A New Method to Quantify within Dive Foraging Behaviour in Marine Predators

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Abstract

Studies on diving behaviour classically divide a dive into three phases: the descent, bottom and ascent phases, with foraging assumed to occur during the bottom phase. The greater complexity of dive revealed through modern, high resolution data highlights the need to re-assess this approach and to consider a larger number of phases within individual dives. Two southern elephant seals (SES) were fitted with a head mounted Time Depth Recorder (TDR) and an accelerometer from which prey capture attempts were estimated. A Weddell seal was also fitted with a TDR. TDRs for both species recorded depth once per second. We quantified the within dive behaviour using an automated broken stick algorithm identifying the optimal number of segments within each dive. The vertical sinuosity of the segments was used to infer two types of behaviours, with highly sinuous segments indicating "hunting" and less sinuous segments indicating "transiting". Using the broken stick method the seals alternated between "hunting" and "transit" modes with an average of 6±2 and 7±0.02 behavioural phases within each dive for the Weddell seal and SES, respectively. In SES, 77% of prey capture attempts (identified from the acceleration data) occurred in highly sinuous phases ("hunting") as defined by our new approach. SES spent more time in transit mode within a dive, and hunting mostly occurred during the bottom phase. Conversely the Weddell seal spent more time in hunting mode which also occurred during bottom phase but occurred mostly at shallower depths. Such differences probably reflect different foraging tactics and habitat use. For both species, hunting time differs significantly from bottom time previously used as a proxy for the time spent foraging in a dive. The hunting time defined by our method therefore provides a more accurate fine-scale description of the seals' foraging behaviour.

Introduction

Predators maximize resource acquisition by adapting their movement patterns and foraging behaviour to the distribution and density of their prey [1–3]. In environments where resources are patchily distributed, such as the open ocean, predators need to compensate the costs associated with travel from one patch to another and pursuing a prey with food intake [4]. Thus, predators tend to increase the time spent in the vicinity of recent prey captures by decreasing their displacement speed and increasing their turning frequency [5,6]. This behaviour, called Area Restricted Search, (ARS) is frequently observed in free ranging predators in the horizontal dimension [7].

For many marine predators, prey capture occurs in the water column where prey are aggregated [8–10], making it necessary to also consider the vertical dimension for these species. Identifying feeding events in the vertical dimension (i.e. within dives) is still a challenging issue in marine ecology as direct observations are usually impossible. To optimize their foraging strategy when diving, they should decrease their vertical speed and increase the sinuosity of their movements, making what are effectively vertical ARS as indicted on two dimensional dive profiles [11].

Bio-logging devices measure various parameters of free-ranging animal behaviour providing important information on their diving and foraging that are difficult to observe otherwise [12]. Miniaturization, extended battery life and memory size now mean that Time Depth Recorders (TDRs) collect and store data at very high resolutions (one second or less) and for long periods of time (several months) [12,13], enabling the study of diving behaviour at finer spatial and temporal scales than before [7,14,15]. Several foraging metrics (e.g. dive duration, dive depth, descent/ascent rate, bottom time, post dive surface interval) can be calculated from TDR data and are used to classify dives into functional categories [7,16–20], but typically they are not systematically associated with direct information on food intake [21]. However, the greater complexity of dives revealed through both high resolution time-depth datasets and three-dimensional diving studies suggest that this method could lead to an over-simplification of diving behaviour [22,23]. When a seal is spending some time at a particular depth and travelling up and down while at this depth ("wiggles"), it is displaying vertical ARS, and this has been used as an index of foraging activity (not necessarily including prey capture), with several studies providing independent evidence for this in the form of changes in stomach or oesophageal temperature
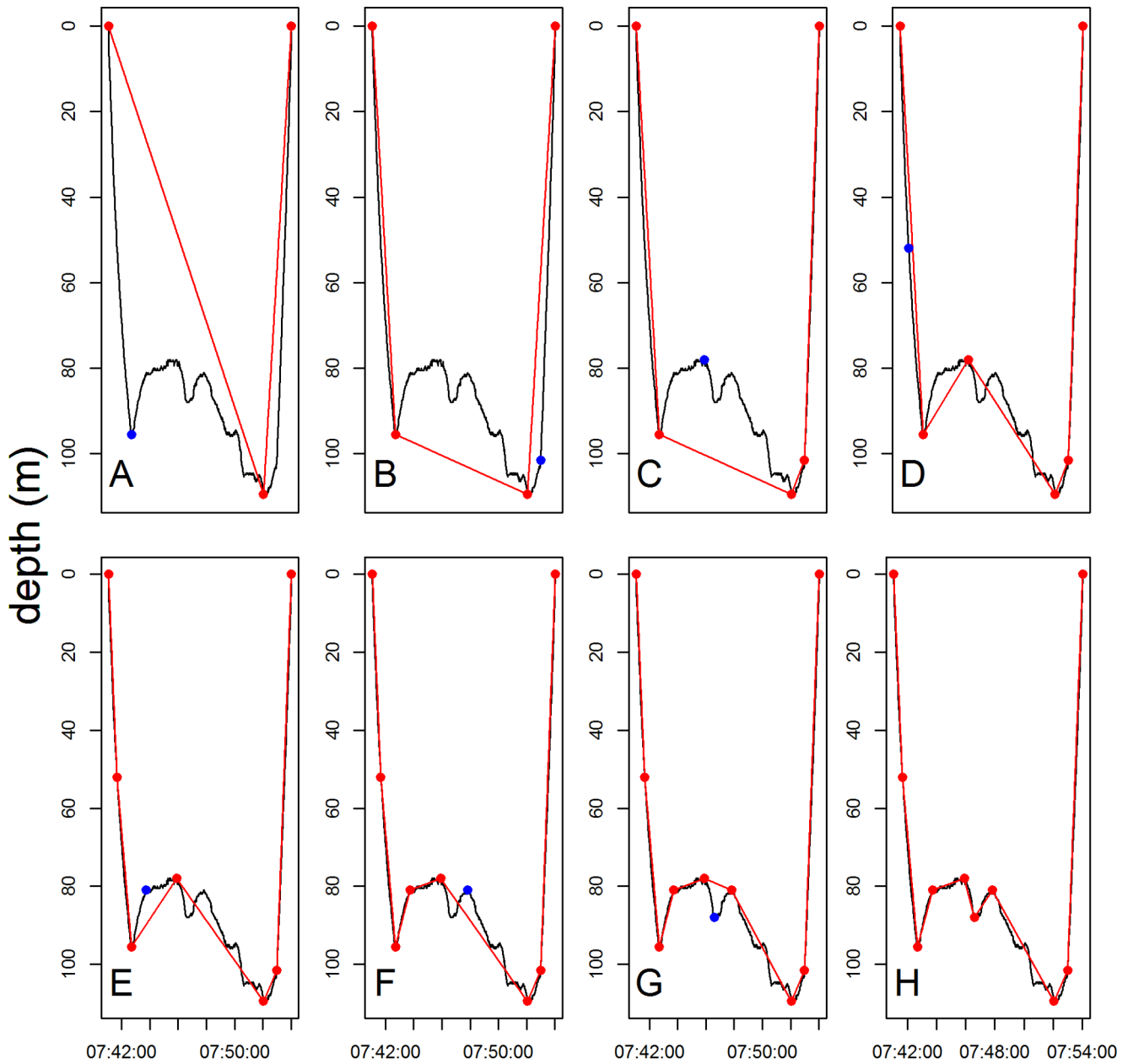
Figure 1. The broken stick algorithm. The iterative process of the broken stick algorithm is presented from panel A to H. The broken stick method iteratively selects the data points (in blue) of maximum difference between the original dive profile (black line) and the dive profile reconstructed by linear interpolation (red lines) between the points selected during the previous iterations (in red). A Weddell seal dive was used as an example for this graph.

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[7,21,24–26]. More recently, accelerometers measuring body acceleration in up to three dimensions (*i.e.* surge, heave and sway observed in movements such as: stroke and rolling) have provided insights into the functionality of dive types and the details of fine-scale foraging [9,25]. Stroke frequency has been used as an index of prey pursuit or feeding success [27,28]. Recent studies have also shown, that for seals, feeding and capture motions are especially visible in the surging axis when using jaw or head accelerometers [25,29,30]. Using high resolution dive data in combination with a new approach to detect likely foraging events within a dive can greatly improve what information can be derived from time-depth data.

Southern elephant seals (*Mirounga leonina*, hereafter SES) have a circumpolar distribution and forage extensively across the Southern Ocean [31]. They are associated with important habitats such as the ice edges and continental shelf and feed mainly on fish and squids [32–34]. They are also very deep divers, diving up to 2000 meters and performing on average 60 dives per day [16,35]. Recent studies have focused on SES fine-scale diving behaviour providing more accurate inferences on their foraging activity [7,25,36]. However, little is known about SES vertical ARS behaviour, which is more likely to respond directly to prey distribution. A detailed analysis of their vertical excursions during
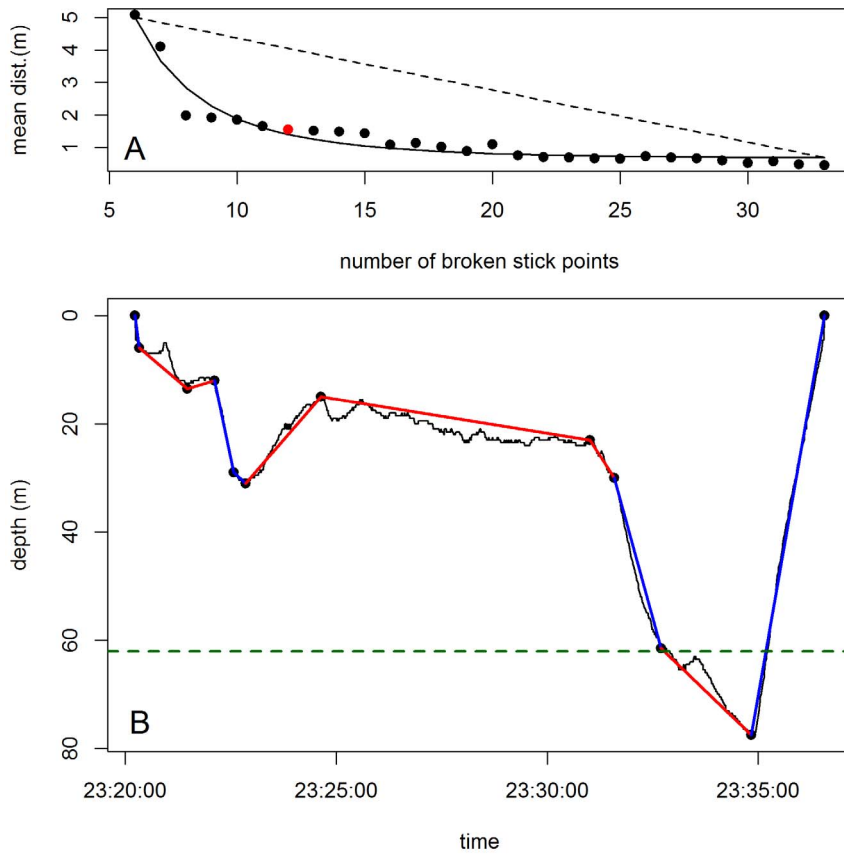
Figure 2. Optimization of the broken stick algorithm. Any number of broken stick points can be chosen depending on the resolution required to describe a dive. A: Mean distance according to the number of broken stick points (from 6 to 33) which are used to describe the dive represented below (B). The mean distance is the average of the differences between each data point of the original profile and the corresponding point of the reconstructed profile obtained by linear interpolation between the broken stick points (from 6 to 33). The inflexion point of the mean distance curve (A, red data point) is determined by calculating the maximal distance between the asymptote curve obtained by fitting a Gompertz model to the mean distance (A, black line) and the linear approximation (A, dashed black line) between its start and end points. B: Original dive profile (B, black line) summarized by the optimal number of broken stick points (B, black data points) as estimated by mean distance represented above (A). The blue lines represent transit segments$_{BS}$ and the red lines represent hunting segments$_{BS}$. The green dashed line represents the depth below which bottom time is calculated with the classical dive analysis method. A Weddell seal dive was used as an example for this graph.
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dives in association with prey capture attempts and prey distribution has yet not been conducted.

