Bottom time does not always predict prey encounter rate in Antarctic fur seals

Morgane Viviant[1], Tiphaine Jeanniard-du-Dot[2], Pascal Monestiez[1,3], Matthieu Authier[1] and Christophe Guinet*[,1]

[1]*Centre d'Etudes Biologiques de Chizé, UMR 7372 ULR-CNRS, 79 360 Villiers en Bois, France;* [2]*Marine Mammal Research Unit, University of British Columbia, 2202 Main Mall, AERL bldg., Vancouver, BC V6T1Z4, Canada; and* [3]*Unité de Biostatistique et Processus Spatiaux, Institut National de Recherche Agronomique, Site Agroparc, Domaine St Paul, 84914 Avignon, France*

Summary

1. Optimal foraging models applied to breath-holding divers predict that diving predators should optimize the time spent foraging at the bottom of dives depending on prey encounter rate, distance to prey patch (depth) and physiological constraints.

2. We tested this hypothesis on a free-ranging diving marine predator, the Antarctic fur seal *Arctocephalus gazella,* equipped with accelerometers or Hall sensors ($n = 11$) that recorded mouth-opening events, a proxy for prey capture attempts and thus feeding events. Over the 5896 dives analysed (> 15 m depth), the mean number of mouth-opening events per dive was 1.21 ± 1.69 (mean $\pm$ SD). Overall, 82% of mouth-openings occurred at the bottom of dives.

3. As predicted, fur seals increased their inferred foraging time at the bottom of dives with increasing patch distance (depth), irrespective of the number of mouth-openings.

4. For dives shallower than 55 m, the mean bottom duration of dives without mouth-openings was shorter than for dives with mouth-opening events. However, this difference was only due to the occurrence of V-shaped dives with short bottom durations (0 or 1 s). When removing those V-shaped dives, bottom duration was not related to the presence of mouth-openings anymore. Thus, the decision to abandon foraging is likely related to other information about prey availability than prey capture attempts (i.e. sensory cues) that seals collect during the descent phase. We did not observe V-shaped dives for dives deeper than 55 m, threshold beyond which the mean dive duration exceeded the apparent aerobic dive limit. For dives deeper than 55 m, seals kept on foraging at bottom irrespective of the number of mouth-openings performed.

5. Most dives occurred at shallower depths (30–55 m) than the 60 m depth of highest foraging efficiency (i.e. of greatest number of mouth-opening events per dive). This is likely related to physiological constraints during deeper dives.

6. We suggest that foraging decisions are more complex than predicted by current theory and highlight the importance of the information collected by the predator during the descent as well as its physiological constraints. Ultimately, this will help establishing reliable predictive foraging models for marine predators based on diving patterns only.

Key-words: aerobic diving limit, Antarctic fur seals, diving behaviour, foraging depth, foraging strategies

Introduction

Unravelling the fine-scale mechanisms by which a predator optimizes its foraging behaviour in relation to prey accessibility is a necessary precursor to understand and ultimately predict impacts of long-term environmental changes on the structure and relative health of food webs. According to optimal foraging theory, a predator should optimize its foraging behaviour to maximize the foraging benefits relative to costs, which ultimately affects its fitness (Stephens & Krebs 1986). It is predicted that at low prey density, the predator is searching most of the time, that every prey item encountered should be consumed and that prey intake increases with prey density. At high prey density, however,

each new prey item is caught almost immediately, the predator may become more selective in its diet and prey handling time and/or digestion time may become the limiting factors of energy ingestion (Stephens & Krebs 1986).

Central place foragers are animals who feed in areas distant from their breeding or resting sites and thus depart from and return to a fixed location, which implies additional temporal and energetic constraints (Orians & Pearson 1979; Pyke 1984; Cézilly & Benhamou 1996). It is assumed that predators should increase their patch residence time (or load size) with increasing distance to the prey patch to maximize the net rate of energy intake (Orians & Pearson 1979). This behaviour has been shown on chipmunks (*Tamias striatus*, Giraldeau & Kramer 1982), starlings (*Sturnus vulgaris*, Kacelnik & Cuthill 1990) and long-eared bats (*Otonycteris hemprichii*, Daniel, Korine & Pinshow 2008) but not in honeybees (*Apis mellifera*, Schmid-Hempel, Kacelnik & Houston 1985) due to a high energetic cost of flight. Thus, distance to prey patch and physiological constraints can interact to play an important role in the predator's decision to stay or leave a prey patch.

In the marine environment, air-breathing predators have similar constraints to central place foragers because they have to dive to forage at depth but need to come back to the surface to breathe. They are limited in their search for food by the magnitude of their oxygen stores and the rate at which they use them (metabolic rate) while diving. The search and acquisition of food is generally assumed to take place mostly at the bottom of dives (Carbone & Houston 1996; Mori 1999; Thompson & Fedak 2001; Wilson *et al.* 2002; Watanabe *et al.* 2003; Austin *et al.* 2006a,b; Fossette *et al.* 2008; Kuhn *et al.* 2009), even though the quality of the environment can also be assessed during the descent phase (Bost *et al.* 2007). Optimal central place foraging theory applied to breath-holding divers predicts maximization of foraging time at the dive bottom and minimization of travelling (descent and ascent duration) and recovery at the surface (post-dive interval) to optimize diving efficiency (bottom duration / (dive + post-dive duration) and rate of energy gain (Carbone & Houston 1996; Mori 1999). However, as dive duration increases, so does post-dive recovery time at the surface, and a small increase in dive duration beyond the aerobic dive limit (ADL) can induce a large increase in the post-dive interval (Kooyman *et al.* 1980; Kooyman 1989).

Initially, studies considered that decisions to terminate each dive were based entirely on body oxygen reserves (Kramer 1988; Houston & Carbone 1992; Thompson, Hiby & Fedak 1993; Carbone & Houston 1996) and predicted an increase in the foraging time at the bottom of dives (or dive duration) with the increasing distance (depth) to the prey patch (Kramer 1988; Mori 1998b). However, these studies did not take into account the effects of quality and accessibility at depth of the prey patch on foraging strategies. More recently, Thompson & Fedak (2001) simultaneously took into account the effect of physiological constraints (aerobic limits), prey patch quality (prey encounters) and distance to the prey patch (depth) in their decision-rules model. Patch quality was assessed by the predator from its recent experience of prey encounters. They showed that it is always beneficial to terminate dives early without fully depleting their oxygen stores if no prey is encountered in the early part of the dive, and these benefits are greatest at the lowest density patches. However, during deeper dives, the benefit of giving up is reduced, and when seals dive to the maximum depth, they can attain aerobically, there will be no benefit to giving up early.

Thompson & Fedak's (2001) model was tested experimentally with captive pinnipeds: the foraging time of captive Steller sea lions (*Eumetopias jubatus*) increased with increasing prey encounter rate (Cornick & Horning 2003). Grey seals (*Halichoerus grypus*) responded to prey density by leaving low-quality patches earlier but, contrary to predictions, responded the same way also for deep dives (Sparling *et al.* 2007). However, to our knowledge, little investigation has been carried out on free-ranging species, which might explain the divergence in results compared to theoretical predictions. In addition, others have tried to investigate foraging strategies in free-ranging marine species (Jodice & Collopy 1999), but seldom with clear information about prey patch quality or prey encounter rate (Heaslip, Bowen & Iverson 2014).

