

Three-dimensional assessment of hunting strategies in a deep diving predator, southern elephant seal *Mirounga leonina*

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ABSTRACT: Few studies have examined the foraging ecology of top marine predators by taking into account the vertical and horizontal dimensions simultaneously. In this study, using 3-dimensional reconstruction of underwater animal paths, we investigated the relationship between area restricted search (ARS) and foraging behaviors in the southern elephant seal *Mirounga leonina*. We equipped 6 post-breeding females on the Kerguelen Islands with an Acousonde™ recording simultaneously sounds, pressure, acceleration and magnetic field-strength in 3-dimensions (n = 879 dives). Using the spherical first passage time analysis, we identified ARS in 46.4% of the dives. They represented 36.9% of the bottom time, but due to a higher prey encounter rate, 67.6% of catch attempts took place in ARS. These areas, occurring within a sphere of 48.2 ± 25.7 m radius, were characterized by an increase in energy expenditure and a strong variability in the roll and heading compared to non-ARS regions. While within an ARS, we identified 3 hunting modes from unsupervised classification based on acceleration properties previous to captures. We found that 32.8% of attempts matched a passive-gliding approach from above the target. The other 2 modes corresponded to an actively swimming approach associated with increases of variance in heading and/or rolling movements for the first one (56.6% of captures), and to a much larger swimming effort for the second one (10.6% of captures). These data revealed a strong link between seals' fine-scale movements and feeding activity, suggesting that seals fed mainly on patchily distributed resources, with different hunting strategies that may be indicative of several prey species targeted.

KEY WORDS: Area restricted search · Foraging · Accelerometer · Acousonde™ · Data mining · Unsupervised classification · Machine learning · Spherical first passage time

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INTRODUCTION

Movement ecology provides a conceptual framework aiming at better understanding how organisms of all kinds move, and how their movement patterns modulate essential features such as survival and reproduction of individuals, as well as the structure and dynamics of populations (Nathan et al. 2008). Therefore, movement can be considered as a crucial behavioral response to diverse processes such as feeding, finding mates, and avoiding predators or other harmful environmental conditions. Yet, the investigation of the mechanisms connecting animal

movement to these key processes is limited by our ability to track animals in sufficiently high spatial and temporal resolution at which they sense and respond to various environmental cues. The recent development of bio-logging technologies has significantly contributed to filling the gap in our knowledge, by relating animal movements to physiology (Butler & Jones 1997, Génin et al. 2015, Day et al. 2017), physical environment (Heupel & Simpfendorfer 2008, Ortega et al. 2009) and exploited resources (Guinet et al. 2014, Kuhn et al. 2015, Goldbogen et al. 2015, Wilmers et al. 2015, Adachi et al. 2017). In this context, high sampling-frequency tracking systems

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and loggers deployed on wild animals have made possible the recording of information that would have been impossible to get otherwise, without being restricted by visibility, observer bias, or geographic scale (Brown et al. 2013).

Such studies on diving animals are important since little is known about their life history under the water compared to terrestrial animals. Indeed, while movements of terrestrial organisms are almost exclusively determined by a 2-dimensional space, aquatic animals evolve in a domain that includes a vertical dimension, modifying the general approach to space use. Advances in bio-logging technologies have greatly improved our ability to monitor the behavior and movements of such animals, since we can now reconstruct their 3-dimensional paths at very fine scale using high-sampling frequency loggers (Mitani et al. 2003, Laplanche et al. 2015). Considering the animal's trajectory underwater in 3 dimensions allows assessment of a level of detail that was not possible using a 2-dimensional representation, i.e. time-depth representation (Harcourt et al. 2000), in particular on the animal track sinuosity (Bailleul et al. 2010b). For instance, Hindell et al. (2002) revealed how the 3-dimensional space use under ice of lactating Weddell seals *Leptonychotes weddellii* can influence reproductive strategies over several consecutive breeding seasons. Narazaki et al. (2009) showed that loggerhead turtles *Caretta caretta* performed highly straight-line courses while diving, and multiple changes in heading at the surface that could be interpreted as direction-searching behavior. In blue whales *Balaenoptera musculus*, Goldbogen et al. (2015) showed that several adaptive foraging strategies were used to maximize prey capture in different ecological contexts, depending on the required energy for manoeuvres. The use of 3-dimensional tracking data associated with high-sampling frequency loggers, such as accelerometers, appears to be then relevant to investigate the foraging behavior of aquatic animals, allowing us to study the relationship between an animal's movement and its feeding behavior.

Therefore, tracking data analyses developed for 2-dimensional data to investigate the spatial distribution of foraging effort have been adapted to 3-dimensional data. Such is the case for the First Passage Time (FPT) method developed by Fauchald & Tveraa (2003) as a measure of search effort along a path. FPT identifies the spatial scale and position of the area-restricted search (ARS; Kareiva & Odell 1987), which is a fundamental aspect of movement pattern analyses. Studies that investigate the foraging ecology of a top marine predator, through both tracking and div-

ing data, can use the FPT method by integrating the vertical dimension (Bailleul et al. 2007b, 2010b, Hoskins et al. 2015, Adachi et al. 2017). This is the case for the approach developed by Bailleul et al. (2010b) to investigate ARS in 3-dimensional movements: the spherical first-passage time (SFPT). This method is similar to FPT, except it considers both the vertical and the horizontal dimensions simultaneously, leading to the concept of time spent inside a sphere rather than a circle.