Weddell seals (*Leptonychotes weddellii*) are the most southerly breeding seal and typically inhabit sea-ice during the whole year [37,38]. Weddell seals are the second deepest phocid diver in the Southern Ocean after the southern elephant seal, attaining 900 m [39]. They are opportunistic predators feeding mainly on fish, but also on cephalopods and crustaceans, in proportions that vary according to age, location and season [40]. Weddell seal diving and foraging behaviour has been extensively studied during summer in the Ross Sea and the Weddell Sea [29,41]. However, because Weddell seals are opportunistic predators it is difficult to associate only one type of foraging dive to their overall behaviour [42,43].

We used high resolution TDR datasets from two SES that travelled to Antarctica during their post-breeding foraging trip and a high resolution TDR dataset covering six winter months from a Weddell seal to develop a new method for identifying the phases within a dive where the seals exhibited foraging behaviour. The concurrent prey capture attempts estimated from high resolution acceleration available for the SES were independently used to validate the method. Our method aimed to: (i) describe the vertical

structure and complexity of seal dives, (ii) determine within each dive the parts where likely foraging occurs and (iii) compare this method to classical dive analysis approach.

Materials and Methods

Fieldwork and data collection were undertaken with approval from the University of Tasmania animal ethics committee (permit A8523), and from IPEV (Institut polaire français Paul Emile Victor) and TAAF (Terres Australes et Antarctiques Françaises) animal ethics committee.

Two adult female SES (length: 266 and 255 cm) were captured at Kerguelen Island (49°20′ S, 70°20′ E) in early November before their post breeding trip. One adult female Weddell seal was captured in February 2008 after its annual moult at Dumont d'Urville (66°40′ S, 140°00 E) (length 230 cm). Similar capture and tagging procedures were adopted for both species. The seals were approached by foot and temporarily restrained with a head bag and an intravenous injection of Zoletil (1:1 mixture of tiletamine and zolazepam, 0.5 mg.kg^{-1}) was administered [44–46]. A TDR combined with an accelerometer (TDR Mk 10 X, Wildlife Computers) and a TDR (Mk 10, Wildlife Computers) was head-glued to the SES and to the back of the Weddell seal,
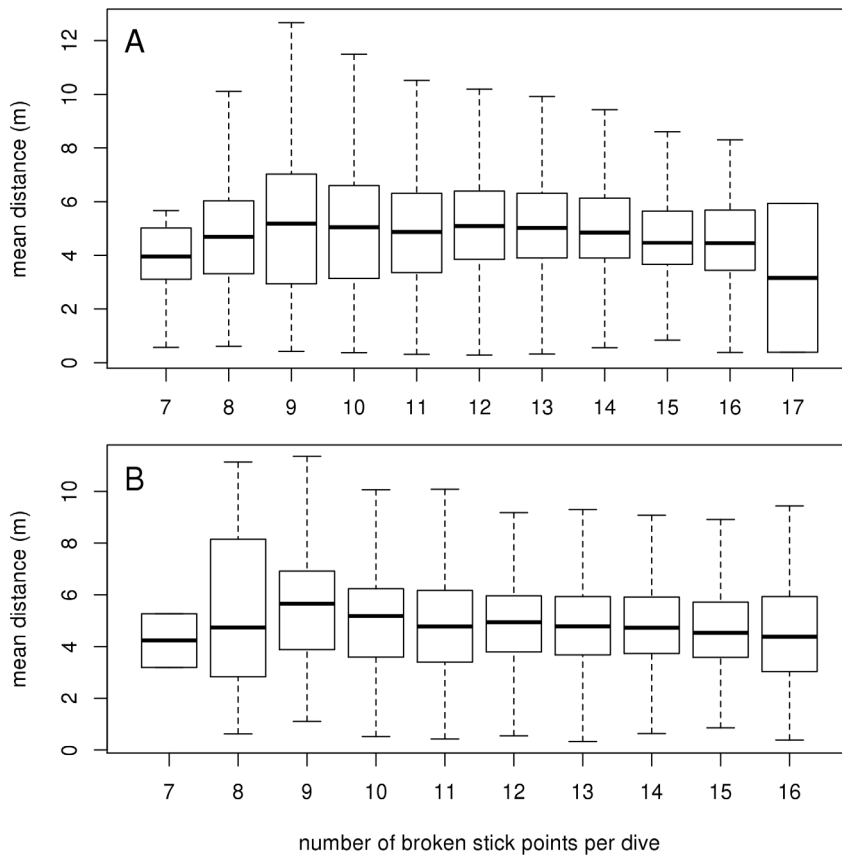
Figure 3. Distribution of the mean distance. Distribution of the mean distance (m) according to the optimal number of broken stick points calculated for each dive for the southern elephant seals (A) and the Weddell seal dataset (B). See figure 2 for calculation of the optimal number of broken stick points.
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respectively, using a two component industrial epoxy (Araldite AW 2101). Seals were observed during recovery from anaesthesia and allowed to enter the water when no longer sedated. The TDRs recorded time and pressure at 1 Hz. Acceleration was recorded in the 3 axis at 16 Hz.

Fine scale analysis of foraging behaviour

1 Surface offset correction. To account for drift in the pressure transducer accuracy and to identify individual dives, we corrected depths using a customised Zero Offset Correction method. We used a moving window of one hour and considered the modal depth between 20 and −20 meters to represent the true surface (assuming that most of the time in this depth range would represent time on the surface. This depth was then subtracted from all depth values in this interval to provide zero offset corrected depths. Only dives below 15 meters were analysed for the SES, while we defined the Weddell seal's dives as being at least 60 seconds long and four meters deep (60% of all dives) taking into account the accuracy of the pressure transducer (0.5 meters), the size of the seal and sea ice thickness during winter (2.5–3 m, [47]). The frequency distribution of the Weddell seal diving depths was bi-modal, with two groups of dive depth separated at 20 m. Dives <20 m were excluded from further analysis (21% of dives longer than 60 sec.) as they may indicate non-foraging activities [48]. SES performed 3941 and 4254 dives with an average (mean ± SD) of 53±1 (max: 68) and 56±1 (max: 104) dives per day, respectively. The Weddell seal performed 11452 dives deeper than

20 m and longer than one minute with an average of 63±24 (max: 115) dives per day. Standard dive parameters were calculated using classical dive analysis methods [16,18,20], dividing each dive into an descent, bottom and ascent phase based on inflection points.

2 Dive analysis with the optimised and automated broken stick method. As an alternative to the classic three-phases (i.e ascent, bottom and descent) dive analysis (CA) we used a method based on a broken stick algorithm (BS). This method selects the data points where the dive trajectory between two points changes the most rapidly (inflexion points). Any number of points can be chosen depending on the resolution required [49]. We started with three points: (i) surface start point, (ii) maximal depth and (iii) surface end point (Fig.1 A). We then iteratively selected the data points of maximum difference between the original dive profile and the dive profile reconstructed by linear interpolation between the points selected during the previous iterations (Fig.1, Script S1 and Dataset S1).