Miniaturized loggers recording individual foraging events allow to fill in this knowledge gap for free-ranging marine predators. Mouth-opening ('m-o') and head-movement detection using Hall sensors (Wilson *et al.* 2002) or accelerometers (Suzuki *et al.* 2009; Naito *et al.* 2010; Okuyama *et al.* 2010; Viviant *et al.* 2010) provide a set of proxies for prey encounter rates. Combined with information on occurrence, number or history of mouth-opening events, classic time-depth data can be used to indirectly assess the quality of the area visited by an animal and investigate the fine-scale behavioural responses of diving predators to habitat quality.

In the light of these technological advances, we tested optimal central place foraging theory, applied to divers, on a free-ranging marine predator, the Antarctic fur seal (*Arctocephalus gazella*; Peters 1875), for which we have simultaneous access to its diving behaviour, recent prey encounters (as determined by mouth-opening events), prey patch distance (depth) and physiological constraints (aerobic dive limit). We first verified that time spent at the bottom of a dive corresponded to the main foraging time and then tested the following hypotheses:

1. Seals should increase their time foraging at the bottom of a dive with increasing distance (i.e. dive depth) to the foraging patch, regardless of the prey encounter rate (Orians & Pearson 1979; Kramer 1988; Mori 1998b).
2. Seals should increase their foraging time at the bottom of dives when mouth-opening events occur compared to dives where no mouth-opening events are detected. In agreement with Thompson and Fedak's prediction

(2001), this pattern should decrease with dive depth and disappear when seals become constrained by their aerobic dive limit.

3. Seals should dive preferentially to depths where their foraging efficiency (i.e. number of mouth-opening events/dive cycle duration) is the highest (Mori 1998a).

Materials and methods

ETHICS STATEMENT

Our study on Antarctic fur seals was approved and authorized by the ethics committee of the French Polar Institute (Institut Paul Emile Victor – IPEV). This Institute does not provide any permit number or approval ID. However, animals were handled and cared for in accordance with the guidelines and recommendations of this committee (dirpol@ipev.fr).

STUDY SITE

We collected data on diving and foraging behaviour of Antarctic fur seals at Pointe Suzanne (49°S, 70°E), on the south-eastern coast of Kerguelen Island, in the southern Indian Ocean, during the breeding seasons 2007–2008 and 2008–2009 (hereafter referred to as '2008' and '2009') from December to February. Antarctic fur seals tend to perform shallow and short dives (Lea *et al.* 2002a). Fur seals breeding on Kerguelen feed mainly on small myctophids that perform diel vertical migrations (*Gymnoscopelus* sp. and *Electrona subaspera* representing 60% and 20% of the diet, respectively (Cherel, Guinet & Tremblay 1997; Lea *et al.* 2002b). These prey species are only accessible to diving fur seals at night when they are close to the surface (Duhamel, Koubbi & Ravier 2000).

INSTRUMENT DEPLOYMENT

Accelerometers (M190L-D2GT; Little Leonardo, Tokyo, Japan) and intermandibular extension sensors (Hall sensors) developed by the CEPE-CNRS (Strasbourg, France) were deployed on adult female fur seals to study their diving activity and detect mouth-opening events. Lactating females were captured ashore during their nursing visits using a hoop net, weighed ($\pm$0·2 kg) and measured (straight-line length, $\pm$0·5 cm). Instruments were attached while animals were under gas anaesthesia (using isoflurane) with two-part fast-setting epoxy adhesive. Seven females were equipped with accelerometers and four with Hall sensor units mounted on nylon webbing with cable ties. Briefly, Hall sensor loggers consist of a magnet attached to the animal's upper jaw and of a sensor glued on the opposite mandible (Appendix S1a, Supporting Information). Mouth-openings induce variations in the electromagnetic field that were recorded by the main recording unit connected to the sensors with a cable and glued on top of the head (Wilson *et al.* 2002). The accelerometers attached to the fur under the animal's jaw (Appendix S1b) record horizontal and vertical accelerations which, in the case of mouth-openings, induce sudden acceleration changes (Suzuki *et al.* 2009; Viviant *et al.* 2010). Hall sensor units and accelerometers were set to sample at frequencies of 16 Hz. Depth sensors ($\pm$0·1 m) were integrated into both loggers and sampled at 1 Hz. Devices were recovered by cutting the fur just under the glued logger after a single foraging trip. Not all females were equipped simultaneously with head-mounted accelerometer/hall sensor and Fastloc GPS, so spatial information was not available for all of them. As this study focuses on diving behaviour, we did not include the spatial component. However, all female Antarctic fur seals breeding at Pointe Suzanne,

Kerguelen Island, tend to forage over the same general area/ oceanographic habitat with no clear spatial variation in the diving behaviour (Lea *et al.* 2008). Diving behaviour of females tagged in this study was not significantly different from previous studies (Lea *et al.* 2002a, 2008).

DIVE ANALYSES

The time series of diving behaviour was reconstructed using a custom-developed R program (R Development Core Team 2010). Pressure sensors on the accelerometer loggers can show an offset in the depth reading when seals are at the surface which was corrected according to the interdive and interdiving bout surface sequences. When animals exhibited prolonged periods of nearly constant minimum depth between 0 and -5 m suggesting that they were at the surface, the offset was automatically corrected using a custom-developed R program. The surface values were offset corrected to $0 \pm 0\cdot2$ (SD). Individual dives were defined as any depth exceeding 15 m based on the previously described bimodal distribution of dive depths for Antarctic fur seals at Kerguelen Island (Lea *et al.* 2002a). Furthermore, dives shallower than 15 m were short (9 ± 9 s) and generally lacked a bottom phase, so foraging time adjustments at bottom appear meaningful only for dives deeper than 15 m. For each dive deeper than 15 m, the following parameters were determined: time at the beginning and at the end of the dive, maximum depth (m), descent duration (s), bottom duration (s), ascent duration (s), dive duration (s) and post-dive surface interval (s). The termination of the descent was defined as the point at which the rate of a continuous descent was <0·4 m s^{-1}. The commencement of ascent was defined as the point at which the rate of a continuous ascent exceeded 0·4 m s^{-1}. This value corresponded to a threshold after which a net change in descent and ascent rates was observed and was empirically validated for the entire data set. We defined the bottom duration as the time between the end of the descent and the beginning of the ascent.

We excluded dives that were at the end of a diving bout (i.e. not followed by another dive) in the analysis of time allocation over the dive cycle since post-dive intervals could correspond to other behaviours than post-dive recovery (post-dive interval). Sequential dives were allocated into dive bouts according to Luque & Guinet (2007), in which the bout ending criterion is determined using maximum likelihood estimation and is based on the absolute difference of post-dive interval duration (Boyd & Croxall 1992). Only dives occurring within bouts of at least 3 dives were included in the analyses. Diving efficiency was then calculated as the ratio between bottom duration and dive cycle duration.

MOUTH-OPENING EVENTS

It was impossible to link mouth-openings to true prey ingestion with absolute certainty, so we considered mouth-opening events to reflect prey capture attempts and used them as a proxy of prey encounters. These mouth-opening events were detected using the acceleration data from the lower jaw following the method described in Viviant *et al.* (2010). Horizontal accelerations recorded on the animal's lower jaw were first filtered with a high-pass filter of 3 Hz to smooth out the low-frequency accelerations of the head and body movements. This left only the peaks in accelerations due to mouth-openings. Variance was calculated for a moving window of 1·5 s and highlighted extreme accelerations considered to be real mouth-opening events. Similar analysis was done with the Hall sensor data using a moving window of 5 s (a wider window was necessary for hall sensor data due to the time-lag of the sensor to come back to its basal value after a mouth-opening event). The number and time of occurrences of mouth-opening events were routinely identified for each dive phase (descent, ascent or bottom). The foraging efficiency was

then calculated as the number of mouth-opening events divided by the dive cycle duration in minutes.