By recording a high level of detail through the biomechanics (Cooke et al. 2004) and exercise science (Suzuki et al. 2009), acceleration data also provide a powerful tool to investigate foraging ecology. First, accelerometers can provide an estimate of the energy expenditure based on the variation in acceleration (Halsey et al. 2011). Additionally, the waveform of the signal provides information on the animal's body posture and movements (Shepard et al. 2008). The movements identified using this technique can be used to construct ethograms and differentiate a range of discrete behaviors (Sakamoto et al. 2009, Berman et al. 2014, Bom et al. 2014), by ensuring that these are biologically meaningful. To date, 3 methods have been developed for assigning acceleration data to behavioral categories based on signal properties (Brown et al. 2013): (1) manual examination, which consists of detecting reference patterns and fixing thresholds (Collins et al. 2015), e.g. mouth opening detection interpreted as prey catch attempts (Viviant et al. 2010); (2) supervised machine learning algorithms, based on algorithms which are trained on data generated from known behaviors (Nadimi et al. 2008); and (3) unsupervised machine learning algorithms (Sakamoto et al. 2009, Chimienti et al. 2016). This latter method presents the advantage of inferring categories from the dataset itself by finding hidden structure, rather than from a labelled dataset. Considering acceleration data without prior knowledge gives the opportunity to detect, in a more objective way, new behaviors that no one has observed or described before (Chimienti et al. 2016).

Southern elephant seals *Mirounga leonina* (SES) spend several months at sea after the breeding season on land. During this period at sea, several foraging habitats have been identified for the Kerguelen Islands population, depending on age and sex. Juveniles of both sexes, i.e. under 5 yr old, and adult females mainly feed in the Antarctic pelagic zone (marginal sea-ice zone) and the Subantarctic zone (interfrontal zone) (Bailleul et al. 2007a, 2010a, Ducatez et al. 2008, Chérel et al. 2008) on small bio-

luminescent fishes (myctophids) (Cherel et al. 2008). For adults, isotope analyses suggest a higher trophic level for males, which likely feed on cephalopods (Slip 1995, Daneri et al. 2000).

The purpose of this study was to investigate the foraging behaviors of 6 post-breeding female SES by combining acceleration data analysis and 3-dimensional trajectory analysis. Using the 3-dimensional reconstruction of animals' paths underwater, we therefore aimed at (1) determining the 3-dimensional spatial scale of the ARS, (2) comparing foraging behaviors inside and outside the ARS region within the dive bottom phase, and (3) identifying hunting behaviors within an ARS, using an unsupervised classification approach.

MATERIALS AND METHODS

Deployment of devices and data collection

Six post-breeding female SES (mean mass = 277 ± 47 kg; mean length = 238 ± 11 cm; Table 1) were each equipped on the Kerguelen Islands ($49^{\circ} 20' S$, $70^{\circ} 20' E$) with an Argos-GPS satellite tag (Splash 10-F, Wildlife Computer, USA), and an autonomous acoustic/accelerometer/magnetometer and pressure logger (Acousonde™, model 3A; Acoustimetrics, Greeneridge Sciences, Santa Barbara, CA). The 6 Splash 10-F tags were glued to the fur on the seals' heads, and the Acousondes™ were glued on the back of the animals on the longitudinal axis, 10 cm behind the scapula. Two animals were equipped in 2011 and the other 4 in 2012. Data loggers were set to collect and archive pressure every second, while tri-axial acceleration and magnetometer data were sampled at 5 Hz. All sensors were calibrated by their respective manufacturers. Because sound recording requires high levels of energy consumption, Acousondes™ were programmed to record sound for 3 h every 12 h in 2011 and for 4 h every 24 h for the

4 individuals equipped in 2012. The sampling frequency of the sound was set at 6 kHz in 2011 and 12.2 kHz in 2012.

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 female SES returned to shore to molt (i.e. January–February following deployments). Seals were located using their Argos locations.

Unless otherwise stated, most of our analyses were conducted using R (R Core Team 2015). All scripts used here for data treatment and analyses are available upon request.

Diving behavior parameters

We considered the seal to be diving when its depth exceeded 15 m. This threshold was chosen to avoid identifying brief subsurface movements as dives. Each dive was then divided into 3 different phases (descent, bottom and ascent) by using a vertical speed criterion chosen after a sensitivity analysis. Descent and ascent phases were characterized as a period when the vertical speed from or towards the surface, fitted to a 4th degree polynomial, was higher than 0.75 m s^{-1} (Vacqu e-Garcia et al. 2015a). 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^{-1} , in absolute terms. Using a custom script, this analysis was performed with a commercial software package (MATLAB 8.1; The MathWorks, Natick, MA).

Data from the accelerometers were used to calculate a swimming effort index based on stroke rate and amplitude, by using a band pass filter (lower cut-off frequency: 0.44 Hz; higher cut-off frequency: 1 Hz) on the lateral axis. The swimming effort (m s^{-2}) was then defined as the summed absolute values of the filtered lateral acceleration (Richard et al. 2014, Jouma'a et al. 2016). Acceleration data were also used to calculate a proxy of the energy expenditure called the vector of dynamic body acceleration (VeDBA; Qasem et al. 2012). For this purpose, we used a high-pass filter with a cut-off fre-

Table 1. Descriptive information about the 6 post-breeding female southern elephant seals *Mirounga leonina*

Seal	Body mass (kg)	Size (cm)	Departure date	<i>n</i> days recorded	— <i>n</i> dives —		Acousonde ID
					Total	With sound	
1	230	232	2012-10-28	24	1945	227	626019
2	362	235	2012-11-03	12	409	60	626020
3	282	248	2012-10-28	4	288	46	626022
4	292	225	2012-11-01	29	1777	212	626040
5	255	254	2011-10-26	13	821	123	A031
6	245	238	2011-10-28	13	1081	211	A032

quency of 0.5 Hz to remove the static acceleration on each channel, and then calculated following the formula:

$$VeDBA = \sqrt{A_x^2 + A_y^2 + A_z^2} \quad (1)$$

where A refers to the filtered acceleration.

Body orientation in 3 dimensions, i.e. the pitch, the roll and the heading were calculated using the R package *animalTrack* (Farrell & Fuiman 2013) by using filtered acceleration and geomagnetism obtained with a 0.5 Hz low-pass filtering. Using the same filter for both acceleration and geomagnetism data allows us to limit the occurrence of artefacts in

calculated headings (Shiomi et al. 2010). Therefore, to assess the animal movement in 3 dimensions, the circular average of the pitch as well as the circular variance of the roll and the heading were calculated using respectively the *circ.mean* and *circ.disp* functions from the R package *CircStats* (Agostinelli 2012).