We then estimated the optimal number of broken stick points (from 6 to 33) that best summarize the dive shape. For this, we calculated a mean distance based on the average of the differences between each data point and its corresponding position on the line between the broken stick points (Fig. 1, averaged depth differences between the black curve and the red lines). The mean distance was calculated for each dive summarised with 6 to 33 broken stick points (Fig. 2 A, Script S1 and Dataset S1). For each dive we plotted the mean distance for a range of broken stick points and we
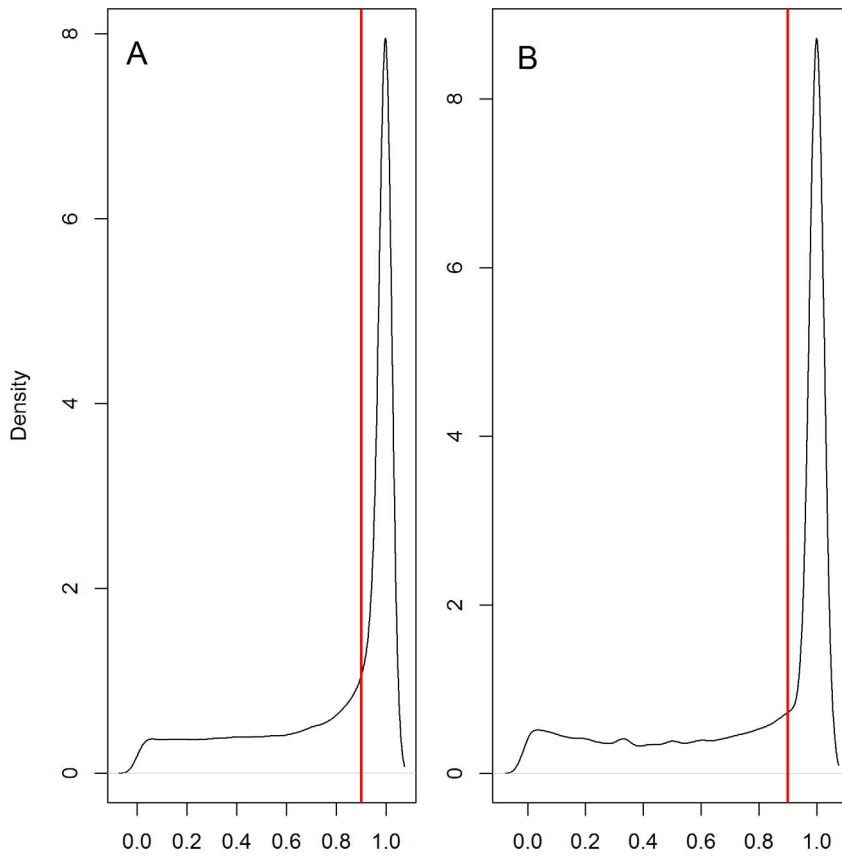
Figure 4. A bimodal behaviour. Density plots representing the distribution of the vertical sinuosity calculated for each broken stick segment from the elephant seal dives (A) and the Weddell seal dives (B). The 0.9 sinuosity threshold represented by the vertical red line was used to discriminate "transit" mode$_{BS}$ versus "hunting" mode$_{BS}$.
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determined the inflexion point of this curve (i.e the point after which the amount of new information explained by increasing the number of segments$_{BS}$ began to decline). To do this in an automated way, each integrated distance curve was smoothed by fitting to a Gompertz model [50]. The inflexion point of this curve was then determined by calculating the maximum distance between the Gompertz curve and the linear approximation between its start and end points (Fig. 2 A, Script S1 and Dataset S1). The number of corresponding broken stick points was then used to optimally describe each dive (Fig. 2, Script S1 and Dataset S1). There was no trend in the relationship between the mean distance and the number of broken stick points per dive (mean ± SD, 5±0.02 m, min: 0.3 m, max: 18 m and 1.2±0.8 m, min: 0.15 m, max: 7.8 m, for the SES and the Weddell seal respectively) (Fig. 3), showing that there is no bias associated with dive complexity.

3 Detection of intensive foraging within dives. Based on the definition of Area Restricted Search (ARS) in the horizontal dimension when animals are at the surface [5], we expected diving predators such as the SES and the Weddell seal to adjust their diving behaviour in order to increase the time spent in a patch of prey, by decreasing their vertical velocity and increasing the vertical sinuosity of their trajectory. Therefore for each segment between two broken stick points (hereafter segment$_{BS}$) we calculated, (i) the vertical descent/ascent rate (in m/s) and (ii) the vertical sinuosity (Script S1 and Dataset S1) adapted from [7] as:

$$Sinuosity = \frac{Dist_{brokenstick}}{Dist_{observed}}$$

where $Dist_{broken\ stick}$ is the vertical distance swum between the two broken stick points considered, and the $Dist_{observed}$ is the sum of all the vertical distances from the original dive profile between the two corresponding depth points. Vertical sinuosity ratio (hereafter sinuosity) takes a value of 1 when the individual swims in a straight path during this part of the dive. Any deviation from a straight path decreases the sinuosity ratio toward 0.

The distribution of the sinuosity index of all dive segments$_{BS}$ and for both species was distinctly bi-modal (sinuosity comprised between 0 and 0.9 and sinuosity >0.9, Fig. 4) suggesting two behavioural modes. We used the 0.9 sinuosity threshold to discriminate vertical search mode$_{BS}$ (0< sinuosity >0.9) from directed travel mode$_{BS}$ (0.9≤ sinuosity ≥1) within each dive. Hunting mode$_{BS}$ was characterized by a more sinuous path, possibly indicating intra-patch movements, whereas directed travel mode$_{BS}$ showed a straighter path probably occurring during inter-patch movements or when transiting from surface to/from depth. Successive broken stick segments of the same behavioural mode$_{BS}$ were then grouped in hunting or transiting phases$_{BS}$ allowing us to quantify the phases$_{BS}$ within each dive (Fig.2 B). For each dive, we characterized each phase$_{BS}$ using the behavioural mode$_{BS}$ (i.e. hunting vs transit), the number of broken stick segments making up each phase$_{BS}$, its duration, its mean depth and its mean ascent/

Table 1. General information on tag transmission and diving behaviour.

	Tag deployment	Tag retrieval	Transmission duration (days)	Number of dives	Number of dives per day	Dive maximum depth (m)	Dive duration (min)
SES 1	2010-10-31	2011-01-21	72	3941	53±1 max: 68	511±4 max: 1260	23±0.01 max: 56
SES 2	2010-01-11	2011-01-15	73	4254	56±1 max: 104	475±4 max: 1296	21±0.1 max: 50
Weddell seal	2003-02-23	2008-10-20	182	11452	63±24 max: 115	67±54 max: 645	10±6 max: 46

Data are given for two adult female southern elephant seals (SES) captured at Kerguelen Island (49°20′ S, 70°20′ E) and one adult female Weddell seal captured at Dumont d'Urville (66°40′ S, 140°00′ E). Both species were fitted with TDRs. Accelerometers were also head-mounted on SES.
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descent rate (Script S1 and Dataset S1). For the SES data set, we also counted the number of prey capture attempts that occurred in each behavioural phase$_{BS}$. They were calculated from the concurrent high resolution acceleration data [51,52]. Briefly, acceleration data were used to identify rapid head movements that may be associated with prey encounter events and these are visible as spikes in the filtered acceleration profiles [25]. Acceleration profiles with more than one spike above a given threshold (in m/s^2) visible both in the surge and heave axes were considered to be related to prey encounter events. A full description of the acceleration data filtration process and definition of the threshold for the spike occurrence are given in [25] and [52].

4 Comparison of the two behavioural modes$_{BS}$. In the Weddell seal data set a number of segments$_{BS}$ showed very high vertical ascent/descent rates, which may result from depth measurement errors by the sensor. Davis et al. [42] used a velocity sensor recording swimming speed and observed mean maximum speeds up to 5.1±1 m/s depending on the type of dive and location. We therefore removed dives containing segments$_{BS}$ with ascent/descent rates >7 m/s (23 dives in the Weddell seal dataset). In SES the maximum ascent/descent rates of the broken stick segments was 3.5 m/s, therefore all the SES dives were retained.

We compared the number of prey capture attempts (when available), duration, depth, and ascent and descent rates between the two behavioural modes$_{BS}$ estimated with our method (i.e. hunting vs transit) using unilateral Welch tests on two datasets of 10% of the dives randomly selected for each behaviour. We also compared the time spent in hunting mode$_{BS}$ with the bottom time$_{CA}$ identified in the classical method, using unilateral Welch tests on two datasets of 10% of total dives randomly selected [53] [50]. The Welch test allows comparing samples with different variances. "Unilateral" means that we tested if the mean of one sample was significantly greater than the other one.

Results

General diving behaviour

The TDRs recorded the diving behaviour of two southern elephant seals for 72 and 73 days from early November to January 2010 (Table 1). The seals performed 3941 and 4254 dives with an average (mean ± SD) of 53±1 and 56±1 dives per day, respectively (Table 1). The mean maximum dive depths were 511±4 m and 475±4 m with average dive durations of 23±0.01 min and 21±0.1 min, respectively (Table 1).

The diving behaviour of the Weddell seal was recorded for 182 days from late February to late August 2008 (Table 1). The seal performed 11452 dives deeper than 20 m and longer than one minute with an average of 63±24 dives per day (Table 1). The mean maximum dive depths were 67±54 m with average dive durations of 10±6 min (Table 1).

Foraging behaviour

1 Comparison between the broken stick analysis and prey capture attempts in SES. Dives included an average of 12±0.02 (max: 16, SES 1), 12±0.02 (max: 17, SES 2) and 12±2 (max: 17, Weddell seal) broken stick segments using the broken stick algorithm. However, the fit of the Gompertz model included in the method did not work for 6% of the SES dives and 4% of the Weddell seal dives which were removed from the dataset. For these dives, the relationship between the mean distance and the number of broken stick points was more linear (Fig. S1). Consequently, the model could not detect an inflexion point, which is necessary for determining the optimal number of

Table 2. Comparison of dives with or without prey capture attempts as inferred from acceleration data in southern elephant seals.

	Dives w/o PrCA	Dives w PrCA	t	df	p-value
Depth (m)	394±7	514±7	12	1998	<0.001
Duration (min)	21±0.2	22±0.14	5.3	1765	<0.001
Number of behavioural phases$_{BS}$	5±0.06	7±0.06	23	1998	<0.001
Time spent in hunting mode$_{BS}$ (min)	8±0.15	9±0.1	4	1974	<0.001

Duration, depth, complexity (number of behavioural phases$_{BS}$) and time spent in hunting mode$_{BS}$ for 1000 dives randomly selected that are associated (w) or not (w/o) with prey capture attempts (PrCA) were compared using unilateral Welch tests.
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broken stick points needed to summarize the dive (Fig. S1). In these cases, the number of broken stick points can be determined subjectively by the user (e.g could be determined to suit the averaged mean distance for all dives).

SES dives were rarely associated with more than 40 prey capture attempts, therefore these dives with >40 prey capture attempts were also removed from the dataset (0.1% of the SES dives). Of the remaining SES dives, there were 1369 dives that were not associated with prey capture attempts (17% of the SES dives) but during which the SES spent 8±13 min in hunting mode$_{BS}$. These dives were, on average, 393±6 m deep, 20±2 min long and characterized by 5±0.05 behavioural phases$_{BS}$. The remaining dives (6814) were associated with an average of 11±0.1 prey capture attempts and on average 9±0.05 min were spent in hunting mode$_{BS}$. Foraging dives (dives with >0 prey capture attempts) were on average 512±3 m deep, 22±0.05 min long and

characterized by 7±0.02 behavioural phases$_{BS}$. Dives with prey capture attempts were significantly deeper, longer, more complex (as they were characterized by more behavioural phases$_{BS}$) and more time was spent in hunting mode$_{BS}$ than dives without prey capture attempts (Table 2).

Hunting phases$_{BS}$ (defined by the broken stick method) of the SES foraging dives were associated with four times more prey capture attempts than transit phases$_{BS}$ (hunting mode$_{BS}$: 2.5±0.02, transit mode$_{BS}$: 0.6±0.007; Table 3, Fig. 5). Of the total prey capture attempts, 77% and 23% occurred during hunting and transit phases$_{BS}$, respectively.