AEROBIC DIVE LIMIT

The dive duration beyond which the post-dive interval abruptly rises was taken as a behavioural proxy of the aerobic dive limit. Past this threshold, the oxygen store might not be completely exhausted but the individual might rely on an increasing proportion of anaerobic metabolism. It generally results in an increase in blood lactate concentration which needs to be eliminated while the animal is at the surface (Costa 2007). For each individual, nonlinear models with piecewise linear relationships (broken-line models) between post-dive interval and dive duration were used to determine the break point of slope changes ('segmented' package in R; Muggeo 2003). Similarly, the dive depth beyond which the post-dive interval abruptly rises was determined.

ANALYSES

A broken-line model fitted on the relationship between post-dive intervals and dive depth showed a break point at $56 \cdot 2 \pm 0 \cdot 85$ m, with an increase in post-dive intervals past this threshold (slope estimate $\pm$ SE for dives less than and >56 m are $1 \cdot 43 \pm 0 \cdot 03$ and $1 \cdot 26 \pm 0 \cdot 02$, respectively; $P < 0 \cdot 0001$; Fig. 1). This suggested that individuals exceeded on average their behavioural aerobic dive limit at more or less 55 m, so we rounded it to 55 m in the subsequent analyses.

We modelled bottom duration for dives above and below this 55 m threshold separately to determine whether foraging behaviour at the bottom of dives was influenced by such physiological constraints. Linear mixed-effect models were fitted using the 'lme' function in the R package (R Development Core Team 2010) to identify the variables influencing foraging time (bottom duration). Bottom durations were square-root-transformed to stabilize the variance and normalize the residuals. Fixed effects were the maximum dive depth, previous surface durations and presence–absence of mouth-opening events. Individual was included as a random effect. An autoregressive variance–covariance matrix (corAR1) representing an order 1 autocorrelation structure was used to model the serial correlation among observations for each individual (Zuur *et al.* 2009). Model selection was based on the Akaike's information criterion (AIC; Burnham & Anderson 2004). Because our interest lied in the identification of variables significantly
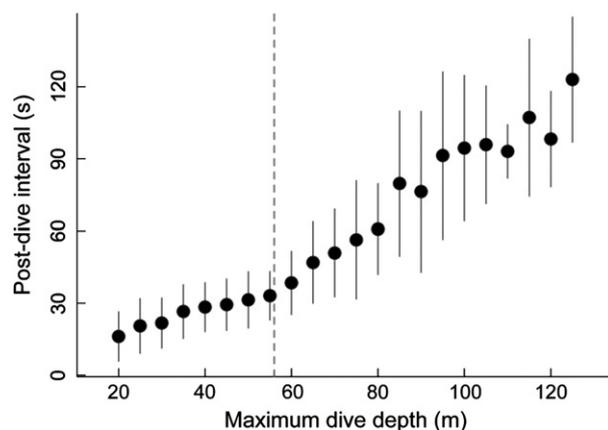
influencing bottom duration, we reported results from the best model only. When models were within two points of the model exhibiting the lowest AIC, the most parsimonious one was selected.

We found evidence of two to three modes in the distribution of bottom duration per depth class. The distributions were thus identified for each 10-m depth class using generalized additive mixture models (Rigby & Stasinopoulos 2005). The number of mixture components was determined with AIC (Burnham & Anderson 2004). Dives within these distributions were then analysed separately using the same linear mixed models presented in the previous paragraph, as each distribution might correspond to different foraging behaviours. Results are presented in mean $\pm$ SD unless stated otherwise.

Results

Among the 13 deployments (Hall or accelerometer), one logger was lost and one logger did not collect any data. We consequently collected complete data (dive profile + mouth-opening events) from 11 individuals in total. Hall sensors recorded during six consecutive days while accelerometers during $2 \cdot 5 \pm 0 \cdot 5$ days only on average. Thus, sample size might differ between loggers because of different memory constraints. In total, 41 different nights of foraging were collected (Table 1).

LOGGER EFFECTS

No effects on foraging trip duration (equipped: $9 \cdot 0 \pm 2 \cdot 3$ days, $n = 13$, non-equipped: $8 \cdot 3 \pm 3 \cdot 3$ days, $n = 22$, t-test $= 0 \cdot 72$, $P = 0 \cdot 48$) could be detected as a consequence of logger deployment, suggesting that the animals were unaffected or able to compensate for the additional disturbance induced by the deployed equipment (Boyd, McCafferty & Walker 1997). Similarly, the dive depth range was consistent with what had been found for Antarctic fur seals on Kerguelen Island using only small time-depth recorders (MK9, Wildlife Computers) deployed on the lower back of the animals (Lea *et al.* 2002a), suggesting no impact of the data loggers on diving behaviour. There was no difference between the data recorded by Hall sensors and accelerometers in terms of diving patterns and number of mouth-opening events. Furthermore, analyses of bottom duration carried out separately on dives from the two logger types showed similar results. Thus, the data of the two loggers were pooled for subsequent analyses.

DIVE ANALYSES

A total of 5896 dives (>15 m) were recorded (Table 1), with 99·8% occurring during night time. Overall, mean dive duration and dive depth were $97 \cdot 4 \pm 41 \cdot 5$ s and $50 \cdot 4 \pm 22 \cdot 4$ m, respectively. Bottom duration and diving efficiency were $42 \cdot 9 \pm 30$ s and $0 \cdot 3 \pm 0 \cdot 16$, respectively. Bottom duration increased with increasing diving depth up to 80 m then stabilized and tended to decrease with increasing depths (Fig. 2, Tables 2A, B). For dives shallower than 55 m, bottom duration increased with

Fig. 1. Plots of the post-dive interval as a function of the maximum dive depth (mean $\pm$ SD). The vertical grey dashed line represents the depth threshold after which there is a sudden change in slope (56 m).

Table 1. Individuals' diving and foraging characteristics (mean ± SD). 'Acc' = accelerometers; 'Hall' = Hall sensors; diving efficiency = bottom duration / dive cycle duration, 'm-o' = mouth-openings, bADL = behavioural aerobic dive limit