Three dimensional reconstruction and speed estimation

Knowing the depth and the orientation of the animal allows us to reconstruct the path of the animal under water (Fig. 1a) by using the *dead_reckoning* function from the R package *animalTrack* (Farrell & Fuiman 2013), and therefore to have a better representation of the animal's path than in 2 dimensions (Fig. 1b). Such a reconstruction must make assumptions of the animal's speed. Here, the speed of the animal was calculated from the low frequency flow noise on the acoustic recorder (Fletcher et al. 1996, Burgess et al. 1998, Goldbogen et al. 2006, Simon et al. 2009, Génin et al. 2015). For each individual, the noise power was computed with a 110 Hz low-pass filter during periods under 200 m depth, with an animal's pitch between -90° and -75° and an acceleration on the 3 axes below 1 m s^{-2} . We used these descent periods for the speed–noise calibration because in this situation, the absolute descent speed of the seal can be easily estimated from the pitch angle and the vertical speed. We then fitted a single-term exponential curve between the flow noise (Simon et al. 2009), and the absolute descent speed. This relation was used to estimate the swimming speed in any part of the dataset that includes sound recordings.

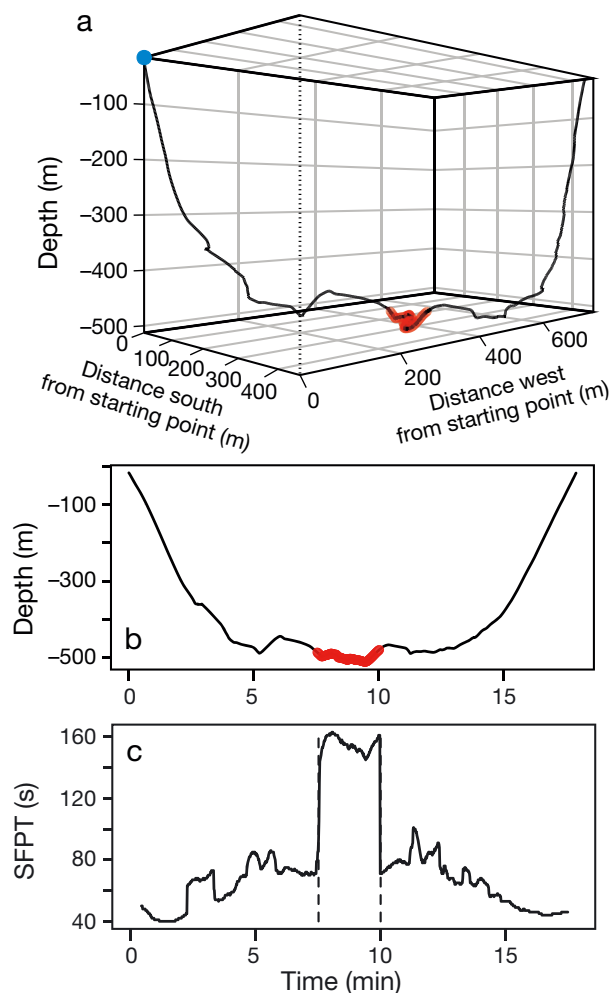


Fig. 1. (a) Three-dimensional trajectory of dive 994 from southern elephant seal 1, starting at the blue point, with an area-restricted search (ARS) identified in red, and (b) the same dive in 2 dimensions, highlighting the necessity of using a third spatial dimension to assess path sinuosity. (c) Spherical first passage time (SFPT) associated with this dive across time. Using Lavielle's method, we then identified an ARS that took place, in a sphere of 37.9 m radius and where southern elephant seal 1 spent 142 s

Spherical first passage time

SFPT has been developed in the case of 3-dimensional movements to account for the vertical dimension in ARS scale identification and description (Bailleul et al. 2010b). Based on FPT Fauchald & Tveraa (2003), the SFPT is defined as the time required to cross a sphere with a given radius. To determine the optimal radius of the sphere used for ARS detection, we tested different radii, range 10–300 m (10 m increments), and visually chose the one providing the highest contrast in SFPT, i.e. a radius of 50 m in this study. Then we used the *lavielle* function from the R package *adehabitatLT* (Calenge 2006) that performs a non-parametric segmentation on time series based on Lavielle's method (Lavielle

2005), to finally identify ARS in SFPT time series (Fig. 1c). To estimate the scale of an ARS, we considered the radius and the time spent inside a sphere centered on the ARS centroid, which included 95% of the ARS positional estimates for that animal.

Detection of prey catch attempts

Mouth opening events indicative of prey catch attempts can be detected from acceleration data (Naito et al. 2010, Viviant et al. 2010, Gallon et al. 2013). Here we used a method derived from Viviant et al. (2010) and adapted by Vacquié-Garcia et al. (2015b) to identify rapid head movement, interpreted to be associated with prey encounter events, with a custom script performed with MATLAB. This method developed for head-mounted accelerometers provided similar results for back-mounted accelerometers (Pearson's product moment correlation coefficient = 93%; Le Bras et al. 2016). We first applied a high-pass filter of 2.64 Hz to the signal in order to remove noise corresponding to swimming movements. Then, a fixed window of 1 s was used to calculate the standard deviation every second on each channel. Signals reduced in this way were smoothed using a moving standard deviation with a 5-s window size. Lastly, a 2-mean clustering was performed on the final 3 signals. Prey catch attempt was defined as a continuous sequence of samples in which all of the 3 axes were classified in the high-variance cluster.

Behavioral comparison of foraging effort inside and outside ARS during the bottom phase

For each SES, in dives where ARS were detected, we calculated both proportion of prey catch attempts and the associated catch attempts rate occurring during the bottom phase, first inside and then outside ARS. We focused on the bottom phase to avoid the effect of directed movements associated with the ascent and the descent phase. Then focusing on hunting behavior, defined as the animal's behavior before prey catch attempts, the average speed, the sum of the swimming effort and the VeDBA, as well as the circular variance of the heading and the roll, and the circular mean of the pitch were calculated during the 20 s preceding the catch attempts. Using Wilcoxon-Mann-Whitney tests for paired data, we then compared averaged values for each SES of these variables inside vs. outside ARS, since the normality assumption was not met.