2 Comparison of behavioural modes$_{BS}$ defined by the broken stick analysis. Within dive behaviour was characterized by two behavioural modes$_{BS}$: (i) hunting and (ii) transit mode$_{BS}$ (Fig. 1, 6 and 7). On average, dives were summarized by 7±0.03 (max: 15, SES 1), 7±0.03 (max: 13, SES 2) and 6±2
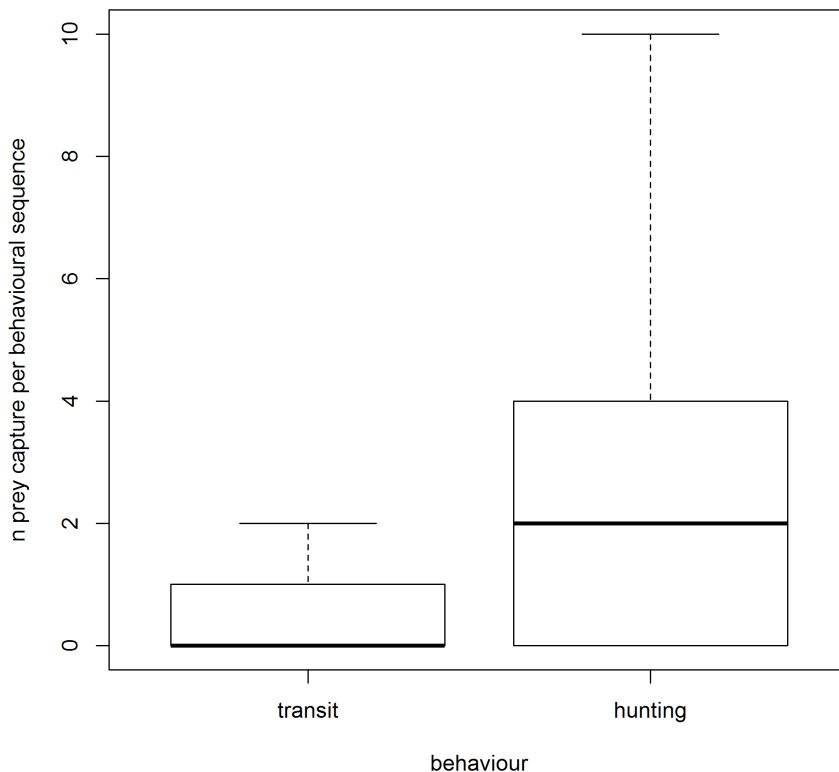
Figure 5. Behavioural differences in prey capture attempts in SES. Distribution of the number of prey capture attempts calculated for each segments$_{BS}$ according to transit mode$_{BS}$ and hunting mode$_{BS}$, respectively for the elephant seal foraging dives.
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Table 3. Comparison of within dive behavioural modes$_{BS}$ in southern elephant seals and Weddell seal.

	Species	Hunting mode$_{BS}$	Transit mode$_{BS}$	t	df	p-value
Depth (m)	SES	386±4	304±3	15	5363	<0.001
	Weddell seal	49±0.9	38±0.6	9.9	5567	<0.001
Duration (min)	SES	2.8±3	2.9±3	1.9	5604	<0.05
	Weddell seal	2.5±3.4	0.9±0.9	27	3314	<0.001
Ascent/descent rate (m.s^{-1})	SES	0.3±0.004	1.23±0.006	126	9153	<0.001
	Weddell seal	0.13±0.001	1.2±0.01	72	7842	<0.001
Number of prey capture attempts	SES	2.5±0.07	0.6±0.02	27	3047	<0.001

Duration, depth, absolute values of ascent and descent rates (mean ± se) and the number of prey captures attempts (SES) between the two foraging modes$_{BS}$ were compared using unilateral Welch tests for two independent sets of 10% of the total dives randomly selected for each modes$_{BS}$. SES stands for southern elephant seals.
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(max: 13, Weddell seal) behavioural phases$_{BS}$. This provides considerably more detail than the simple three phases$_{CA}$ (descent, bottom and ascent phases$_{CA}$) found with the classic dive analysis method (Fig.6 and 7). For the SES, dives with three hunting phases$_{BS}$ were the most frequent (35% of all dives, Fig. 8 a and Fig.6 f-g), followed by those with two (Fig.6 d-e), four (Fig.6 h-i) and one (Fig.6 b-c) hunting phases$_{BS}$ representing, 25%, 24% and 9% of all dives, respectively (Fig. 8 a). Dives with five, six, zero (Fig.8 a) and seven hunting phases$_{BS}$ were scarce, representing 6 to 0.2% of the dives, respectively (Fig. 8 a). Weddell seal's dives with two hunting phases$_{BS}$ were the most frequent (36% of all dives, Fig. 8 b and Fig.7 d-e), followed by those with three (Fig.7 f-g), one (Fig.7 b-c) and four (Fig.7 h-i) hunting phases$_{BS}$ representing, 28%, 20% and 11% of all dives, respectively (Fig. 8 b). Dives with five, zero (Fig.7 a) and six hunting phases$_{BS}$ were scarce, representing 2.7 to 0.2% of the dives, respectively (Fig. 8 b).

SES hunting phases$_{BS}$ were deeper than transit phases$_{BS}$ as they were localized at 80±0.12% (393±1 m) and 64±0.12% (312±1 m) of the maximal dive depth, respectively (Table 3, Fig. 9 b). Hunting phases$_{BS}$ were shorter than transit phases$_{BS}$ representing 14±0.1% (3±0.01 min) and 15±0.1% (3.3±0.01 min) of the dive duration, respectively (Table 3, Fig. 9 a). When displaying hunting behaviour, SES decreased their instantaneous vertical velocity compared to the one adopted during transit behaviour (hunting mode$_{BS}$: 0.3±0.001, transit mode$_{BS}$: 1.22±0.002; Table 3, Fig. 10 a).

The Weddell seal hunting phases$_{BS}$ were deeper than transit phases$_{BS}$ as they were localized at 66±26% (47±45 m) and 51±23% (36±35 m) of the maximal dive depth, respectively (Table 3, Fig. 9 b). Hunting phases$_{BS}$ were also longer than transit phases$_{BS}$ representing 25±23% (3±3 min) and 12±14% (1±1 min) of the dive duration, respectively (Table 3, Fig. 9 c). The Weddell seal decreased its instantaneous vertical velocity during hunting mode$_{BS}$ compared to the one adopted during transit behaviour (hunting mode$_{BS}$: 0.13±0.13, transit mode$_{BS}$: 1.3±1.9; Table 3, Fig. 10 b).

3 Comparison between the Broken stick and the Classical dive analysis. The SES spent 41% and 59% of their total time foraging when considering the sum of time spent in hunting mode$_{BS}$ and bottom time$_{CA}$ for all dives, respectively. The mean bottom time$_{CA}$ per dive calculated from the classical method was 13±0.05 min whereas time spent in hunting mode$_{BS}$ per dive (i.e. the sum of the different hunting phases$_{BS}$ within a dive) was 9±0.05 min, representing 59±0.2% and 42±0.2% of the corresponding dive duration, respectively. Statistical comparison on 10% of the dives, revealed that bottom time$_{CA}$ was significantly longer than time spent in hunting mode$_{BS}$ (Table 4). The time spent in transit per dive represented 58±0.2% of the corresponding dive duration for the BS method compared to 41±0.2% for the classical approach.

The Weddell seal spent 67% and 46% of its total time foraging when considering the sum of time spent in hunting mode$_{BS}$ and bottom time$_{CA}$ for all dives, respectively. The mean bottom time$_{CA}$ per dive calculated from the classical method was 4±4 min whereas the time spent in hunting mode$_{BS}$ per dive was 6±5 min, representing 42±26% and 59±25% of the corresponding dive duration, respectively. Unlike the SES, the mean bottom time$_{CA}$ per dive was significantly shorter than the time spent in hunting mode$_{BS}$ per dive (Table 4). The time spent in transit represented 41±24% of the corresponding dive duration for the BS method compared to 58±24% for the classic approach.

In SES 43% of the hunting phases$_{BS}$ occurred above the bottom phase$_{CA}$ identified by the classical approach. For the Weddell seal, 61% hunting phases$_{BS}$ occurred above the bottom phase$_{CA}$ identified by the classical approach (Fig. 7).

Discussion

In natural systems, predators perceive and react to environmental heterogeneity. These reactions are detected through changes in movement characteristics of animals (*e.g.* direction, speed, sinuosity) [5,54], that are likely to reflect changes in the presence, or availability, of prey.

