reid, K. & Bevan, R.M. (1995) Swimming speed and allocation of time during the dive cycle in Antarctic fur seals. *Animal Behaviour*, **50**, 769–784.
- Butler, P.J. & Jones, D.R. (1997) Physiology of diving of birds and mammals. *Physiological Reviews*, **77**, 837–899.
- Carbone, C. & Houston, A.I. (1994) Patterns in the diving behaviour of the pochard, *Aythya ferina*: a test of an optimality model. *Animal Behaviour*, **48**, 457–465.
- Carbone, C. & Houston, A.I. (1996) The optimal allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. *Animal Behaviour*, **51**, 1247–1255.
- Cook, T.R., Lescroël, A., Tremblay, Y. & Bost, C.-A. (2008) To breathe or not to breathe? Optimal breathing, aerobic dive limit and oxygen stores in deep-diving blue-eyed shags. *Animal Behaviour*, **76**, 565–576.
- Cornick, L.A. & Horning, M. (2003) A test of hypotheses based on optimal foraging considerations for a diving mammal using a novel experimental approach. *Canadian Journal of Zoology*, **81**, 1799–1807.
- Costa, D.P., Gales, N.J. & Goebel, M.E. (2001) Aerobic dive limit: how often does it occur in nature? *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology*, **129**, 771–783.
- Costa, D., Kuhn, C., Weise, M., Shaffer, S. & Arnould, J. (2004) When does physiology limit the foraging behaviour of freely diving mammals?
- Crocker, D.E., Le Boeuf, B.J. & Costa, D.P. (1997) Drift diving in female northern elephant seals: implications for food processing. *Canadian Journal of Zoology*, **75**, 27–39.
- Dragon, A., BarHen, A., Monestiez, P. & Guinet, C. (2012) Horizontal and vertical movements as predictors of foraging success in a marine predator. *Marine Ecology Progress Series*, **447**, 243–257.
- Falke, K.J., Hill, R.D., Qvist, J., Schneider, R.C., Guppy, M., Liggins, G.C. *et al.* (1985) Seal lungs collapse during free diving: evidence from arterial nitrogen tensions. *Science*, **229**, 556–558.
- Fedak, M.A., Lovell, P. & Grant, S.M. (2001) Two approaches to compressing and interpreting time-depth information as collected by time-depth recorders and satellite-linked data recorders. *Marine Mammal Science*, **17**, 94–110.
- Field, I.C., Bradshaw, C.J.A., McMahon, C.R., Harrington, J. & Burton, H.R. (2002) Effects of age, size and condition of elephant seals (*Mirounga leonina*) on their intravenous anaesthesia with tiletamine and zolazepam. *The Veterinary Record*, **151**, 235–240.
- Fossette, S., Gleiss, A.C., Myers, A.E., Garner, S., Liebsch, N., Whitney, N.M. *et al.* (2010) Behaviour and buoyancy regulation in the deepest-diving reptile: the leatherback turtle. *The Journal of Experimental Biology*, **213**, 4074–4083.
- Génin, A., Richard, G., Jouma'a, J., Picard, B., El Ksabi, N., Vacquie Garcia, J. *et al.* (2015) Characterization of postdive recovery using sound recordings and its relationship to dive duration, exertion and foraging effort of southern elephant seals (*Mirounga leonina*). *Marine Mammal Science*. doi: 10.1111/mms.12235
- Guinet, C., Vacquie-Garcia, J., Picard, B., Bessigneul, G., Lebras, Y., Dragon, A.C. *et al.* (2014) Southern elephant seal foraging success in relation to temperature and light conditions: insight into prey distribution. *Marine Ecology Progress Series*, **499**, 285–301.
- Heithaus, M.R. & Frid, A. (2003) Optimal diving under the risk of predation. *Journal of Theoretical Biology*, **223**, 79–92.
- Houston, A.I. (2011) Assessing models of optimal diving. *Trends in Ecology & Evolution*, **26**, 292–297.
- Houston, A.I. & Carbone, C. (1992) The optimal allocation of time during the diving cycle. *Behavioral Ecology*, **3**, 255–265.
- Houston, A.I. & McNamara, J.M. (1985) The variability of behaviour and constrained optimization. *Journal of Theoretical Biology*, **112**, 265–273.