Unsupervised hunting behavior classification inside ARS

To identify different hunting behaviors inside ARS, we based our classification on acceleration signal properties from the 3 channels by considering an arbitrary time window before prey catch attempts. We present the outputs for a 20 s time window, but a sensitivity analysis revealed a similar classification for a time window ranging from 10 to 60 s (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m573p255_supp.pdf).

The calculated signal properties were the mean, the maximum, the minimum, the skewness and the kurtosis (respectively *skewness* and *kurtosis* from the R package *moments*; Komsta & Novomestky 2015), as well as the main frequency that composed the signal and the associated power spectral density (*pspectrum* from the R package *psd*; Barbour & Parker 2014) for each raw acceleration axis. The same parameters were calculated on acceleration data filtered with a 0.5 Hz low-pass and a 0.5 Hz high-pass filter, respectively, to retain the gravitational part of the signal, and the one due to animal's movements.

A PCA analysis was conducted to create a set of orthogonal variables. The optimal number of factors to extract from the PCA, was determined with Kaiser's rule (Kaiser 1960) through the *nScree* function from the R package *nFactors* (Raiche 2010).

We finally performed an agglomerative hierarchical clustering on results from the factor analysis using the *HCPC* function from the R package *FactoMineR* (Husson et al. 2015), by computing the Euclidean distance matrix and following Ward's criterion. The suggested partition was the one with the higher relative loss of inertia.

Assuming each cluster is a specific hunting behavior, we described these behaviors in terms of average speed, swimming effort and VeDBA, circular average roll and pitch, circular variance of heading, and average prey capture rate during the time window of 20 s before prey catch attempts. We tested the independence of the proportion of prey catch attempts associated with each cluster, between the 6 southern elephant seals, using a chi-squared test.

RESULTS

Detection and scale of ARS

The average percentage of dives with ARS (Table 2) was $46.4 \pm 0.9\%$ (range: 34.1–58.7%, for Seal 6 and

Table 2. Descriptive information calculated from dives with sound (see Table 1) about area restricted search (ARS) for the 6 post-breeding female southern elephant seals *Mirounga leonina*

Seal	ARS sphere parameters		Dives with ARS (%)
	Time inside (s)	Radius (m)	
1	131.5 ± 61.5	39.7 ± 19.9	55.5
2	138.6 ± 60.6	42.1 ± 21.8	43.3
3	176.1 ± 121.4	54.9 ± 37.9	58.7
4	182.2 ± 132.9	44.6 ± 30.9	39.6
5	230.3 ± 188.2	63.1 ± 15.9	47.2
6	131.5 ± 91.6	44.7 ± 28.0	34.1

Seal 3, respectively). Overall, the scale of an ARS was similar for the 6 elephant seals, with an average radius of 48.2 ± 25.7 m, and a median of 36.6 m (Fig. 2a). This represents an average of 165.1 ± 109.4 s spent inside the ARS, with a median of 123 s (Fig. 2b).

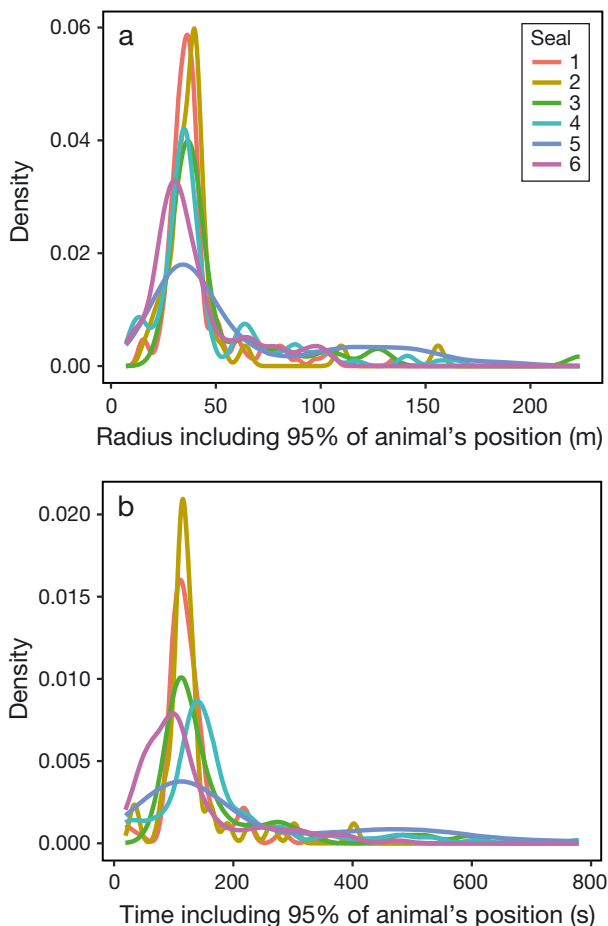


Fig. 2. Density distributions of (a) the radius for a sphere centred on the centroid of each ARS identified within the bottom phase of dives made by southern elephant seals *Mirounga leonina* and (b) the time spent inside this sphere. Including 95% of the positional estimates, the median sphere radius is 36.6 m and the median time is 123 s

Differences of foraging behaviors inside and outside ARS

When ARS were detected within a dive, they represented an average $36.9 \pm 7.6\%$ of the bottom time, with an associated mean prey capture attempts rate of $1.2 \pm 0.3 \text{ min}^{-1}$ (Table 3). Non-ARS represented $63.1 \pm 7.6\%$ of bottom time for each animal, with a significant lower mean capture attempts rate of $0.3 \pm 0.2 \text{ min}^{-1}$ (Wilcoxon-Mann-Whitney, $p < 0.01$).