We present a new method to quantify the within-dive complexity of diving predators, and demonstrate it using high resolution TDR datasets from two SES and a Weddell seal. We assessed within-dive behavioural phases$_{BS}$ (*e.g.* hunting vs transit) using concepts derived from ARS analyses developed for horizontal track analysis. Our results show: (i) the seals alternated between hunting and transit modes$_{BS}$ at the scale of a dive; (ii) the dives were mainly characterized by numerous behavioural phases$_{BS}$ instead of the three previously described phases$_{CA}$ (descent, bottom and ascent), of which only one (the bottom) was deemed to be involved in foraging; (iii) 77% of total SES actual prey capture attempts occurred in our identified hunting mode$_{BS}$ and intra-dive hunting phases$_{BS}$ were associated on average with four times more prey capture attempts (SES) than transit phases$_{BS}$; (iv) hunting mode$_{BS}$ was adopted two or three times in a dive and was shorter (SES) or longer (Weddell) than that classically estimated from bottom time$_{CA}$. Even though based on a small sample of individuals, this study demonstrates on two seal species that our simple algorithm represents a powerful tool to identify within a dive the parts where the individual intensify its foraging behaviour.
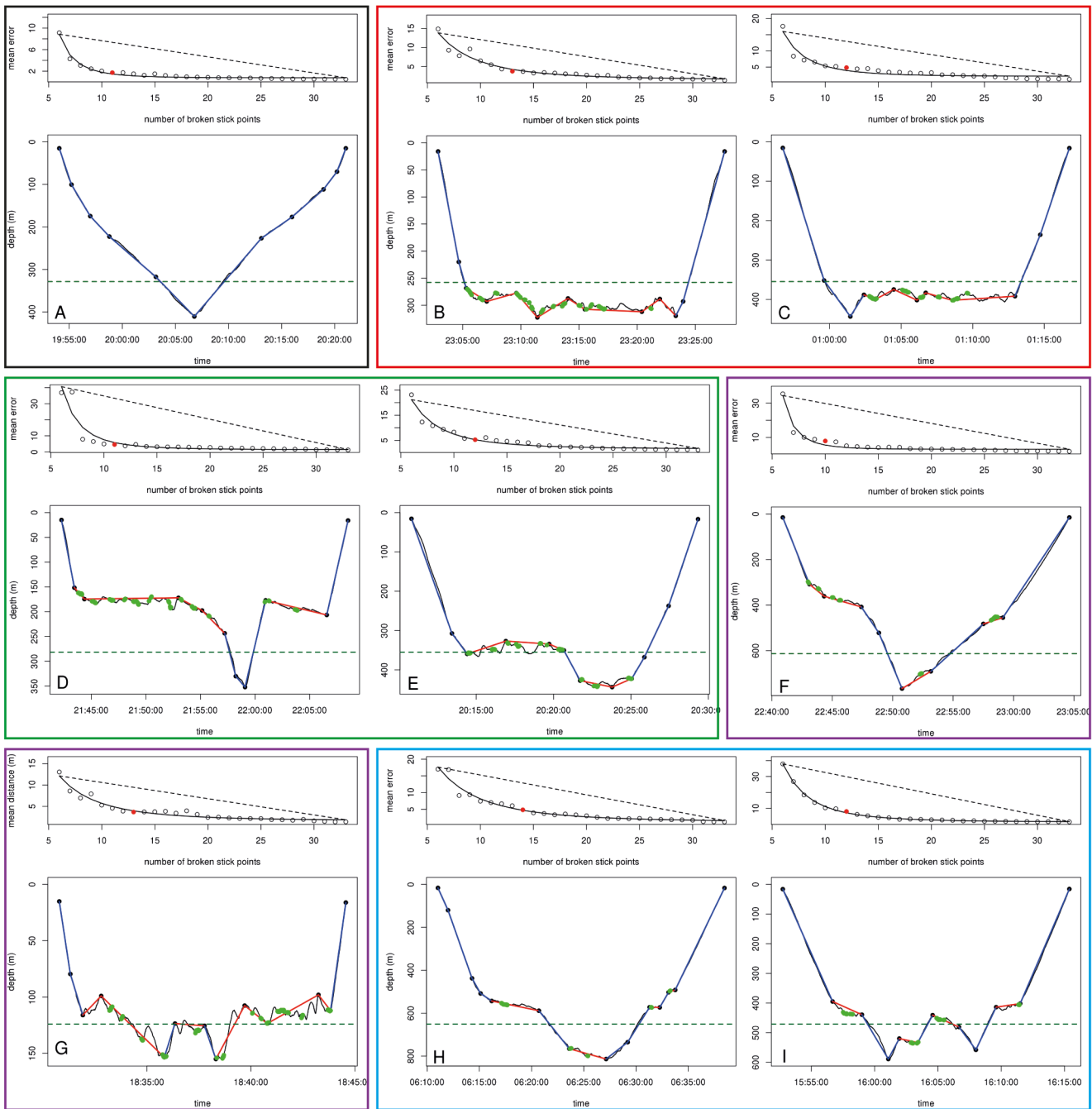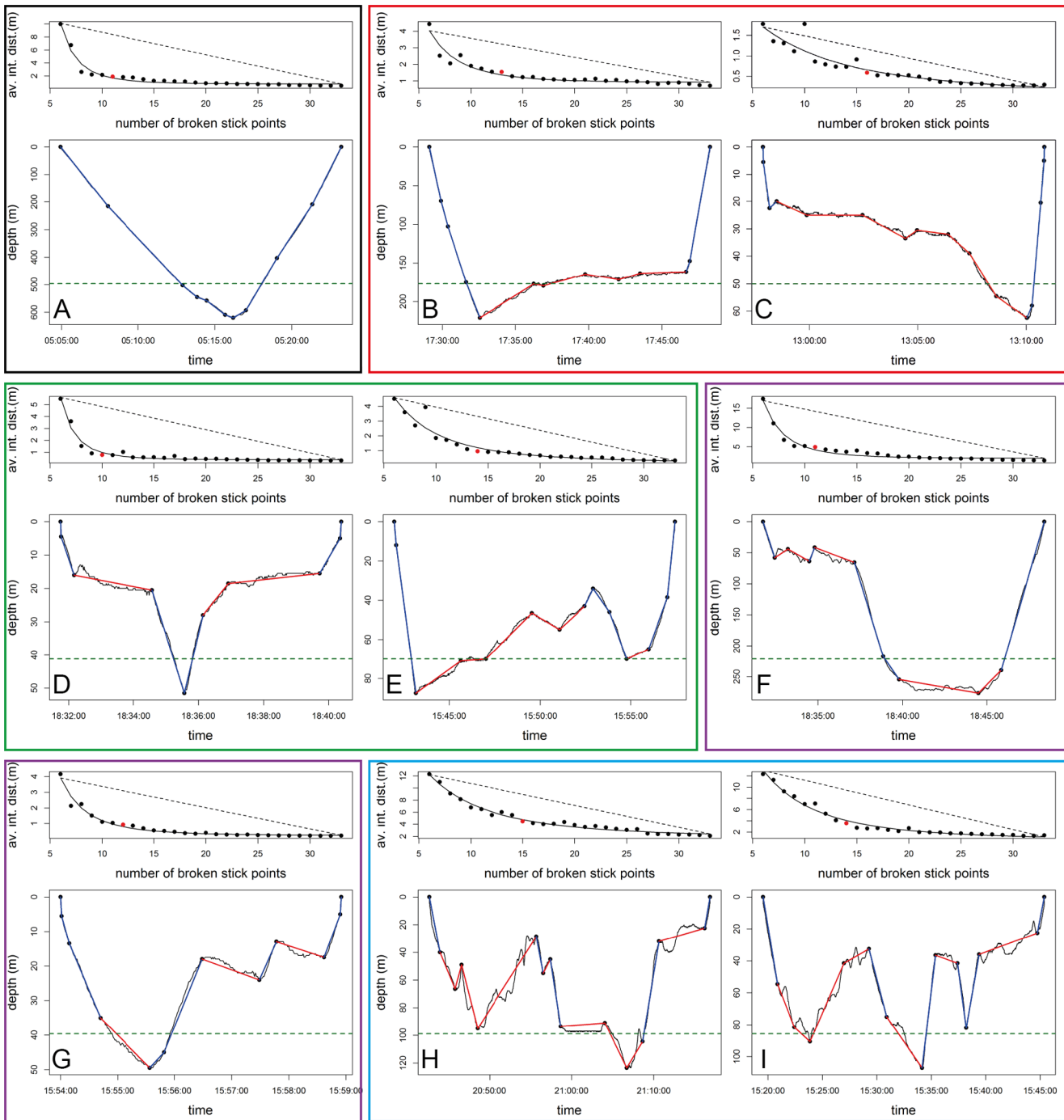
Figure 6. Complexity of the dives for the southern elephant seals. For each panel, the top graph represents the mean distance according to the number of broken stick points in order to select the optimal number of broken stick points to best describe each dive. See figure 2.A for a full description. The lower graph of each panel represents the original dive profile (black line) summarized by the optimal number of broken stick points (black data points). The blue lines represent transit segments$_{BS}$, the red lines represent hunting segments$_{BS}$ and the green dots indicate prey capture attempts (estimated from acceleration data). The green dashed line represents the depth below which bottom time is calculated with the classical dive analysis method. Figures are represented from A to I, from the simplest to the most complex dives, with zero (A, grey frame) to four (H and I, blue frame) hunting phases$_{BS}$.

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Detection of intensive foraging activity within dives

Simple depth and time data give a greatly simplified representation of what are very complex and dynamic 3D behaviours. Nonetheless, they still have provided very valuable inferences about key ecological parameters such as foraging, at very relevant temporal and spatial scales [7,15,16,18,19]. Our approach was based on the transposition of ARS to the vertical dimension. In the horizontal dimension, ARS is characterized by an increase of the trajectory sinuosity and a decrease of displacement speed [5,6], and is often used as a proxy for intensification of the foraging behaviour [7,36,55,56]. Weimerskirch et al. [57] showed in seabirds, that while food intake could occur outside ARS, it was

Figure 7. Complexity of the dives for the Weddell seal. For each panel, the top graph represents the mean distance according to the number of broken stick points in order to select the optimal number of broken stick points to best describe each dive. See figure 2.A for a full description. The lower graph of each panel represents the original dive profile (black line) summarized by the optimal number of broken stick points (black data points). The blue lines represent transit segments$_{BS}$ and the red lines represent hunting segments$_{BS}$. The green dashed line represents the depth below which bottom time is calculated with the classical dive analysis method. Figures are represented from A to I, from the simplest to the most complex dives, with zero (A, grey frame) to four (H and I, blue frame) hunting phases$_{BS}$.
doi:10.1371/journal.pone.0099329.g007

more predictable in these areas. Here, we identified ARS in the vertical dimension in order to identify those parts of the dive during which the seal increased its foraging activity.

One limit of our study could be that it was based on data from three individuals, though this is compensated to some extent by the very large number of high resolution dives included in the analysis.

Nonetheless, two behavioural modes$_{BS}$ were clearly identified in the vertical dimension according to the sinuosity of the dive segments$_{BS}$ identified with the broken stick method.

In our study, 77% of the SES prey capture attempts measured independently occurred during hunting phases$_{BS}$. Acceleration data cannot discriminate between successful prey capture attempts
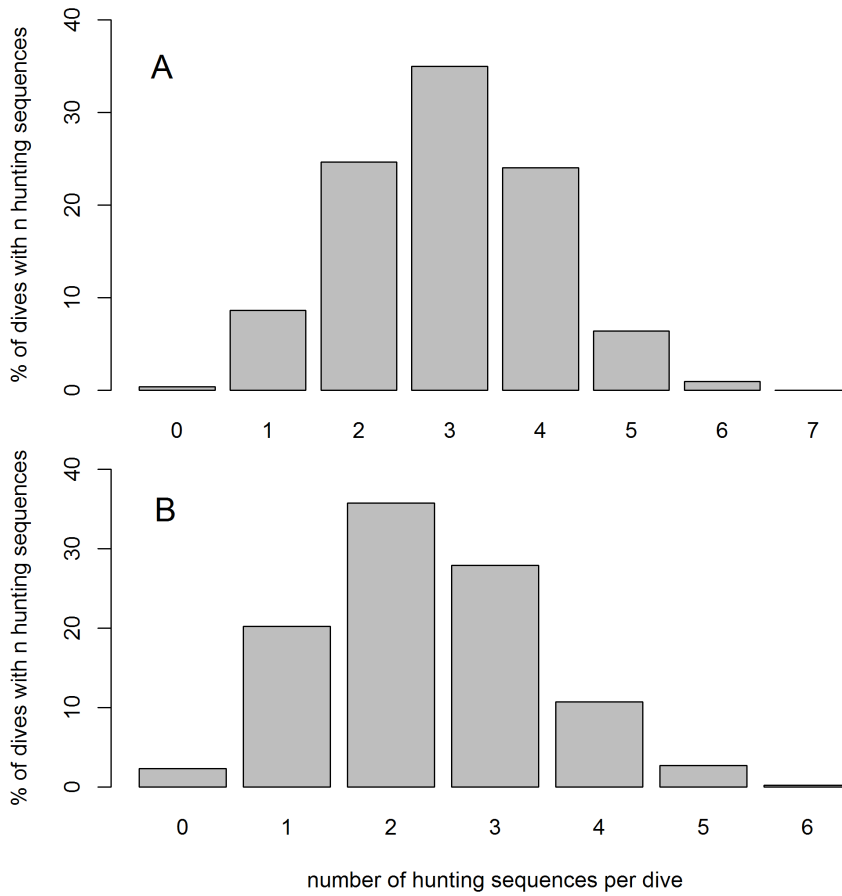
Figure 8. Occurrence of hunting mode_BS. Proportion of dives containing from zero to seven hunting phases_BS (%) for the southern elephant seals (A) and the Weddell seal (B).
doi:10.1371/journal.pone.0099329.g008