id	Year	Deployment date	Duration (h)	Logger	Body mass (kg)	Body length (cm)	No. of dives	Depth (m)	Bottom duration (s)	Diving efficiency	No. of 'm-o' per dive	bADL (s)
126	2008	2007/12/21 16 h	27	Acc	31·9	119	296	57 ± 22	45 ± 27	0·32 ± 0·14	1·5 ± 2·2	146
145	2008	2008/01/01 15 h	32	Acc	28·75	111·5	211	62 ± 32	73 ± 38	0·38 ± 0·08	0·7 ± 1·5	132
223	2009	2009/01/04 16 h	52	Acc	25·5	111	240	50 ± 14	51 ± 13	0·38 ± 0·09	1·8 ± 1·7	113
233	2009	2009/01/19 16 h	30	Acc	29·75	119	311	52 ± 26	20 ± 25	0·14 ± 0·15	1·4 ± 2·4	107
238	2009	2009/01/26 15 h	53	Acc	33·5	116	519	55 ± 24	52 ± 28	0·36 ± 0·14	2·4 ± 2·8	128
220	2009	2009/01/04 16 h	50	Acc	31	115	486	52 ± 22	33 ± 16	0·29 ± 0·11	1·1 ± 1·5	105
222	2009	2009/01/04 16 h	50	Acc	26	107	291	48 ± 20	41 ± 17	0·33 ± 0·1	0·9 ± 1·6	99
115	2008	2007/12/21 17 h	22	Hall	25·45	108	676	46 ± 11	52 ± 15	0·36 ± 0·07	1·1 ± 1·2	148
118	2008	2008/01/04 18 h	23	Hall	38·2	119·5	688	41 ± 14	77 ± 28	0·48 ± 0·1	1·3 ± 1·3	133
138	2008	2007/12/20 21 h	18	Hall	32·3	115	956	56 ± 25	29 ± 20	0·22 ± 0·12	1·1 ± 1·4	124
224	2009	2009/01/05 16 h	21	Hall	37·75	127	1222	48 ± 24	29 ± 31	0·21 ± 0·15	0·8 ± 1·2	114
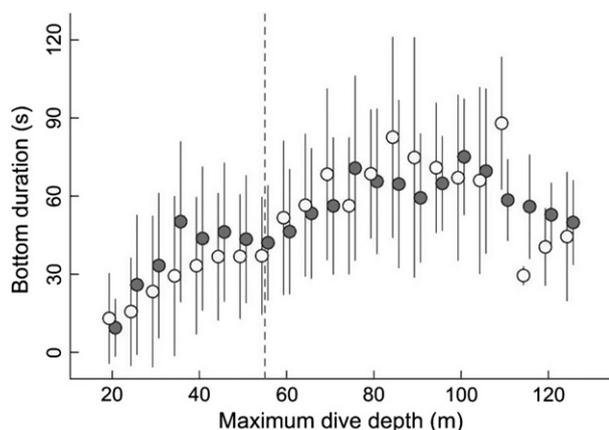
Fig. 2. Dive bottom duration as a function of the maximum dive depth (mean ± SD). Dives are plotted with (grey) and without (white) mouth-opening events. The vertical grey dashed line shows the threshold of 55 m depth below which the bottom duration is significantly higher in dives with mouth-opening events than dives without mouth-opening events. This pattern is not observed for deeper dives (Table 2).

increasing depth as well as with increasing descent rate. For dives deeper than 55 m, bottom duration increased with increasing surface interval prior to the dive and with increasing descent rate.

Mixture models revealed that the bottom duration was composed of three distributions for depths ranging from 15 to 55 m, two distributions for depths ranging from 55 to 95 m and only one distribution for depths >95 m (Fig. 3). The first distribution, occurring at depth shallower than 55 m, was composed of short bottom durations ranging from 0 to 1 s, which likely corresponded to exploratory dives. We called these dives, 'V-shaped' dives. It is important to note that these V-shaped dives occurred inside dive bouts and thus were not solitary dives.

MOUTH-OPENING EVENTS

We detected 196 ± 109 (range 18–539) mouth-opening events per night and per individual. Among the 5896 dives

deeper than 15 m sampled, 3267 were associated with at least one mouth-opening event (i.e. 55·4%) among which 1583 with only one mouth-opening event. The overall mean number of mouth-opening events recorded per dive was 1·21 ± 1·69 (range 0–15) (for dives with and without mouth-opening events) (i.e. the mean of the mean can be calculated from the values presented in Table 1). It was 0·11 ± 0·40, 0·98 ± 1·53 and 0·10 ± 0·36 in the descent, bottom and ascent phases, respectively. A total of 7164 mouth-opening events were detected, 81·9% of those occurred at the bottom while only 9·7% and 8·4% occurred in the descent and ascent phases, respectively. This suggests that the bottom phase of the dives corresponded to the most important feeding period (Appendix S2).

Bottom durations were greater in the presence of mouth-opening events than in the absence of mouth-opening events (Fig. 2; Table 2A, Appendix S4) for dives shallower than 55 m; variations in individual seal accounted for 52·6% of the linear mixed model's total variance (Table 2A). For dives deeper than 55 m, no evidence for an effect of the occurrence of mouth-opening events was detected (Fig. 2; Table 2B, Appendix S4); individual variations accounted for 40·8% of the linear mixed model's total variance (Table 2B). A linear mixed model was fitted on shallow dives (<55 m) but excluding V-shaped dives and revealed that in dives where a bottom phase was present (>1 s), the presence of mouth-opening events had no detectable effect on the bottom duration (Table 2, Appendix S4).

AEROBIC CONSTRAINTS

Behavioural aerobic dive limit (bADL) is summarized in Table 1. Examples of broken-line models fitted for post-dive interval and dive duration for two individuals are presented in Appendix S3. Mean behavioural aerobic dive limit for all individuals was 123 ± 16 s. Animals exceeded their behavioural aerobic dive limit on 16 ± 4% of dives (mean of the percentage of the dives exceeding the

Table 2. Final model (selected by AIC. see Appendix S4) explaining the bottom duration in relation to depths, descent rates, previous surface durations (PrevSurfT) and the presence–absence of mouth-opening events ('m-o'). Estimate of the correlation (auto-regression of order 1) and individual variations (in % of total variance) are given. Models were fitted on dives shallower than 55 m (A), deeper than 55 m (B) and shallower than 55 m but with bottom duration >1 s (C)

Dives used in the model	Parameters	Estimate ± SE	t-value	*P*-value	Id variation	Corr
A: Depths <55 m	Intercept	−1·599 ± 0·636	−2·5	0·012	52·6	0·30
	Depth	0·088 ± 0·005	18·8	<0·001		
	Descent rate	2·308 ± 0·150	15·4	<0·001		
	Presence of mouth-openings	0·236 ± 0·055	4·3	<0·001		
B: Depth >55 m	Intercept	4·206 ± 0·595	7·06	<0·001	40·8	0·31
	Previous surface time	0·014 ± 0·003	5·70	<0·001		
	Descent rate	1·556 ± 0·305	5·11	<0·001		
C: Depths <55 m and bottom duration >1 s	Intercept	1·530 ± 0·520	2·94	0·0033	49·3	0·30
	Depth	0·068 ± 0·004	15·25	<0·001		
	Descent rate	1·099 ± 0·145	7·60	<0·001		
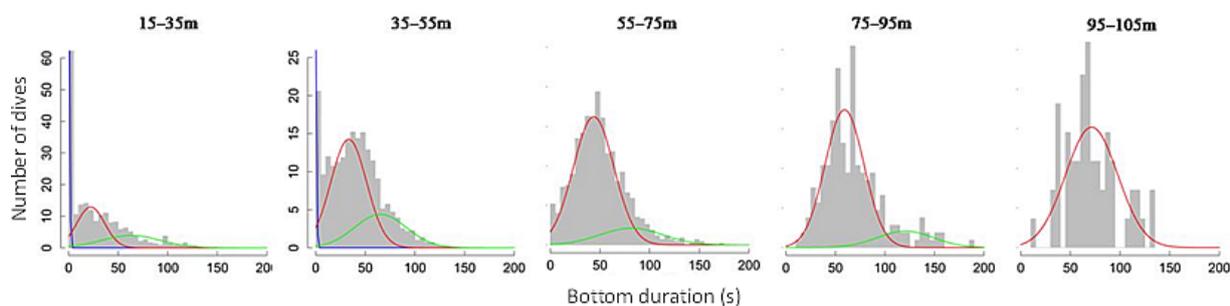
Fig. 3. Frequency distribution of bottom duration according to five depth classes (grey bars). Blue lines correspond to the frequency distribution of bottom duration for V-shaped dives deeper than 15 m and with bottom time shorter than 1 s (with and without mouth-opening events) and are only observed for dive categories 15–35 and 35–55 m. Red lines corresponds to distribution for similar dives except with intermediate bottom durations and are observed for all diving depth categories, and green lines show the distribution for dives with long bottom durations and are observed for all dive categories except for the 95–105 m one.

behavioural ADL found for each individual using the breaking point approach (Muggeo 2003)), and the proportion of dives exceeding the behavioural aerobic dive limit increased with dive depth.