At the bottom phase of these dives, before a prey catch attempt, only the circular variance of the heading and the roll were significantly different outside and inside ARS (Fig. 3; Wilcoxon-Mann-Whitney, $p < 0.01$). Indeed, during the 20 s preceding the prey catch attempts, both parameters were higher in ARS than outside. The sum of the swimming effort and the circular mean of the pitch were not significantly different inside vs. outside ARS (Fig. 3; Wilcoxon-Mann-Whitney, $p > 0.05$). We found the same result for the average speed and the sum of VeDBA, even if visual inspection tends to suggest lower values inside ARS.

Characterization of hunting behaviors inside ARS at the bottom

Using Kaiser's rule to reduce the number of variables as inputs for the classification, we only considered the first 18 component scores of the PCA (Fig. S2 in the Supplement). The hierarchical clustering (Fig. 4), through the higher loss of inertia by partitions, revealed the presence of 3 related clusters obtained from the factor map. High values of prey catch attempt rates associated with each cluster (Table 4) compared to values in Table 3, come from the number of prey catch attempts that occur during the 20 s preceding a prey catch attempt, averaged over a minute.

Table 3. Proportion of bottom time spent inside and outside area restricted search (ARS), with the associated prey catch attempts rate for southern elephant seals *Mirounga leonina*

Seal	ARS		non ARS	
	Proportion (%)	Prey catch attempts min^{-1}	Proportion (%)	Prey catch attempts min^{-1}
1	38.7	1.4	61.3	0.3
2	23.6	1.5	76.4	0.4
3	43.5	1.2	56.5	0.1
4	33.2	1.1	66.8	0.4
5	43.8	0.8	56.2	0.2
6	38.4	1.4	61.7	0.6

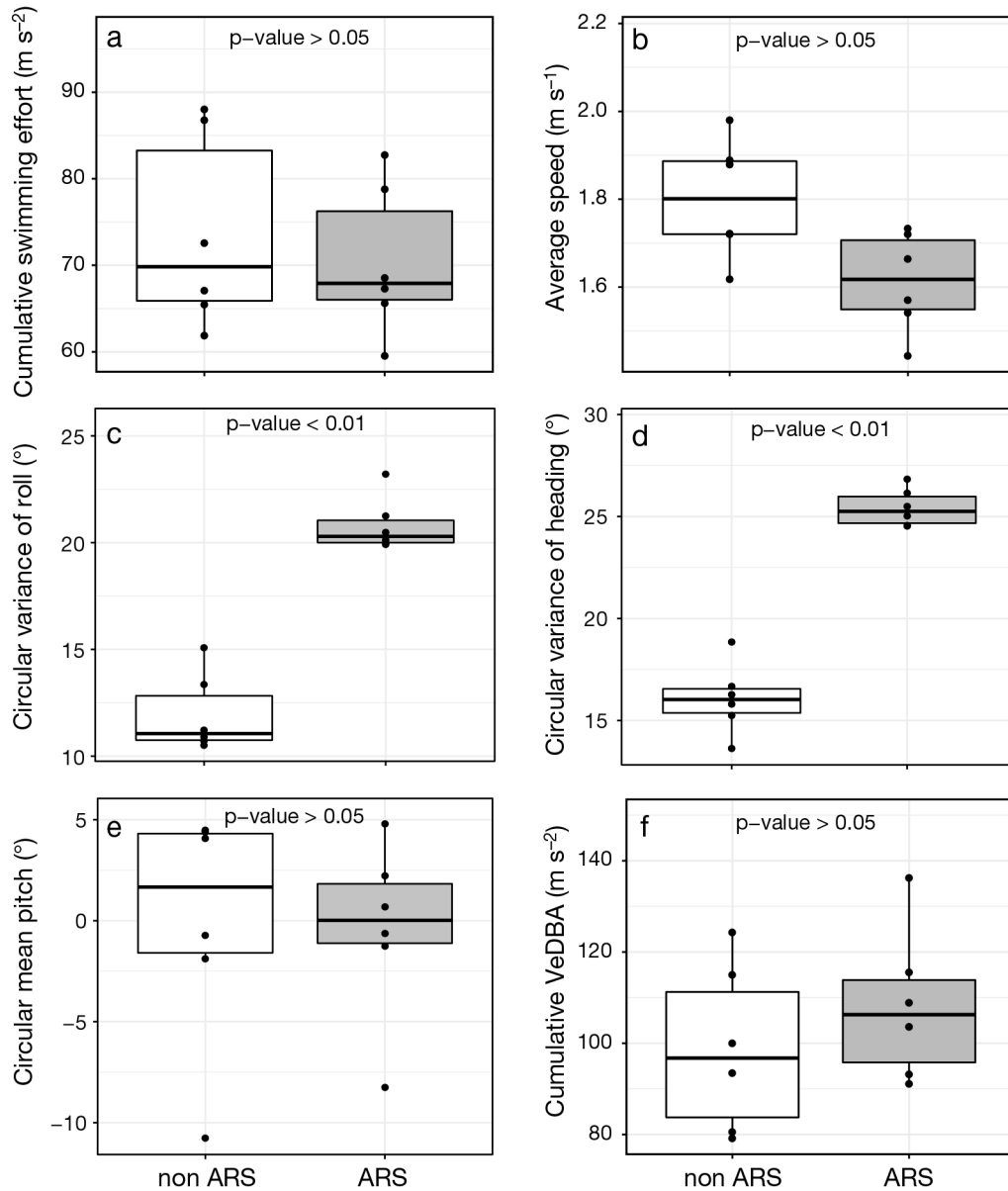


Fig. 3. Behavioural comparison of prey catch attempts occurring during both area restricted search (ARS) and non-ARS regions during the bottom phase of dives made by southern elephant seals *Mirounga leonina* (SES). (a) Average swimming effort, (b) speed, the variance of (c) roll and (d) heading, (e) pitch, and (f) vector of dynamic body acceleration (VeDBA, a proxy of energy expenditure) during the 20 s preceding prey catch attempts. Each point represents the average value for each SES. Horizontal line: median; box: interquartile range (IQR); whiskers: max/min. values $\leq 1.5 \times$ IQR above/below hinge. The p-value is the result of a median 2-sample Wilcoxon test