and unsuccessful ones, thus it doesn't give a true estimation of feeding success. Nonetheless it is a proxy for predators interactions with prey [25,51] and can provide information on the distribution and abundance of prey in the water column [14,29,41,51]. The remaining 23% of the SES prey capture attempts occurred during transit phases_BS suggesting opportunistic interactions with more dispersed prey resource [52]. Our results are consistent with transit phases_BS representing: (i) transit from the surface to depth of interest or (ii) travel between prey within a dive therefore corresponding to "exploratory phases". Conversely, the intensification of the seal vertical foraging behaviour can be interpreted as behavioural responses to local increased densities of prey field. During faster, straight transiting parts within the dive, the seal could explore the water column to reach a region occupied by prey. The seal then probably optimizes the time spent in that area by: (i) making "wiggles"; (ii) decreasing its vertical speed and; (iii) horizontally meander at that depth, which cannot be detected in our dataset but which has been previously observed in 3D movements analysis studies [42,43,58]. Thus, intensive foraging depths likely correspond to the depths where prey patches are located.

Vertical sinuosity (or wiggles) is often used as an index of foraging effort and/or feeding success even when no independent information on prey capture is available [16,20,56,59]. In our study, non-foraging SES dives were also characterized by some hunting phases_BS, but they only represented a minority of the dives performed. It is possible that in non-foraging dives SES captured

their prey by suction which wouldn't be detected in acceleration data [51]. Feeding by suction has been previously observed for sea lions, leopard, bearded and hooded seals [51,60–62]. Most likely vertical sinuosity is also indicative of searching to locate prey, and therefore still reflects an intensification of the foraging effort [25]. Within foraging dives more prey capture attempts occurred in sinuous phases_BS (hunting_BS). This is in accordance with [41] who showed that intensification of jaw movements during the bottom phase_CA of Weddell seal dives were associated with wiggles. Several studies of free-ranging penguins using time-depth data have confirmed that vertical sinuosity was correlated to the occurrence of feeding events measured independently with changes in oesophageal temperature, beak opening events and integrated acceleration-video records [24,30,63,64]. In pinnipeds, vertical sinuosity has also been related to prey capture based on drops in stomach temperature [21]. Furthermore, [65] used video and data recorder to study the 3D dive profiles of Weddell seals in relation to prey encounter and confirmed that vertical sinuosity in time-depth profiles actually occurs during prey encounter.

Fine scale foraging strategy of Weddell and southern elephant seal

While we are unable to make formal statistical comparisons between the two species due to our sample size, qualitatively we noticed two principal behavioural differences between the SES and Weddell seal: (i) transit phases_BS were shorter than hunting phases_BS for the Weddell seal whereas they were longer for SES;
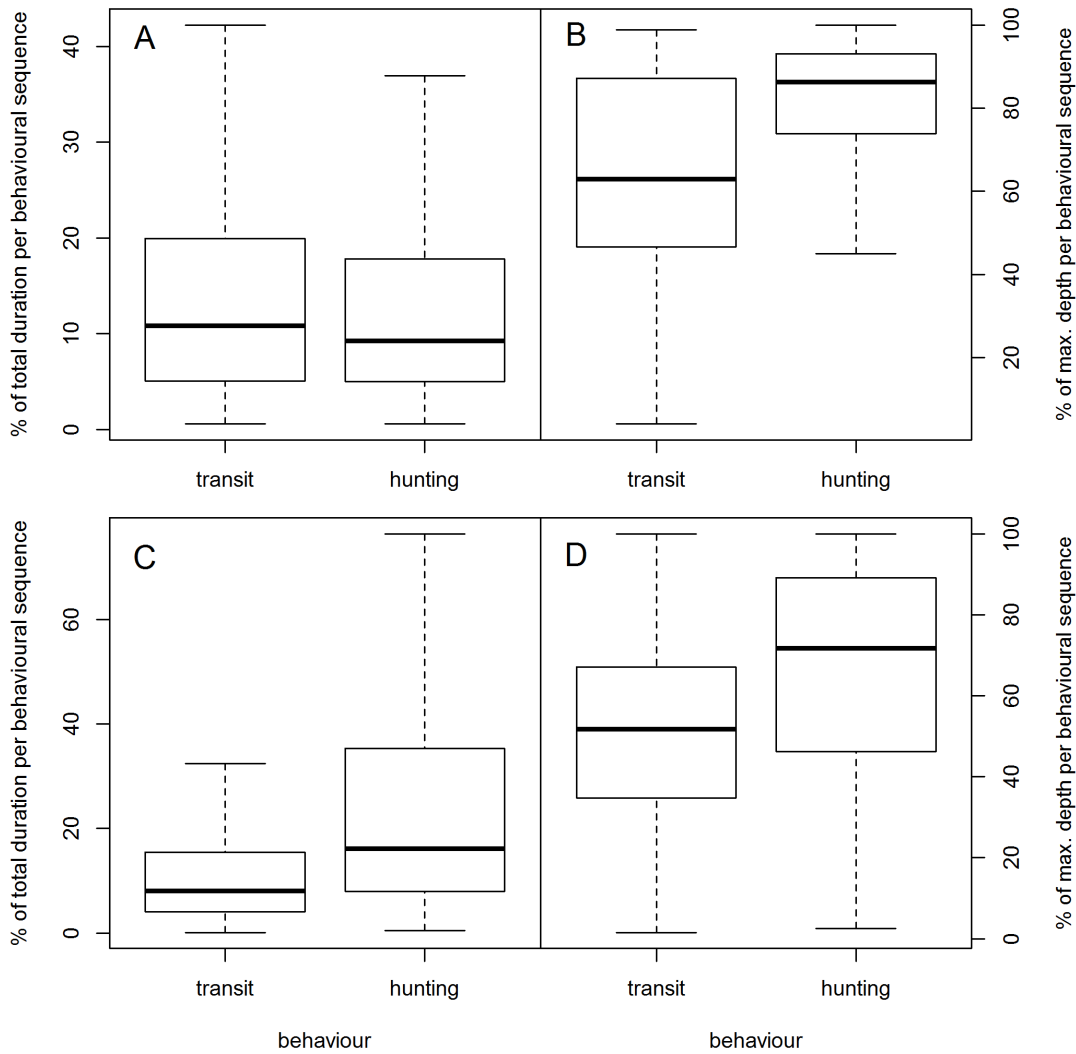
Figure 9. Behavioural mode$_{BS}$ differences. Distribution of each behavioural phase$_{BS}$ duration (sec.) expressed in percentage of the corresponding dive total duration (sec.) for transit mode$_{BS}$ and hunting mode$_{BS}$, respectively (A: southern elephant seals, C: Weddell seal). Distribution of each behavioural phase$_{BS}$ depth (m) expressed in percentage of the corresponding dive maximal depth (m) for each of the two modes$_{BS}$ (B: southern elephant seals, D: Weddell seal). The horizontal bold line of the box shows the median. The bottom and top of the box show the 25th and 75th percentiles.
doi:10.1371/journal.pone.0099329.g009

(ii) hunting phases$_{BS}$ mostly occurred above the bottom phase$_{CA}$ for the Weddell seal whereas they occurred mostly in the bottom phase$_{CA}$ for the SES. These differences probably reflect different foraging strategies between the two species.

Similarly to previous studies, the two SES females essentially used the Antarctic shelf break at sea-ice margin whereas the Weddell seal essentially dived in the fast-iced shallow coastal area in front of Dumont D'Urville [32,39]. SES performed deeper dives than the Weddell seal and must allocate more time travelling to and from the surface, therefore decreasing the time spent in hunting mode$_{BS}$. Previous studies of Weddell seals using animal borne video and data recorder have shown that the bottom phase$_{CA}$ of dives was associated with significantly higher prey availability than the descent and ascent phase$_{CA}$ [10,66]. Even though we found that hunting mode$_{BS}$ also occurred during the bottom phase$_{BS}$, it mostly occurred at shallower depths for the Weddell seal. Weddell seals are opportunistic predators feeding both on pelagic prey such as *Pleuragramma antarcticum* and squid, and benthic prey such as *Trematomus* fish species and invertebrates

[37,67,68]. Their opportunistic behaviour has also been observed during summer where the three dimensional use of the space under the ice by the Weddell seals suggested that they were searching for prey throughout their dive instead of targeting one depth [58].

In contrast, even though we found SES mostly intensified their foraging activity at the bottom of their dive, 43% of their hunting phases$_{BS}$ still occurred above the bottom phase$_{CA}$. This could be related to a more consistent pattern in their foraging strategy due to a more specialized diet. Indeed, SES females essentially perform pelagic dives and a recent study has shown that they were mostly feeding on myctophid fishes [16,34]. However, our results suggest that considering only the bottom phase$_{CA}$ to fully describe a SES's foraging strategy is probably misleading.