Fur seals concentrated 68·4% of their dives between 30 and 55 m (Fig. 4a). We found a clear segregation in the dive duration distribution between dives shallower and dives deeper than 15 m. The mean duration of dives deeper than 15 m was 96 s, while mean dive duration of dives shallower than 15 m was 20 s; therefore, deep dives represent 85% of the total number of dives but 96% of the diving time. When all dives (with and without mouth-opening events) were taken into account, diving efficiency first increased with dive depth, reaching a maximum at 0·3 between 35 and 80 m. It then progressively decreased with increasing depths (Fig. 4b). This shows that fur seals tried to maintain a bottom duration corresponding to 30% of the dive cycle at these depths on average. Detailed analysis of data at 35–55 m revealed that diving efficiency was greater at these depths than at 55–80 m when mouth-opening events occurred (0·025 ± 0·009, t = 2·72, *P* = 0·0065; Appendix S5).

A broken-line model showed a break point in the relationship between foraging efficiency and dive depths at 59·5 ± 2·6 m (mean ± SE). Indeed, foraging efficiency increased with increasing dive depths up to ~ 60 m (mean ± SE slope estimate: 0·012 ± 0·001; *P* < 0·0001) before stabilizing (Fig. 4c). Hence, fur seals dove mostly at depths shallower than the depth at which their foraging efficiency was the highest.

Discussion

Using accelerometers and Hall sensor loggers, we showed that free-ranging Antarctic fur seals adjust their foraging time in the bottom phase of the dive mainly according to the prey patch accessibility (depth) and to their physiological constraints (behavioural aerobic dive limit), rather than their prey encounters (mouth-opening events). These results are important in the sense that they help us understand the factors determining a predator's foraging strategies, foraging efficiencies and interaction with prey and their environment, which ultimately affect their fitness.

We first confirmed, as previously hypothesized for fur seals, that most of the foraging activity takes place during the bottom phase of the dive (82% of mouth-opening events; Hooker *et al.* 2002). This result is consistent with findings obtained from other marine species foraging in
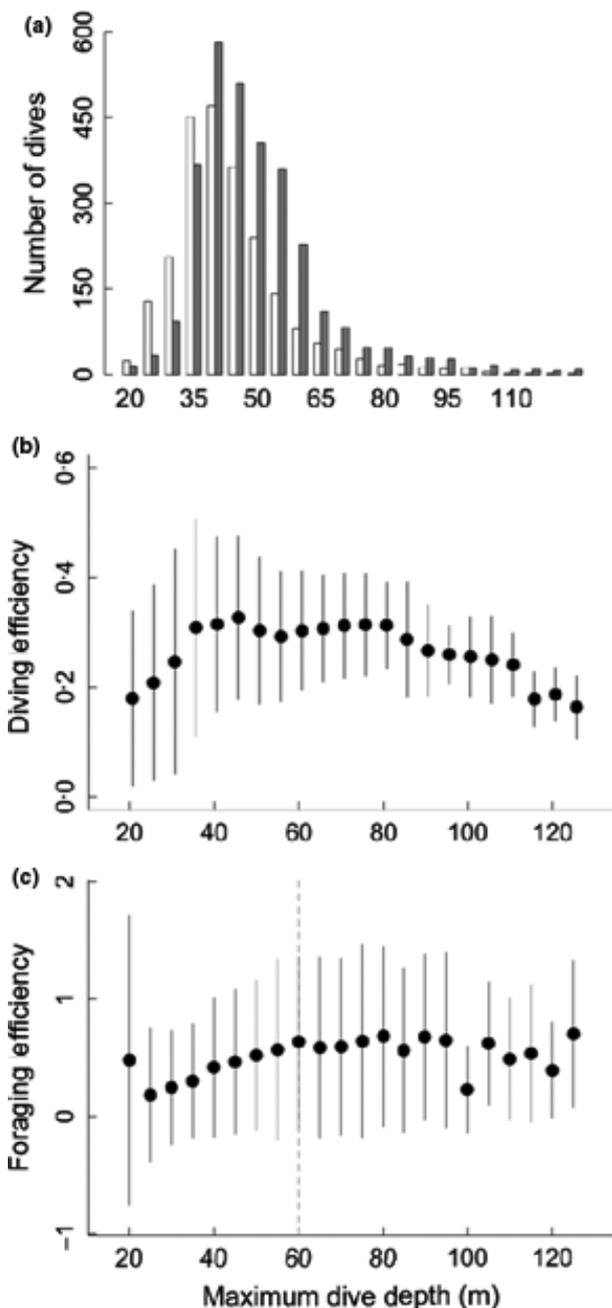
Fig. 4. Dive frequency (a), diving efficiency (bottom duration / dive cycle) (b) and foraging efficiency (mouth-opening events per minute of dive cycle) as a function of maximum dive depth (mean ± SD). Dives with and without mouth-opening events are plotted in grey and white, respectively. The combination of both is plotted in black. The vertical grey dashed line in graph (c) represents the depth thresholds of 60 m after which there is a change in slope.

bottom of dives as the prey patch location, although it is worth mentioning that the 'active' patch is one that the predator preferentially chooses to forage in.

In addition, our first prediction stated that diver predators should increase their patch residence time (or load size) with increasing distance between the prey patch (dive bottom) and the surface of the water (Orians & Pearson 1979; Kramer 1988; Mori 1998b). This prediction was confirmed by our findings. Antarctic fur seals increased their foraging time at the dive bottom when the vertical distance (diving depth) to reach the prey patch increased independently of prey encounters. This adjustment enabled them to maintain a high diving efficiency which conforms to our first prediction.

In accordance with our second prediction, we also found that fur seals spent more time on average at the bottom of shallow dives when they encountered prey items (with mouth-opening events) compared to when they did not. However, this result was driven by the occurrence of 'V-shaped' dives. These dives are likely exploratory dives in which the seal decided in subsequent dives to either to forage in the patch or to move to another location (Austin et al. 2006a,b, Lesage, Hammill & Kovacs 1999). Nonetheless, 'V-shaped' dives were present inside dive bouts and were not isolated dives separated by greater surface duration. This suggests that seal aborted their dive in absence of prey encounters. However, this behaviour of performing 'V-shaped' dives disappeared for dives deeper than 55 m. At such depths, seals might keep on foraging at bottom to maintain a greater diving efficiency as there is no benefit to giving up anymore. These results are consistent with Thompson and Fedak's prediction (2001) which says that diving predators should end their dive earlier when no prey is found compared to when at least one prey item is encountered early in the dive. Furthermore, when a predator dives to the maximum depth it can attain aerobically, there is no benefit to giving up early, as validated in captive seals (Cornick & Horning 2003; Sparling et al. 2007).