Table 4. Summary of the behaviour during the 20 s preceding prey catch attempts performed by 6 post-breeding female southern elephant seals *Mirounga leonina* within area restricted searches, in each cluster identified from the unsupervised classification (cf. Fig. 4). Mean values and circular mean values are respectively given with \pm SD and circular variance

Cluster	n	Σ VeDBA (m s ⁻²)	Σ Swimming effort (m s ⁻²)	μ Speed (m s ⁻¹)	θ_c^2 Roll (°)	θ_c^2 Heading (°)	μ_c Pitch (°)	Prey catch attempts min ⁻¹
1	826	138.15 \pm 45.94	80.44 \pm 26.03	1.6 \pm 0.26	32.49 \pm 1.14	37.61 \pm 1.08	-1.47 \pm 2.02	5.65 \pm 2.47
2	155	132.13 \pm 38.83	124.31 \pm 33.14	1.76 \pm 0.3	8.68 \pm 1.04	12.56 \pm 1.39	41.76 \pm 1.92	3.64 \pm 1.45
3	479	54.77 \pm 30.46	45.57 \pm 27.76	1.64 \pm 0.34	5.06 \pm 0.48	9.65 \pm 1.03	-12.04 \pm 2.97	3.61 \pm 1.43

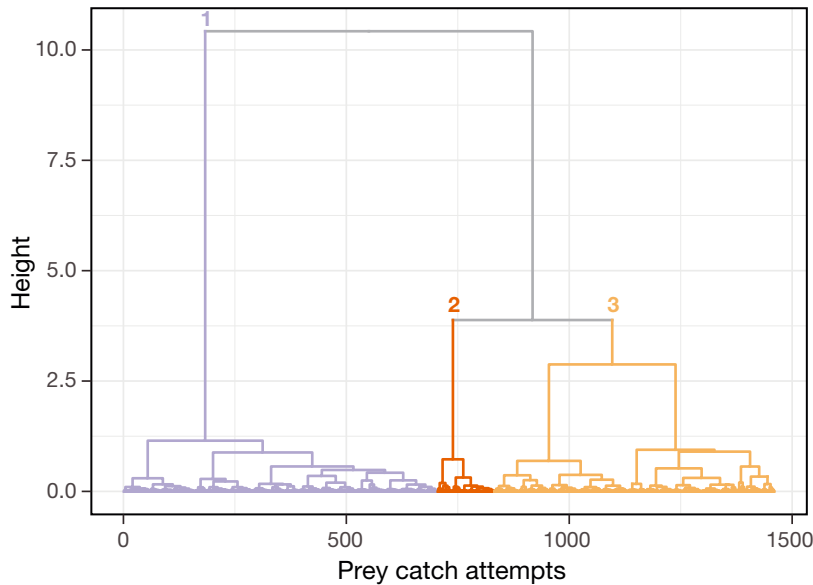


Fig. 4. Hierarchical clustering of prey catch attempts within area restricted searches during the bottom phase of dives, based on southern elephant seals' behavioural features during the 20 s previous to captures. Using the higher relative loss of inertia, the prey catch attempts are partitioned into 3 clusters

The first cluster ($n = 826$; Table 4) was characterized by high values of circular variance for the heading ($37.6 \pm 1.2^\circ$) and the roll ($32.5 \pm 1.1^\circ$), and a circular mean for the pitch near zero degrees ($-1.5 \pm 2.0^\circ$). It was also associated with a large prey catch attempt rate of $5.7 \pm 2.5 \text{ min}^{-1}$ and the highest values of VeDBA ($138.2 \pm 45.9 \text{ m s}^{-2}$). Catch attempts contained in the second cluster ($n = 155$) were associated

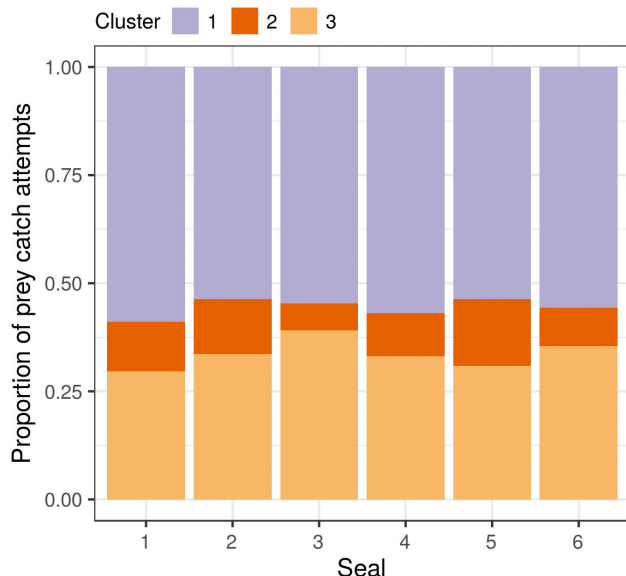


Fig. 5. Partitioning of prey catch attempts identified within area restricted search for 6 southern elephant seals *Miromounga leonina*, among the 3 clusters identified through the hierarchical clustering on principle components (cf. Fig. 4)

with slightly lower values of VeDBA and high values of swimming effort (respectively $132.1 \pm 38.8 \text{ m s}^{-2}$ and $124.3 \pm 33.1 \text{ m s}^{-2}$), a circular mean for the pitch of $41.8 \pm 1.9^\circ$ and a low capture rate of $3.6 \pm 1.5 \text{ min}^{-1}$. The last behavior associated with the third cluster ($n = 479$) included catch attempts with the lowest values of swimming effort ($45.6 \pm 27.8 \text{ m s}^{-2}$), a circular mean for the pitch of $-12.0 \pm 3.0^\circ$, a capture rate of $3.6 \pm 1.4 \text{ min}^{-1}$ and the lowest values for VeDBA ($54.8 \pm 30.5 \text{ m s}^{-2}$).

The proportion of these 3 classes of hunting mode leading to prey catch attempts did not depend on individuals (Fig. 5; chi-squared test, $p > 0.05$). Cluster 1 contained the largest proportion of prey catch attempts, followed by Cluster 3 and Cluster 2 (respectively 56.6%, 32.8% and 10.6% of attempts).