- Insley, S., Robson, B., Yack, T., Ream, R. & Burgess, W. (2008) Acoustic determination of activity and flipper stroke rate in foraging northern fur seal females. *Endangered Species Research*, **3**, 147–155.
- Jouma'a, J., Bras, Y.L., Richard, G., Vacquie-Garcia, J., Picard, B., Ksabi, N.E. *et al.* (2015) Data from: adjustment of diving behaviour with prey encounters and body condition in a deep diving predator: the Southern Elephant Seal. *Figshare*. doi: 10.6084/m9.figshare.1452900.
- Kacelnik, A., Houston, A.I. & Schmid-Hempel, P. (1986) Central-place foraging in honey bees: the effect of travel time and nectar flow on crop filling. *Behavioral Ecology and Sociobiology*, **19**, 19–24.
- Kooyman, G.L. & Ponganis, P.J. (1998) The physiological basis of diving to depth: birds and mammals. *Annual Review of Physiology*, **60**, 19–32.
- Kooyman, G.L. & Sinnett, E.E. (1982) Pulmonary shunts in harbor seals and sea lions during simulated dives to depth. *Physiological Zoology*, **55**, 105–111.
- Kooyman, G.L., Wahrenbrock, E.A., Castellini, M.A., Davis, R.W. & Sinnett, E.E. (1980) Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior. *Journal of Comparative Physiology*, **138**, 335–346.
- Kooyman, G.L., Castellini, M.A., Davis, R.W. & Maue, R.A. (1983) Aerobic diving limits of immature Weddell seals. *Journal of Comparative Physiology*, **151**, 171–174.
- Kramer, D.L. (1988) The behavioral ecology of air breathing by aquatic animals. *Canadian Journal of Zoology*, **66**, 89–94.
- Le Boeuf, B.J., Crocker, D.E., Grayson, J., Gedamke, J., Webb, P.M., Blackwell, S.B. *et al.* (2000) Respiration and heart rate at the surface between dives in northern elephant seals. *Journal of Experimental Biology*, **203**, 3265–3274.
- Lesage, V., Hammill, M.O. & Kovacs, K.M. (1999) Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Canadian Journal of Zoology*, **77**, 74–87.
- Luque, S.P. (2007) Diving behaviour analysis in R. *R News*, **7**, 8–14.
- McConnell, B.J., Chambers, C. & Fedak, M.A. (1992) Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science*, **4**, 393–398.
- McDonald, B.I. & Ponganis, P.J. (2012) Lung collapse in the diving sea lion: hold the nitrogen and save the oxygen. *Biology Letters*, **8**, 1047–1049.
- McMahon, C.R., Burton, H., McLean, S., Slip, D. & Bester, M. (2000) Field immobilisation of southern elephant seals with intravenous tiletamine and zolazepam. *The Veterinary Record*, **146**, 251–254.
- Miller, P.J.O., Johnson, M.P., Tyack, P.L. & Terray, E.A. (2004) Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *The Journal of Experimental Biology*, **207**, 1953–1967.
- Miller, P.J.O., Biuw, M., Watanabe, Y.Y., Thompson, D. & Fedak, M.A. (2012) Sink fast and swim harder! Round-trip cost-of-transport for buoyant divers. *Journal of Experimental Biology*, **215**, 3622–3630.
- Mitani, Y., Andrews, R.D., Sato, K., Kato, A., Naito, Y. & Costa, D.P. (2010) Three-dimensional resting behaviour of northern elephant seals: drifting like a falling leaf. *Biology Letters*, **6**, 163–166.
- Mori, Y., Takahashi, A., Mehlum, F. & Watanuki, Y. (2002) An application of optimal diving models to diving behaviour of Brünnich's guillemots. *Animal Behaviour*, **64**, 739–745.
- Naito, Y., Bornemann, H., Takahashi, A., McIntyre, T. & Plötz, J. (2010) Fine-scale feeding behavior of Weddell seals revealed by a mandible accelerometer. *Polar Science*, **4**, 309–316.
- Naito, Y., Costa, D.P., Adachi, T., Robinson, P.W., Fowler, M. & Takahashi, A. (2013) Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes on small prey. *Functional Ecology*, **27**, 710–717.
- Okuyama, J., Kawabata, Y., Naito, Y., Arai, N. & Kobayashi, M. (2009) Monitoring beak movements with an acceleration datalogger: a useful