However, when fur seals decided to continue foraging at depth (bottom duration >1 s), the amount of time spent at the bottom did not depend on prey encounters, contrary to Thompson and Fedak's (and to our 2d) prediction (2001). This suggests that seals might use other cues (e.g. visual, acoustic or vibratory) to assess prey density and/or might make decisions based on a larger time-scale (data from previous dives). Myctophid species are bioluminescent. Consequently, Antarctic fur seals might use visual clues to evaluate the prey patch density. This behaviour has been observed in southern elephant seals which have been shown to use bioluminescence when foraging at depth (Vacquié-Garcia et al. 2012). Fur seals might also rely on their whiskers to help them detect and track prey items through the hydrodynamic trail prey leave in their wake (Hyvärinen 1989).

It is also important to mention that prey behaviour (escape behaviour for example) or the prey patch structure likely impacts predators' strategies. For example, if a prey

mesopelagic waters such as Weddell seals *Leptonychotes weddelli* (Watanabe et al. 2003), Magellanic penguin *Spheniscus magellanicus* (Wilson et al. 2002), leatherback turtles *Dermochelys coriacea* (Fossette et al. 2008) and southern elephant seals (*Mirounga leonina*, Guinet et al. 2014). This emphasizes the importance of the bottom phase as the most active foraging part of the dive and the

patch is not tightly aggregated, fur seals might decide to keep foraging at the bottom even though they do not encounter prey in a given dive as probability of encountering prey is still high. So if animals obtain additional information on prey patch quality/density/location, this might skew their response compared to theory that considers no prior knowledge. Consequently, our second prediction is partly verified since the seals spent more time at the bottom of shallow dives when they encounter prey compared to when they do not, but our data suggest a more subtle pattern as this pattern is no longer verified when excluding 'V-shaped' dives that do not include bottom (or foraging) time with seal spending less time at the bottom of their dive when encountering preys.

Finally, we tested the third prediction (Mori 1998a) that optimal foraging depth for a diving predator corresponds to the depth at which the highest foraging efficiency is achieved. Mori (1998a) also specifies that it is always slightly shallower than the depth at which prey density is the highest, even if the depth of the highest prey density is within easy reach. Watanabe *et al.* (2003) showed how Weddell seals mostly dive to depths at the shallower end of the depths range of highest prey densities, supporting Mori's model (1998a). Likewise, emperor penguins *Aptenodytes forsteri* focus their foraging effort at depths where overall gain is greatest (Zimmer *et al.* 2010). However, Antarctic fur seals did not conform to these behaviours. They concentrated 68·4% of their dives between 30 and 55 m even though their foraging efficiency increased up to 60 m. The fact that animals foraged mostly at depths above the depth of maximum foraging efficiency is likely explained by physiological constraints.

The behavioural aerobic dive limit gives a useful indication of average physiological constraint, which influences foraging strategies adopted by the seals. Post-dive intervals steadily increased after 55 m dive depth while dive duration exceeded the behavioural aerobic dive limit around 55–60 m, which means fur seals seem to be physiologically more constrained past the threshold limit of 55 m. When all dives were considered (with or without mouth-opening events), fur seals did not forage at depths that yielded the highest foraging efficiency. When only dives with mouth-opening events were considered, they actually chose to dive at shallower depths, which corresponded to the highest foraging efficiency. By diving at shallow depths, fur seals might keep more flexibility to explore and adjust their dive bottom duration according to other cues of prey availability.

It is interesting to note that the behavioural aerobic dive limit we recorded (123 ± 16 s) is lower than the one estimated for the Crozet Island population (150 s; Luque, Arnould & Guinet 2008) but greater than the aerobic dive limit calculated for this species at South Georgia (96 ± 24 s; based on direct measurements of oxygen stores and metabolic rates; cADLCosta, Gales & Goebel 2001). It should be kept in mind that ADL is affected by oxygen stores in metabolically active tissues and, thus, by differences in body composition between studies, sites and/or

individuals. Body mass did not explain this observed inter-site variation in bADL (30·9 ± 4·5 kg at Kerguelen (this study), 32·7 ± 0·36 kg at Crozet (Bailleul *et al.* 2005; Luque *et al.* 2007) and 41·9 ± 5 kg at South Georgia (Costa 2007), and no relationship between body mass (or size) and behavioural aerobic dive limit was found in our study.

The interindividual, intersite differences in aerobic dive limits require further investigation such as the energy expenditure when diving according to prey types with dive limit varies with metabolic rate and thus with swimming and/or prey-chasing behaviour or environmental conditions, such as sea temperature associated with the foraging zone (Enstipp, Grémillet & Jones 2007). Antarctic fur seals from South Georgia feed mostly on krill while species on Crozet and Kerguelen target fish (myctophids) and cephalopods (Reid & Arnould 1996; Lea *et al.* 2002a,b). The difference in prey type and/or prey distribution might affect the rate at which fur seals spend their energy chasing prey, and thus their bADL. This could also explain why some dives exceeded the behavioural aerobic dive limit below 55 m in our study. Furthermore, the high variances among individuals could reflect either a difference in quality or distribution of prey patches encountered during a foraging trip, a difference in prey targeted during dives, a difference in individual foraging specialization or the abundance of competing predators. Hooker *et al.* (2002) found several Antarctic fur seals feeding on the same krill swarm on Bird Island, suggesting a possible role for competition or cooperative feeding in foraging decisions (increasing the phenomenon of prey depletion or escape). Unfortunately, whether several fur seals also forage simultaneously on myctophid schools is unknown. Animal-borne cameras would be a useful way to address some of these questions in the future.

In any case, our results did not confirm our third prediction, as Antarctic fur seals did not dive mostly at the depths at which their foraging efficiency was the greatest. However, it is important to note that other uncontrollable factors might have influenced the predator's foraging decisions. Foraging efficiency can be affected by the energetic profitability of prey consumed (in size or energy density) (Bowen *et al.* 2002). Trade-offs between predation risks (Kotler 1997) or competition (Lair, Kramer & Giraldeau 1994) and foraging efficiency could also prevent fur seals to forage at specific depths even though these depths would yield a greater energy gain. In addition, body condition (through the predator's motivation or its buoyancy; Caraco 1981; Biuw *et al.* 2003) could impact differently the depths at which foraging efficiency is the greatest.

The proportion of successful vs. unsuccessful feeding attempts with depth could also play a major role. This would be particularly true if the degree of prey aggregation and/or the distribution of prey species vary with depth. We are unable with our method to determine whether mouth-opening events corresponded to successful vs. unsuccessful feeding attempts, or whether the proportion of successful vs. non-successful feeding attempts vary by depth. This could affect how we interpret our results in the light of our

third prediction. Consequently, our results suggest that these Antarctic fur seals at Kerguelen Island do not comply with Mori's (1998b) and our third prediction, but numerous other factors might affect our observed conclusion.

Finally, predators may maximize another currency than gross rate of energy intake that we have been measuring here (mouth-opening events / dive cycle duration), such as net rate of energy intake or energetic efficiency which takes into account the energy spent while foraging ((mouth-opening event – energy spent)/ dive cycle duration). In this case, decisions would also take into account how much energy animals have to spend to catch a prey at a specific depth. Knowing that energy expenditure increases past the bADL (here at 55 m), foraging at 60 m might not result in the greatest (net) foraging efficiency, but at a shallower depth (possible between 30–55 m). Changing the currency that animals might optimize can change the optimal foraging strategies and could explain why Antarctic fur seals did not comply with our third prediction.