DISCUSSION

Path reconstruction

Despite recent advances in the bio-logging field, many biases have still to be considered when using new tools to study the paths of marine animals. When predicting the position of an animal underwater, the term 'pseudo-track' is preferred over 'track', to reinforce the idea that absolute position is unknown (Hazen et al. 2009). Such differentiation is crucial, as the reconstruction process relies on multiple assumptions. For instance, to simplify the reconstruction we assume that the animal frame is the same as the tag frame, which is not always the case (Laplanche et al. 2015). To make a reliable estimation of the speed, we also assume that recording sound under a certain frequency is proportional to the animal's speed due to the noise of the water flow. However, in some situations (e.g. if the seal is swimming with the current, or moving into a position in which its head disturbs the flow of water over the tag, thereby diminishing the flow noise), this estimation can be misleading. As mentioned by Laplanche et al. (2015), the implementation of these approximations can have considerable impacts on the estimated track. However, new methods based on Bayesian statistics (Laplanche et al. 2015, Wensveen et al. 2015), developed to compen-

sate for these approximations, are time-consuming and thus impractical for analyzing large numbers of dives. Therefore, dealing with a relatively large number of dives, we consider the method employed in our study as a likely acceptable trade-off between accuracy and processing time.

Areas of increased foraging effort

A reliable estimation of the animal's track underwater is required to assess and understand the role of marine predators within their ecosystem. Because they perceive and react to environmental heterogeneity, their reactions detected through changes in movements are usually interpreted as interaction and response to physical and/or biological changes (Gordon 1991, Nathan et al. 2008). In a foraging context, an inaccurate estimation of the scale at which animals are searching could lead to misinterpreting their response to environmental changes or disturbances. By using the SFPT (Bailleul et al. 2010b) we accounted for the vertical dimension to improve movement analyses in 3 dimensions. Based on tracking and diving data, this is the first study to implement this innovative method for looking at ARS in order to differentiate behavioral states, thanks to unsupervised classification. Our study revealed that SESs perform active search in an optimal sphere of 48.2 ± 25.7 m radius (Table 2). The smaller radii (9 and 18 m) found by Adachi et al. (2017) could be due to behavioral differences between the 2 species (*Mirounga angustirostris* vs. *Mirounga leonina*), or between prey targeted. In addition, the method used by Adachi et al. (2017) is different from ours, since they considered the radius of the sphere used to detect ARS as the actual radius of the ARS. In our study, we showed that using a sphere of 50 m radius for ARS detection allows us to detect ARS within a sphere of 36.6 m median radius (Fig. 2a). Detected in half of the dives, our ARS represent just 36.9% of bottom times, but due to higher prey capture rate, they represent 67.6% of the total prey catch attempts performed during the bottom phase of dives. Our results are consistent with those from Adachi et al. (2017) that most feeding events occurred in ARS zones (78 and 86% for small and large ARS, respectively). SESs appear therefore to have higher encounter rates in small regions of the bottom phase, considered as the main foraging phase in southern elephant seals (Guinet et al. 2014, Jouma'a et al. 2016). These results would suggest prey aggregation, which seems consistent with the patchy distribution of their main

prey, the myctophids (Auster et al. 1992, Cherel et al. 2008). However, since a substantial proportion of prey catch attempts occurred outside ARS, i.e. 32.4%, we would define a prey aggregation as an area where the local prey density is higher than the average overall prey density in the environment, and so the distribution of prey as a continuum.

Regarding swimming behaviors before prey catch attempts at the bottom level, the hunting behavior inside vs. outside ARS was different. ARS appeared to be zones with a higher swimming activity, where animals seemed to reduce speed, but showed a significant increase of horizontal sinuosity, i.e. high values of circular variance for heading, and high values in the circular variance for the roll, meaning that animals tend to have a rotating movement when capturing prey (Fig. 3). The increase of sinuosity within an ARS suggests that such behavior results from higher resource concentration, as revealed in satellite tracking studies in birds (Veit & Prince 1997, Pinaud & Weimerskirch 2005) and mammals (Haskell 1997, Thums et al. 2011). In this study, we showed that SESs increase their 3-dimensional track sinuosity at the dive scale in relation to a higher prey catch attempt rate (Fig. 3, Table 3). This is a finding consistent with the increase of both horizontal and vertical sinuosity detected in relation to the increasing number of prey catch attempts (Le Bras et al. 2016).

We interpret the likely reduction of speed before prey catch attempts within an ARS as a way to improve precision by favoring specific hunting strategies over just fast swimming. During the bottom phase, the animal could capture prey on its way and alter its behavior, such as reducing speed, as a result of higher prey density. This tactic of switching from extensive to intensive search mode by regulating speed has also been found in plaice *Pleuronectes platessa* (Hill et al. 2002). Because the horizontal speed of an animal is linked to its swimming effort (Sato et al. 2013), we would then expect higher swimming effort before a catch attempt outside ARS. Such a difference was not observed, and this could be due to our proxy of the speed which is known to be limited when an animal's path sinuosity increases, because of interference noises. Another explanation would be that an SES, by reducing its speed, would reallocate energy saved in this case for rolling movements or quick direction changes, potentially responsible for the reduction in travelling speed compared to more linear tracks outside ARS. The fact that pursuing prey inside ARS seems to require more energy, i.e. higher value of VeDBA, than chasing outside, by increasing sinuosity for instance, could be partly bal-

anced by reducing speed. However, these hypotheses need to be taken with caution since no significant differences in swimming speed and VeDBA were detected outside vs. inside ARS (Fig. 3). The other way SESs have to compensate for the extra energy required to chase inside ARS would be to increase efficiency inside these areas, by catching more prey.