For both species the foraging behaviour revealed by the broken stick was complex. Dives contained on average six or seven behavioural phases$_{BS}$ instead of just three, and hunting mode$_{BS}$ was exhibited on average two and three times a dive, for the Weddell seal and the SES, respectively. Bottom time$_{CA}$ was also
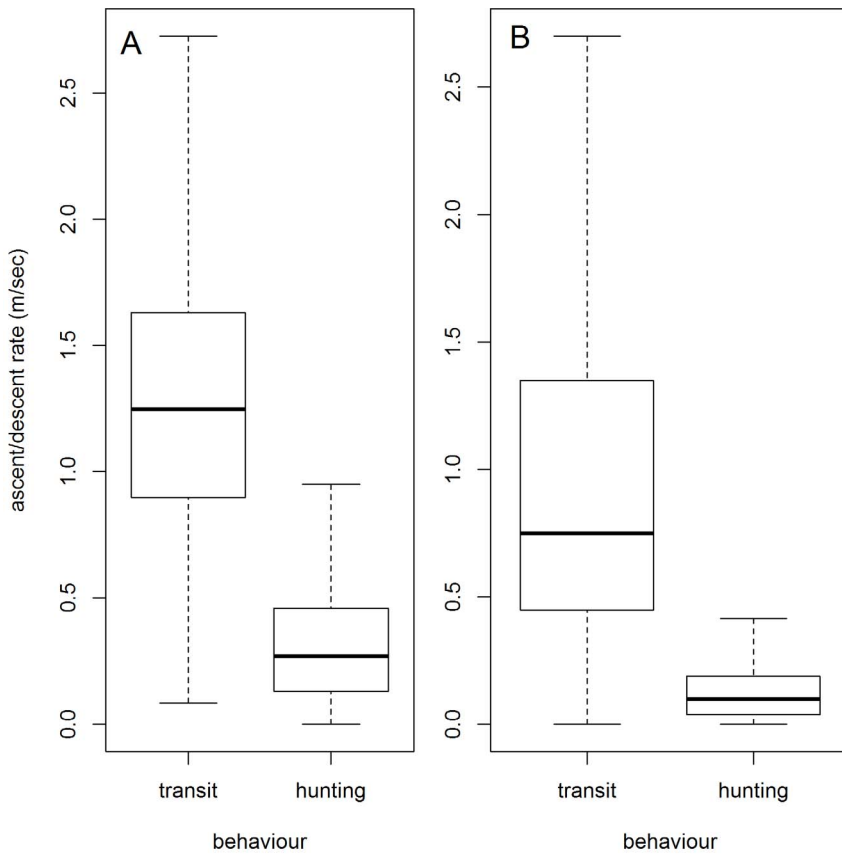
Figure 10. Behavioural differences in ascent/descent rates. Distribution of the ascent/descent rates (m.sec^{-1}) calculated for each segments$_{BS}$ according to transit mode$_{BS}$ and hunting mode$_{BS}$, respectively for the southern elephant seals (A) and the Weddell seal (B). The horizontal bold line of the box shows the median. The bottom and top of the box show the 25th and 75th percentiles.
doi:10.1371/journal.pone.0099329.g010

significantly higher and lower than hunting time$_{BS}$ for SES and the Weddell seal, respectively, giving a different estimation of the time spent foraging when compared to the time spent hunting$_{BS}$. It is therefore likely that instead of targeting only one type of prey at a particular depth, SES and Weddell seals may also change behaviour mid-dive, to accommodate the sudden appearance of prey. Our novel method allows a more accurate description of the within dive foraging behaviour than when using the bottom time$_{CA}$ only.

Conclusion

Our study emphasizes the complexity of SES and Weddell seals diving behaviour, suggesting that using bottom time$_{CA}$ only as an index of intensive foraging may lead to an inaccurate estimation of

their foraging activity. Our results also suggest that the Weddell seal is an opportunistic feeder capable of chasing prey in different parts of the water column during a single dive whereas the SES mostly increased their foraging effort during the bottom part of their dives. The integration of instrumentation such as video recorders or stomach/oesophageal temperature sensors, from which prey capture success could be inferred, would help validate the method further [21,24,30,42]. This study was based on three individuals of two species but it relies on a broken stick method which detects changes in a dive profile and metrics that can be easily implemented in all diving animals. The consistency observed in foraging strategies across different species [19] suggests that this method could be applied to other species and would be a useful tool to detect behavioural changes when only time-depth data of a sufficient resolution are available.

Table 4. Comparison of the broken stick and the classical dive analysis.

	Species	Hunting mode$_{BS}$	Bottom time$_{CA}$	n	T	df	p-value
Duration per dive (min)	SES	9±0.07	13±0.08	818	36	7947	<0.001
Duration per dive (min)	Weddell seal	6±0.1	4±0.1	1144	12	2197	<0.001

Duration of the time spent foraging estimated from bottom time (classical dive analysis) and the time spent in hunting mode$_{BS}$ (broken stick method) were compared using unilateral Welch tests for two independent sets of 10% of the total dives selected randomly for both species. SES stands for southern elephant seals.
doi:10.1371/journal.pone.0099329.t004

Supporting Information

Figure S1 Examples of dives for which the Gompertz model did not work. Upper graph: Mean distance according to the number of broken stick points (from 6 to 33) that could be used to describe the dive represented below. The mean distance is the average of the differences between each data point of the original profile and the corresponding point of the reconstructed profile obtained by linear interpolation between the broken stick points (from 6 to 33). Lower graph: original dive profile. Graphs A and B are two examples of SES dive types for which the Gompertz model did not work. For these dives, the relationship between the mean distance and the number of broken stick points was more linear. Consequently, the model could not detect an inflexion point.
(TIFF)

Script S1 Algorithm of the automated and optimised broken stick method. R script that allow to apply the broken stick method on high-resolution dives: (i) selection of the optimal number of broken stick points to summarize the dive, (ii) calculation for each broken stick segment of the vertical sinuosity index, descent/ascent rates, duration and depth associated with and (iii) determination of the behavioural mode$_{BS}$ (hunting vs transit) according to the 0.9 vertical sinuosity threshold (see Methods and Fig.4).
(R)

Dataset S1 Training dataset to run the automated and optimised broken stick algorithm. Dataset of 1000 dives randomly selected from the Weddell seal dives. Depth was sampled every second by the TDRs during six winter months in 2008 in the Dumont D'Urville coastal area.
(RDATA)

Author Contributions

Conceived and designed the experiments: JBC MH CG. Performed the experiments: JBC MH CG. Analyzed the data: KH JBC MH. Contributed reagents/materials/analysis tools: KH JBC MH. Wrote the paper: KH JBC MH.

References

1. Charnov EL (1976) optimal foraging, the marginal value theorem. Theoretical Population Biology 9: 129–136.
2. Fauchald P, Erikstad KE (2002) Scale-dependent predator-prey interactions: the aggregative response of seabirds to prey under variable prey abundance and patchiness. Marine Ecology Progress Series 231: 279–291.
3. Fauchald P, Erikstad KE, Skarsfjord H (2000) Scale-dependent predator-prey interactions: the hierarchical spatial distribution of seabirds and prey. Ecology 81: 773–783.
4. MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. American Naturalist: 603–609.
5. Fauchald P, Tveraa T (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. Ecology 84: 282–288.
6. Kareiva P, Odell G (1987) Swarms of Predators Exhibit "Preytaxis" if Individual Predators Use Area-Restricted Search. The American Naturalist 130: pp. 233–270.
7. Dragon AC, Bar-Hen 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. doi:doi: 10.3354/meps09498.
8. Fuiman LA, Davis R, Williams T (2002) Behavior of midwater fishes under the Antarctic ice: observations by a predator. Marine Biology 140: 815–822. doi:10.1007/s00227-001-0752-y.
9. Mitani Y, Sato K, Ito S, Cameron MF, Siniff DB, et al. (2003) A method for reconstructing three-dimensional dive profiles of marine mammals using geomagnetic intensity data: results from two lactating Weddell seals. Polar Biology 26: 311–317.
10. Watanabe Y, Mitani Y, Sato K, Cameron MF, Naito Y (2003) Dive depths of Weddell seals in relation to vertical prey distribution as estimated by image data. Marine Ecology Progress Series 252: 283–288.
11. Dragon AC (2011) Modélisation des stratégies d'approvisionnement des éléphants de mer austraux - influence de la variabilité de la production primaire et des conditions océanographiques physiques. Paris: Université Pierre et Marie Curie. Available: https://www.locean-ipsl.upmc.fr/~AnneCecile.Dragon/manuscript/AC-Dragon_PhD-thesis.pdf.
12. Evans K, Lea M-A, Patterson TA (2012) Recent advances in bio-logging science: Technologies and methods for understanding animal behaviour and physiology and their environments. Deep Sea Research Part II: Topical Studies in Oceanography. Available: http://linkinghub.elsevier.com/retrieve/pii/S0967064512001865. Accessed 18 March 2013.
13. Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, et al. (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475: 86–90. doi:10.1038/nature10082.
14. Naito Y, Costa DP, Adachi T, Robinson PW, Fowler M, et al. (2013) Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes on small prey. Functional Ecology 27: 710–717. doi:10.1111/1365-2435.12083.
15. Scheffer A, Bost C, Trathan P (2012) Frontal zones, temperature gradient and depth characterize the foraging habitat of king penguins at South Georgia. Marine Ecology Progress Series 465: 281–297. doi:10.3354/meps09884.
16. Hindell MA, Slip DJ, Burton HR (1991) The Diving Behavior of Adult Male and Female Southern Elephant Seals, Mirounga-Leonina (Pinnipedia, Phocidae). Australian Journal of Zoology 39: 595–619.
17. Kooyman GL (1968) An analysis of some behavioural and physiological characteristics related to diving in the Weddell seal. Biology of the Antarctic seas. Antarctic Research series. Washington D.C., U.S.A.: G.A. Llano, W.L. Schmidt, Vol. 3. pp. 227–261.
18. Le Boeuf BJ, Costa DP, Huntley AC, Feldkamp SD (1988) Continuous, deep diving in female northern elephant seals, Mirounga angustirostris. Canadian Journal of Zoology 66: 446–458. doi:10.1139/z88-064.
19. Schreer JF, Kovacs KM, O'Hara Hines RJ (2001) Comparative diving patterns of pinnipeds and seabirds. Ecological Monographs 71: 137–162. doi:10.1890/0012-9615(2001)071[0137:CDPOPA]2.0.CO;2.
20. Schreer JF, Testa JW (1996) Classification of Weddell Seal Diving Behavior. Marine Mammal Science 12: 227–250. doi:10.1111/j.1748-7692.1996.tb00573.x.
21. Horsburgh JM, Morrice M, Lea M, Hindell MA (2008) Determining feeding events and prey encounter rates in a southern elephant seal: a method using swim speed and stomach temperature. Marine Mammal Science 24: 207–217. doi:10.1111/j.1748-7692.2007.00156.x.
22. Harcourt RG, Hindell MA, Bell DG, Waas JR (2000) Three-dimensional dive profiles of free-ranging Weddell seals. Polar Biology 23: 479–487.
23. Simpkins MA, Kelly BP, Wartzok D (2001) Three-dimensional diving behaviors of ringed seals (phoca hispida). Marine mammal science 17: 909–925.
24. Bost C-A, Handrich Y, Butler PJ, Fahlman A, Halsey LG, et al. (2007) Changes in dive profiles as an indicator of feeding success in king and Adélie penguins. Deep Sea Research Part II: Topical Studies in Oceanography 54: 248–255.
25. Gallon S, Bailleul F, Charrassin J-B, Guinet C, Bost C-A, et al. (2012) Identifying foraging events in deep diving southern elephant seals, Mirounga leonina, using acceleration data loggers. Deep Sea Research Part II: Topical Studies in Oceanography. Available: http://www.sciencedirect.com/science/article/pii/S0967064512001671. Accessed 2013 March 6.
26. Zimmer I, Wilson RP, Beaulieu M, Ropert-Coudert Y, Kato A, et al. (2010) Dive efficiency versus depth in foraging emperor penguins. Aquatic Biology 8: 269–277.
27. Sato K, Daunt F, Watanuki Y, Takahashi A, Wanless S (2008) A new method to quantify prey acquisition in diving seabirds using wing stroke frequency. Journal of Experimental Biology 211: 58–65. doi:10.1242/jeb.009811.
28. Ropert-Coudert Y, Kato A, Wilson R, Cannell B (2006) Foraging strategies and prey encounter rate of free-ranging Little Penguins. Marine Biology 149: 139–148.
29. 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.
30. Watanabe YY, Takahashi A (2013) Linking animal-borne video to accelerometers reveals prey capture variability. Proceedings of the National Academy of Sciences 110: 2199–2204. doi:10.1073/pnas.1216244110.