To summarize, our result confirm the growing evidence that bottom duration can be used as a simple proxy for foraging success. In grey seals, cumulated bottom duration is the best predictor of the number of feeding events per diving bout (Wilson *et al.* 2002; Watanabe *et al.* 2003; Fossette *et al.* 2008). At the foraging trip scale, cumulated daily bottom duration best predicted the number of feeding events (Austin *et al.* 2006a,b) in grey seals (*Halichoerus grypus*). We also found that bottom duration correlated positively with the number of mouth-opening events in dives less than the bADL (<55 m). However, the absence of relationship between bottom duration and presence of mouth-opening events for dives with bottom duration >3 s in fur seals as well as the discrepancy between the diving efficiency and the foraging efficiency shows that bottom duration might not accurately predict the number of mouth-opening events. The presence of exploratory dives might give an indication on the quality of the area visited (whether it is worth or not to forage) but only at depths below the bADL. Consequently, the observed correlation between bottom duration and number of feeding attempts in a marine predator does not imply that the bottom duration alone will be a good predictor of the foraging success. However, these models assume constant prey quality while seals may encounter different sized/quality prey items throughout and between dives such that their decision to terminate dives may not be obligatorily related to bottom duration.

These patterns observed in Antarctic fur seals are likely to be shared by other marine predators, with a magnitude that will depend on the species' physiological capacity as well as the vertical accessibility, mobility and energy density of the targeted prey. Thums, Bradshaw & Hindell (2011) showed that the probability of being in foraging search mode in elephant seals was negatively related to the number of daily speed spikes (a proxy of prey encounters). Consequently, the foraging strategies of diving predators are more complex than initially thought and than predicted by current theory. Ultimately, the understanding of these fine-scale foraging mechanisms will help establishing reliable predictive foraging models for marine predators, based on diving patterns only.

Data accessibility

Data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.ct511 (Viviant *et al.* 2016).

References

Austin, D., Bowen, W.D., McMillan, J.I. & Boness, D.J. (2006a) Stomach temperature telemetry reveals temporal patterns of foraging success in a free-ranging marine mammal. *Journal of Animal Ecology*, **75**, 408–420.

Austin, D., Bowen, W.D., McMillan, J.I. & Iverson, S.J. (2006b) Linking movement. diving. and habitat to foraging success in a large marine predator. *Ecology*, **87**, 3095–3108.

Bailleul, F., Luque, S., Dubroca, L., Arnould, J.P.Y. & Guinet, C. (2005) Differences in foraging strategy and maternal behaviour between two sympatric fur seal species at the Crozet Islands. *Marine Ecology Progress Series*, **293**, 273–282.

Biuw, M., McConnell, B., Bradshaw, C.J.A., Burton, H. & Fedak, M. (2003) Blubber and buoyancy: monitoring the body condition of free-ranging seals using simple dive characteristics. *The Journal of Experimental Biology*, **206**, 3405–3423.

Bost, C.A., Handrich, Y., Butler, P.J., Fahlman, A. & Halsey, L.G. (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.

Bowen, W.D., Tully, D., Boness, D.J., Bulheier, B.M. & Marshall, G.J. (2002) Prey- dependent foraging tactics and prey profitability in a marine mammal. *Marine Ecology Progress Series*, **244**, 235–245.

Boyd, I.L. & Croxall, J.P. (1992) Diving behaviour of lactating Antarctic fur seals. *Canadian Journal of Zoology*, **70**, 919–928.

Boyd, I.L., McCafferty, D. & Walker, T.R. (1997) Variation in foraging effort by lactating Antarctic fur seals: response to simulated increased foraging costs. *Behavioural Ecology and Sociobiology*, **40**, 135–144.

Burnham, K.B. & Anderson, D.R. (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research*, **33**, 261–305.

Caraco, T. (1981) Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*). *Behavioural Ecology and Sociobiology*, **8**, 213–217.

Carbone, C. & Houston, A. (1996) The optimal allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. *Animal Behaviour*, **51**, 1247–1255.

Cézilly, F. & Benhamou, S. (1996) Les stratégies optimales d'approvisionnement. *Revue d'Ecologie la Terre et la Vie*, **51**, 43–86.

Cherel, Y., Guinet, C. & Tremblay, Y. (1997) Fish prey of Antarctic fur seals *Arctocephalus gazella* at Ile de Croy, Kerguelen. *Polar Biology*, **17**, 87–90.

Cornick, L.A. & Horning, M. (2003) A test of hypotheses based on optimal foraging considerations using a novel experimental approach. *Canadian Journal of Zoology*, **81**, 1799–1807.

Costa, D.P. (2007) *Diving Physiology of Marine Vertebrates. eLS*. John Wiley & Sons Ltd, Chichester, UK.

Costa, D.P., Gales, N.J. & Goebel, M.E. (2001) Aerobic dive limit: how often does it occur in nature? *Comparative Biochemistry and Physiology A*, **129**, 771–783.

Daniel, S., Korine, C. & Pinshow, B. (2008) Central place foraging in nursing, arthropod- gleaning bats. *Revue Canadienne de Zoologie*, **86**, 623–626.

Duhamel, G., Koubbi, P. & Ravier, C. (2000) Day and night mesopelagic fish assemblages off the Kerguelen Islands (Southern Ocean). *Polar Biology*, **23**, 106–112.

Enstipp, M.R., Grémillet, D. & Jones, D.R. (2007) The effect of depth, temperature and food ingestion on the foraging energetic of a diving endotherm, the double-crested cormorant (*Phalacrocorax auritus*). *The Journal of Experimental Biology*, **209**, 845–859.

Fossette, S., Gaspar, P., Handrich, Y., Le Maho, Y. & Georges, J.Y. (2008) Dive and beak movement patterns in leatherback turtles *Dermochelys coriacea* during internesting intervals in French Guiana. *Journal of Animal Ecology*, **77**, 236–246.

Giraldeau, L.-A. & Kramer, D.L. (1982) The marginal value theorem: a quantitative test using load size variation in a central place forager, the eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, **30**, 1036–1042.

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

Heaslip, S.G., Bowen, W.D. & Iverson, S.J. (2014) Testing predictions of optimal diving theory using animal-borne video from harbour seals (*Phoca vitulina concolor*). *Canadian Journal of Zoology*, **92**, 309–318.

Hooker, S.K., Boyd, I.L., Jessopp, M., Cox, O., Blackwe, J., Boveng, P.L. *et al.* (2002) Monitoring the prey-field of marine predators: combining digital imaging with datalogging tags. *Marine Mammal Science*, **18**, 680–697.

Houston, A.I. & Carbone, C. (1992) The optimal allocation of time during the diving cycle. *Behavioral Ecology*, **3**, 255–265.

Hyvärinen, H. (1989) Diving in darkness: whiskers as sense organs of the ringed seal (*Phoca hispida saimensis*). *Journal of Zoology*, **218**, 663–678.

Jodice, P.G.R. & Collopy, M.W. (1999) Diving and foraging patterns of Marbled Murrelets (*Brachyramphus marmoratus*): testing predictions from optimal breathing models. *Canadian Journal of Zoology*, **77**, 1409–1418.

Kacelnik, A. & Cuthill, I. (1990) Central place foraging in starlings (*Sturnus vulgaris*). II Food allocation to chicks. *Journal of Animal Ecology*, **59**, 655–674.