Behavioral classification

Techniques based on acceleration data for animal movement classification are beginning to emerge in the ecological literature (Shepard et al. 2008, Nathan et al. 2012, Brown et al. 2013, Collins et al. 2015). An increasing number of studies have developed supervised algorithm classification, but only a few suggested using unsupervised methods (Sakamoto et al. 2009, Chimienti et al. 2016). Here, like Sakamoto et al. (2009), the classification was based on *k*-means clustering, except that the number of clusters was estimated using hierarchical clustering on principle components. We believe that our method reduces the decision-biases associated with supervised methods. This innovative method enabled us to identify objectively 3 different clusters, interpreted as hunting modes, in ARS.

The first cluster is likely related to a substantial horizontal sinuosity as though SESs were chasing fishes all round them within the patch, while remaining at the same depth, i.e. low variability in the pitch (Table 4), suggesting a distribution of prey in a thin vertical layer. This hunting mode agrees with findings by Le Bras et al. (2016) that female elephant seals were found to be more successful when foraging inside a prey patch distributed in narrow vertical layers. During this hunting mode, SESs appear to roll, alternating almost from one side to the other, which is not observed in any other cluster. These variations in the roll have been documented in northern fur seals (Battaile et al. 2015) and sperm whales (Miller et al. 2004). In this latter case, this behavior was associated with active clicking, indicative of prey catch attempts. Here, these variations are in part responsible for the associated high-energy expenditure. Indeed, this hunting mode appeared to be the most costly in energy with the highest values of VeDBA. In addition to 3-dimensional movements, this energy expenditure is also due to the swimming effort necessary to maintain these negatively buoyant animals at the same depth (Richard et al. 2014). According to the associated high capture rate (5.65 ± 2.67 prey catch attempts

min^{-1} , almost twice as high as the other identified modes) we believe that SESs compensate for the energy required to catch these prey, by catching as much prey as possible and potentially by feeding on prey with high energy density. With their patchy distribution (Auster et al. 1992) and their lethargic behavior (Barham 1971), small myctophids, which are high energy density fishes (Lenky et al. 2012) are the most plausible candidate prey.

We interpreted the second mode as an active chase, as SESs attack from below with a large swimming effort (Table 4). Here, the energy expenditure is almost exclusively due to the animal's stroke, as if the only purpose of the animal was to charge into prey. Depending on the depth and the prey, SESs could in this case use the prey shadow to better target them. As the associated prey catch attempt rate was also found to be low, we hypothesized that SESs would compensate for the extra energy required to catch fast moving prey while ascending, by favoring large prey such as squid or larger myctophid species (e.g. *Gymnoscopelus bolini*).

Finally, the last cluster reveals a passive hunting mode that would consist of catching prey from above, by gliding down on them at a relatively shallow angle (Table 4). All females were found to remain negatively buoyant during post-breeding foraging trips (Richard et al. 2014), particularly during the first weeks following their departure from the colony, and therefore to glide when moving down (Davis & Weihs 2007). This attitude, while being interpreted as an energy-saving strategy, i.e. low values for VeDBA, could also be interpreted as opportunistic captures, by catching prey by stealth during the approach phase. In this case, the associated low sinuosity could be perceived as if SESs travelled in a straight direction, gliding down at a shallow angle and capturing low density prey on their way.

While ARS are associated with a higher prey encounter rate, these 3 foraging strategies were also found to be the same outside these areas (Fig. S3 in the Supplement), highlighting that hunting behavior is not dependent on ARS. Presumably, areas of increasing foraging effort are contingent upon prey aggregation, revealing 3-dimensional ARS regions as a way to assess the heterogeneity of resource distribution. Although we may associate different foraging strategies based on energy balance associated with each behavioral mode, it is also possible that SESs pursue a variety of prey and that their behavior is simply a result of pursuing different species.

Foraging ecology

Marine ecosystems are difficult to access and study. However, the combination of diving and tracking data from top predators can be extremely useful to improve our understanding of the role and the structure of marine resources. Following the conceptual framework of the optimal foraging theory (Charnov 1976), predators should adjust their movements to prey encounters or environmental conditions. In a favorable environment, or when prey is encountered, predators are expected to increase their turning rate (Davis et al. 1991) and decrease their speed (Patlak 1953, Turchin 1991), as we found in SESs (Fig. 3, Table 3).

As no differences in the proportion of hunting modes were observed between individuals, our results on hunting classification seem generalizable, but the small number of individuals, the short recording periods (Table 1) and the geographical bias (all animals went east) do not allow us to draw conclusions at the population level. This also applies to the analysis of hunting strategies, since only subsampled data from 6 elephant seals were used for the classification. Here, 3 different strategies emerge from the unsupervised classification. One of them is associated with opportunistic attempts and represents 32.8% of prey captures. It consists of catching prey at a lower rate, by adopting an apparently energy-saving strategy. The other 2 strategies are much more energy consuming for these animals, in part because of the swimming effort required to counteract their natural negative buoyancy. In addition to this effort, the energy expenditure was also found to be related to 3-dimensional movement for the main hunting behaviors used in 56.6% of the prey catch attempts. We believe the extra energy required by employing this hunting mode would be compensated with a greater number of captured prey, particularly if these prey have higher energy density. As this strategy seems to be preferred over the others, we believe the associated energy balance (energy intake vs. energy expenditure) is more favorable than the others.

These findings challenge the general assumption that elephant seals mainly adopt energy-saving foraging behaviors. Based on previous studies (Adachi et al. 2014, Richard et al. 2014, Maresh et al. 2015, Jouma'a et al. 2016), we believe that SESs adopt an energy saving strategy when transiting between patches, through the minimal cost of transport (Miller et al. 2012), but increase their swimming costs when actively pursuing prey. While this classification is

indicative of different foraging strategies, one can consider that it may also be indicative of different prey species. Further investigations, such as these initiated by Vacquié-Garcia et al. (2015b) on the delineation of SESs' foraging environments defined by temperature, light level and depth, or Bailleul et al. (2015) on the dissolved oxygen in water masses visited by SESs, would be interesting to assess the distribution and the ecology of their prey.

Ethics statement. The Ethics Committee of the French Polar Institute validated all scientific procedures applied on elephant seals. All animals in this study were handled and cared for in accordance with its guidelines and recommendations.

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