- technique for assessing the feeding and breathing behaviors of sea turtles. *Endangered Species Research*, **10**, 39–45.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core team. (2013) *Nlme: Linear and Nonlinear Mixed Effects Models*.
- Pyke, G.H. (1984) Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics*, **15**, 523–575.
- R Development Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Richard, G., Vacqu  -Garcia, J., Jouma'a, J., Picard, B., G  nin, A., Arnould, J.P.Y. *et al.* (2014) Variation in body condition during the post-moult foraging trip of southern elephant seals and its consequences on diving behaviour. *The Journal of Experimental Biology*, **217**, 2609–2619.
- Sato, K., Mitani, Y., Cameron, M.F., Siniff, D.B. & Naito, Y. (2003) Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *The Journal of Experimental Biology*, **206**, 1461–1470.
- Sato, K., Aoki, K., Watanabe, Y.Y. & Miller, P.J.O. (2013) Neutral buoyancy is optimal to minimize the cost of transport in horizontally swimming seals. *Scientific Reports*, **3**, 2205.
- Sparling, C.E., Georges, J.-Y., Gallon, S.L., Fedak, M. & Thompson, D. (2007) How long does a dive last? Foraging decisions by breath-hold divers in a patchy environment: a test of a simple model. *Animal Behaviour*, **74**, 207–218.
- Suzuki, I., Naito, Y., Folkow, L.P., Miyazaki, N. & Blix, A.S. (2009) Validation of a device for accurate timing of feeding events in marine animals. *Polar Biology*, **32**, 667–671.
- Thompson, D. & Fedak, M.A. (2001) How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Animal Behaviour*, **61**, 287–296.
- Thompson, D., Hiby, A.R. & Fedak, M. (1993) How fast should I swim? Behavioural implications of diving physiology. *Symposium Zoology Society London*, **66**, 349–368.
- Thums, M., Bradshaw, C.J.A., Sumner, M.D., Horsburgh, J.M. & Hindell, M.A. (2013) Depletion of deep marine food patches forces divers to give up early (ed G Hays). *Journal of Animal Ecology*, **82**, 72–83.
- Tuck, K. (2007) Tilt sensing using linear accelerometers. Freescale Semiconductor, AN3461 Rev. 2.
- Tucker, V.A. (1975) The energetic cost of moving about: walking and running are extremely inefficient forms of locomotion. Much greater efficiency is achieved by birds, fish—and bicyclists. *American Scientist*, **63**, 413–419.
- Viviant, M., Trites, A.W., Rosen, D.A.S., Monestiez, P. & Guinet, C. (2010) Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. *Polar Biology*, **33**, 713–719.
- Watwood, S.L., Miller, P.J.O., Johnson, M., Madsen, P.T. & Tyack, P.L. (2006) Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *Journal of Animal Ecology*, **75**, 814–825.
- Webb, P.M., Crocker, D.E., Blackwell, S.B., Costa, D.P. & Boeuf, B.J. (1998) Effects of buoyancy on the diving behavior of northern elephant seals. *The Journal of Experimental Biology*, **201**, 2349–2358.
- Williams, T.M., Davis, R.W., Fuiman, L.A., Francis, J., Le, B.J., Boeuf Horning, M. *et al.* (2000) Sink or swim: strategies for cost-efficient diving by marine mammals. *Science*, **288**, 133–136.
- Wilson, R., Steinfurth, A., Ropert-Coudert, Y., Kato, A. & Kurita, M. (2002) Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Marine Biology*, **140**, 17–27.
- Ydenberg, R.C. & Clark, C.W. (1989) Aerobiosis and anaerobiosis during diving by western grebes: an optimal foraging approach. *Journal of Theoretical Biology*, **139**, 437–447.

Received 19 August 2014; accepted 2 July 2015

Handling Editor: Daniel Costa

## Supporting Information

Additional Supporting information may be found in the online version of this article:

**Table S1.** Top five ranked linear mixed-effects models by AIC of bottom time as the response variable explained by dive duration, ascent and descent angles, ascent and descent effort, body density and maximum depth.

**Table S2.** Top five ranked linear mixed-effects models by AIC of bottom swimming effort as the response variable explained by bottom time, body density and maximum depth.

**Table S3.** Top five ranked linear mixed-effects models by AIC of surface time as the response variable explained by total swimming effort provided during the last dive and the prey capture attempts availability.

**Table S4.** Estimates and confidence intervals for prey availability, number of prey and the body density in each linear mixed effects models associated to box plot.

**Fig. S1.** Evolution of the relation between total bottom swimming effort and total transit swimming effort according to depth and animal's body density.