31. Biuw M, Boehme L, Guinet C, Hindell M, Costa D, et al. (2007) Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. Proceedings of the National Academy of Sciences 104: 13705–13710.

32. Bailleul F, Charrassin J-B, Ezraty R, Girard-Ardhuin F, McMahon CR, et al. (2007) Southern elephant seals from Kerguelen Islands confronted by Antarctic Sea ice. Changes in movements and in diving behaviour. Deep Sea Research Part II: Topical Studies in Oceanography 54: 343–355. doi:10.1016/j.dsr2.2006.11.005.

33. Bailleul F, Authier M, Ducatez S, Roquet F, Charrassin J-B, et al. (2010) Looking at the unseen: combining animal bio-logging and stable isotopes to reveal a shift in the ecological niche of a deep diving predator. Ecography 33: 709–719. doi:10.1111/j.1600-0587.2009.06034.x.

34. Cherel Y, Ducatez S, Fontaine C, Richard P, Guinet C (2008) Stable isotopes reveal the trophic position and mesopelagic fish diet of female southern elephant seals breeding on the Kerguelen Islands. Marine Ecology Progress Series 370: 239–247. doi:10.3354/meps07673.

35. Mcintyre T, Bornemann H, Plötz J, Tosh CA, Bester MN (2012) Deep divers in even deeper seas: habitat use of male southern elephant seals from Marion Island. Antarctic Science 24: 561–570. doi:10.1017/S0954102012000570.

36. Thums M, Bradshaw CJA, Sumner MD, Horsburgh JM, Hindell MA (2013) Depletion of deep marine food patches forces divers to give up early. Journal of Animal Ecology 82: 72–83. doi:10.1111/j.1365-2656.2012.02021.x.

37. Castellini MA, Kooyman GL, Ponganis PJ (1992) Metabolic rates of freely diving Weddell seals: correlations with oxygen stores, swim velocity and diving duration. Journal of Experimental Biology 165: 181–194.

38. Cornet A, Jouventin P (1980) Le phoque de Weddell (Leptonychotes weddelli L.) à Pointe Géologie et sa plasticité sociale. Mammalia 44: 497–522. doi:10.1515/mamm.1980.44.4.497.

39. Heerah K, Andrews-Goff V, Williams G, Sultan E, Hindell M, et al. (2013) Ecology of Weddell seals during winter: Influence of environmental parameters on their foraging behaviour. Deep Sea Research Part II: Topical Studies in Oceanography. Available: http://www.sciencedirect.com/science/article/pii/S0967064512001658. Accessed 2012 November 29.

40. Lake S, Burton H, van den Hoff J (2003) Regional, temporal and fine-scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica. Marine Ecology Progress Series 254: 293–305.

41. Plötz J, Bornemann H, Knust R, Schröder A, Bester M (2001) Foraging behaviour of Weddell seals, and its ecological implications. Polar Biology 24: 901–909.

42. Davis RW, Fuiman LA, Madden KM, Williams TM (2012) Classification and behavior of free-ranging Weddell seal dives based on three-dimensional movements and video-recorded observations. Deep Sea Research Part II: Topical Studies in Oceanography. Available: http://www.sciencedirect.com/science/article/pii/S0967064512000926. Accessed 2012 November 29.

43. Davis RW, Fuiman LA, Williams TM, Horning M, Hagey W (2003) Classification of Weddell seal dives based on 3-dimensional movements and video-recorded observations. Marine Ecology Progress Series 264: 109–122.

44. Andrews-Goff V, Hindell MA, Field IC, Wheatley KE, Charrassin JB (2010) Factors influencing the winter haulout behaviour of Weddell seals: consequences for satellite telemetry. Endangered species research 10: 83–92.

45. Wheatley KE, Bradshaw CJA, Harcourt RG, Davis LS, Hindell MA (2006) Chemical immobilization of adult female Weddell seals with tiletamine and zolazepam: effects of age, condition and stage of lactation. BMC veterinary research 2: 8.

46. Field IC, McMahon CR, Burton HR, Bradshaw CJA, Harrington J (2002) Effects of age, size and condition of elephant seals (Mirounga leonina) on their intravenous anaesthesia with tiletamine and zolazepam. Veterinary Record 151: 235–240. doi:10.1136/vr.151.8.235.

47. Moline MA, Karnovsky NJ, Brown Z, Divoky GJ, Frazer TK, et al. (2008) High latitude changes in ice dynamics and their impact on polar marine ecosystems. Annals of the New York Academy of Sciences 1134: 267–319.

48. Testa JW (1994) Over-winter movements and diving behavior of female Weddell seals (Leptonychotes weddellii) in the southwestern Ross Sea, Antarctica. Canadian Journal of Zoology 72: 1700–1710. doi:10.1139/z94-229.

49. Fedak MA, Lovell P, Grant SM (2001) Two approaches to compressing and interpreting time-depth information as as collected by time-depth recorders and satellite-linked data recorders. Marine Mammal Science 17: 94–110.

50. R Development Core Team (2008) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Available: http://www.R-project.org.

51. Viviant M, Trites AW, Rosen DAS, Monestiez P, Guinet C (2009) Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. Polar Biology 33: 713–719. doi:10.1007/s00300-009-0750-y.

52. Guinet C, Vacquié-Garcia J, Picard B, Bessigneul G, Lebras Y, et al. (2014) Southern elephant seal foraging success in relation to temperature and light conditions: insight into prey distribution. MEPS 499: 285–301

53. Millot G (2011) Comprendre et réaliser les tests statistiques à l'aide de R - 2ème édition. De Boeck. 767 p.

54. Jonsen ID, Myers RA, James MC (2007) Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. Marine Ecology Progress Series 337: 255–264.

55. Bailleul F, Pinaud D, Hindell M, Charrassin J-B, Guinet C (2008) Assessment of scale-dependent foraging behaviour in southern elephant seals incorporating the vertical dimension: a development of the First Passage Time method. Journal of Animal Ecology 77: 948–957. doi:10.1111/j.1365-2656.2008.01407.x.

56. Dragon A, Bar-Hen A, Monestiez P, Guinet C (2012) Comparative analysis of methods for inferring successful foraging areas from Argos and GPS tracking data. Marine Ecology Progress Series 452: 253–267. doi:10.3354/meps09618.

57. Weimerskirch H, Pinaud D, Pawlowski F, Bost C (2007) Does Prey Capture Induce Area-Restricted Search? A Fine-Scale Study Using GPS in a Marine Predator, the Wandering Albatross. The American Naturalist 170: 734–743. doi:10.1086/522059.

58. Hindell MA, Harcourt R, Waas JR, Thompson D (2002) Fine-scale three-dimensional spatial use by diving, lactating female Weddell seals Leptonychotes weddellii. Marine Ecology Progress Series 242: 275–284.

59. Hindell MA, Crocker D, Mori Y, Tyack P (2010) Foraging behaviour. Marine mammal ecology and conservation - A handbook of techniques. Oxford: Boyd Ian L., Bowen W. Don, Iverson Sarah J. pp. 241–262.

60. Suzuki I, Naito Y, Folkow L, Miyazaki N, Blix A (2009) Validation of a device for accurate timing of feeding events in marine animals. Polar Biology 32: 667–671.

61. Hocking D, Evans A, Fitzgerald EG (2013) Leopard seals (Hydrurga leptonyx) use suction and filter feeding when hunting small prey underwater. Polar Biology 36: 211–222.

62. Marshall CD, Kovacs KM, Lydersen C (2008) Feeding kinematics, suction and hydraulic jetting capabilities in bearded seals (Erignathus barbatus). Journal of Experimental Biology 211: 699–708.

63. Hanuise N, Bost C-A, Huin W, Auber A, Halsey LG, et al. (2010) Measuring foraging activity in a deep-diving bird: comparing wiggles, oesophageal temperatures and beak-opening angles as proxies of feeding. Journal of Experimental Biology 213: 3874–3880. doi:10.1242/jeb.044057.

64. Simeone A, Wilson RP (2003) In-depth studies of Magellanic penguin (Spheniscus magellanicus) foraging: can we estimate prey consumption by perturbations in the dive profile? Marine Biology 143: 825–831. doi:10.1007/s00227-003-1114-8.

65. Fuiman LA, Madden KM, Williams TM, Davis RW (2007) Structure of foraging dives by Weddell seals at an offshore isolated hole in the Antarctic fast-ice environment. Deep Sea Research Part II: Topical Studies in Oceanography 54: 270–289.

66. Mitani Y, Watanabe Y, Sato K, Cameron MF, Naito Y (2004) 3D diving behavior of Weddell seals with respect to prey accessibility and abundance. Marine Ecology Progress Series 281: 275–281.

67. Burns JM, Trumble SJ, Castellini MA, Testa JW (1998) The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. Polar Biology 19: 272–282.

68. Green K, Burton HR (1987) Seasonal and Geographical Variation in the Food of Weddell Seals, Leptonychotes-Weddelii, in Antarctica. Wildlife Research 14: 475–489.