Kooyman, G.L. (1989) *Diverse Divers: Physiology and Behavior*. Springer-Verlag, Berlin, Germany.

Kooyman, G.L., Wahrenbrock, E.A., Castellini, M.A., Davis, R.W. & Sinnett, E.E. (1980) Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior. *Journal of Comparative Physiology B*, **138**, 335–346.

Kotler, B.P. (1997) Patch use by gerbils in a risky environment: manipulating food and safety to test four models. *Oikos*, **78**, 274–282.

Kramer, D.L. (1988) The behavioral ecology of air breathing by aquatic animals. *Canadian Journal of Zoology*, **66**, 89–94.

Kuhn, C.E., Crocker, D.E., Tremblay, Y. & Costa, D.P. (2009) Time to eat: measurements of feeding behaviour in a large marine predator, the northern elephant seal *Mirounga angustirostris*. *Journal of Animal Ecology*, **78**, 513–523.

Lair, H., Kramer, D.L. & Giraldeau, L.-A. (1994) Interference competition in central place foragers: the effect of imposed waiting on patch-use decisions of eastern chipmunks, *Tamias striatus*. *Behavioural Ecology*, **5**, 237–244.

Lea, M.A., Hindell, M., Guinet, C. & Goldsworthy, S. (2002a) Variability in the diving activity of Antarctic fur seals, *Arctocephalus gazella*, at Iles Kerguelen. *Polar Biology*, **25**, 269–279.

Lea, M.A., Cherel, Y., Guinet, C. & Nichols, P.D. (2002b) Antarctic fur seals foraging in the Polar Frontal Zone: inter-annual shifts in diet as shown from fecal and fatty acid analyses. *Marine Ecology Progress Series*, **245**, 281–297.

Lea, M.A., Guinet, C., Cherel, Y., Duhamel, G., Dubroca, L. & Thalmann, S. (2008) Colony-based foraging segregation by Antarctic fur seals at the Kerguelen Archipelago. *Marine Ecology Progress Series*, **358**, 273–287.

Lesage, V., Hammill, M.O. & Kovacs, K.M. (1999) Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Canadian Journal of Zoology*, **77**, 74–87.

Luque, S.P., Arnould, J.P.Y. & Guinet, C. (2008) Temporal structure of diving behaviour in sympatric Antarctic and subantarctic fur seals. *Marine Ecology Progress Series*, **372**, 277–287.

Luque, S.P. & Guinet, C. (2007) A maximum likelihood approach for identifying dive bouts improves accuracy, precision and objectivity. *Behaviour*, **144**, 1315–1332.

Luque, S.P., Arnould, J.P.Y., Miller, E.H., Cherel, Y. & Guinet, C. (2007) Foraging behaviour of sympatric Antarctic and subantarctic fur seals: does their contrasting duration of lactation make a difference? *Marine Biology*, **152**, 213–224.

Mori, Y. (1998a) Optimal choice of foraging depth in divers. *Journal of Zoology of London*, **245**, 279–283.

Mori, Y. (1998b) The optimal patch use in divers: optimal time budget and the number of dive cycles during bout. *Journal of Theoretical Biology*, **190**, 187–199.

Mori, Y. (1999) The optimal allocation of time and respiratory metabolism over the dive cycle. *Behavioural Ecology*, **10**, 155–160.

Muggeo, V. (2003) Estimating regression models with un-known breakpoints. *Statistics in Medicine*, **22**, 3055–3071.

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.

Okuyama, J., Kawabata, Y., Naito, Y., Arai, N. & Kobayashi, M. (2010) Monitoring beak movements with an acceleration datalogger: a useful technique for assessing the feeding and breathing behaviors of sea turtles. *Endangered Species Research*, **10**, 39–45.

Orians, G.H. & Pearson, N.E. (1979) On the theory of central place foraging. *Analysis of Ecological Systems* (eds D.J. Horn, G.R. Stairs & R.D. Mitchell), pp. 155–177. Ohio State University Press, Columbus, OH, USA.

Pyke, G.H. (1984) Optimal foraging theory: a critical review. *Annual Revue of Ecology and Systematics*, **15**, 523–575.

R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Reid, K. & Arnould, J.P.Y. (1996) The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biology*, **16**, 105–114.

Rigby, R.A. & Stasinopoulos, D.M. (2005) Generalized additive models for location, scale and shape. *Applied Statistics*, **54**, 507–554.

Schmid-Hempel, P., Kacelnik, A. & Houston, I. (1985) Honeybees maximize efficiency by not filling their crop. *Behavioural Ecology and Sociobiology*, **17**, 61–66.

Sparling, C.E., Georges, J.Y., Gallon, S.L., Fedak, M. & Thompson, D. (2007) How long does a dive last? Foraging decisions by breath-hold divers in a patchy environment: a test of a simple model *Animal Behaviour*, **74**, 207–218.

Stephens, D. & Krebs, J. (1986) *Foraging Theory*. Princeton University Press, Princeton, NJ, USA.

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

Thompson, D. & Fedak, M. (2001) How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Animal Behaviour*, **61**, 287–296.

Thompson, D., Hiby, A.R. & Fedak, M.A. (1993) How fast should I swim? Behavioural implications of diving physiology. *Symposia of the Zoological Society of London*, **66**, 349–368.

Thums, M., Bradshaw, C.J.A. & Hindell, M.A. (2011) In-situ Measures of foraging success and prey encounter reveal marine habitat-dependent search strategies. *Ecology*, **92**, 1258–1270.

Vacquié-Garcia, J., Royer, F., Dragon, A.-C., Viviant, M., Bailleul, F. & Guinet, C. (2012) Foraging in the darkness of the Southern Ocean: influence of bioluminescence on a deep diving predator. *PLoS ONE*, **7**, e43565.

Viviant, M., Andrew, W.T., Rosen, D.A.S., Monestiez, P. & Guinet, C. (2010) Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. *Polar Biology*, **33**, 713–719.

Viviant, M., Jeanniard-du-Dot, T., Monestiez, P., Authier, M. & Guine, C. (2016) Data from: Bottom time does not always predict prey encounter rate in Antarctic fur seals. *Dryad Digital Repository*, http://dx.doi.org/10.5061/dryad.ct511.

Watanabe, Y., Mitani, Y., Sato, K., Cameron, M.F. & 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.

Wilson, R.P., Steinfurth, A., Ropert-Coudert, Y., Kato, A. & Kurita, M. (2002) Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Marine Biology*, **140**, 17–27.

Zimmer, I., Wilson, R.P., Beaulieu, M., Ropert-Coudert, Y., Kato, A., Ancel, A. *et al.* (2010) Dive efficiency versus depth in foraging emperor penguins. *Aquatic Biology*, **8**, 269–277.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology With R*. Springer, New York, NY, USA.

Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. (a) Hall sensor attachment and (b) accelerometer attachment on Antarctic fur seals.

Appendix S2. Number of prey capture attempts per minute in each phase of a dive (mean ± SD) as identified by numbers of mouth-opening events. The number of mouth-opening events in each phase is in brackets.

Appendix S3. Example of post-dive intervals in relation to dive duration for two individuals. The abrupt slope change defines the behavioural aerobic dive limit (bADL).

Appendix S4. Model selection using Akaike's Information Criterion (AIC) to explain relationships between bottom duration and depths.

Appendix S5. Results of the final Linear Mixed Model describing the diving efficiency (bottom duration/dive cycle duration) for dives between 35 and 80 m deep.