Identifying foraging events in deep diving southern elephant seals, *Mirounga leonina*, using acceleration data loggers

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ABSTRACT

Southern elephant seals (*Mirounga leonina*) range widely throughout the Southern Ocean and are associated with important habitats (*e.g.*, ice edges, shelf) where they accumulate energy to fuel their reproductive efforts on land. Knowledge of the fine scale foraging behaviour used to garner this energy, however, is limited. For the first time, acceleration loggers were deployed on three adult southern elephant seals during a translocation study at Kerguelen Island. The aims of the study were to (1) identify prey capture attempts using 2-D accelerometer tags deployed on the head of southern elephant seals, (2) compare the number of foraging dives identified by simple dive depth profiles and accelerometer profiles and (3) compare dive characteristics between prey encounter and non-prey encounter dives. The 2-D loggers recorded depth every second, surge and heave accelerations at 8 or 16 Hz and were carried for periods between 23 and 121 h. Rapid head movements were interpreted to be associated with prey encounter events. Acceleration data detected possible prey encounter events in 39–52% of dives whilst 67–80% of dives were classified as foraging dives when using dive depth profiles alone. Prey encounters occurred in successive dives during days and nights and lasted between tenths of a second and 7.6 min. Binomial linear mixed effect models showed that seals were diving significantly deeper and increased both descent rate and bottom duration when encountering prey. Dive duration, however, did not significantly increase during dives with prey encounters. These results are in accordance with optimal foraging theory, which predicts that deep divers should increase both their transit rates and the time spent at depth when a profitable prey patch is encountered. These findings indicate that this technique is promising as it more accurately detects possible prey encounter events compared with dive depth profiles alone and thus provides a better understanding of seal foraging strategies.

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1. Introduction

Southern elephant seals, *Mirounga leonina*, are a large and abundant phocid predator at the top of the Southern Ocean food web (Guinet et al., 1996; Hindell et al., 2003). During long migrations, individuals typically make ocean journeys of thousands of kilometres in order to feed sufficiently to fuel their brief reproductive effort on land (McConnell et al., 1992). These deep-diving predators are associated with important habitats such as the ice edges and the continental shelf (Bailleul et al., 2010; Biuw

et al., 2007). The details of their diet, however, are still largely unknown because their stomach contents are usually entirely digested by the time they return to land. Recent studies using isotope analyses suggest that female and juvenile elephant seals feed mainly on myctophids and not predominantly on cephalopods as previously assumed (Bailleul et al., 2010; Cherel et al., 2008; Newland et al., 2011). The spatial and vertical distribution of potential prey is also poorly understood. Several behaviour-derived foraging metrics (*e.g.* transit swim speed, diving depth, diving duration, drift rate, wiggles) have been used to identify foraging habitats and/or foraging success for elephant seals (Biuw et al., 2007; Bailleul et al., 2007, 2008; Dragon et al., 2012a, 2012b; Field et al., 2001; Hindell et al., 1991; McConnell et al., 1992; Robinson et al., 2010; Thums et al., 2011), and although these studies are crucial for investigating key habitats they cannot provide the necessary fine-scale information of when and where these top predators encounter their prey.

Despite its importance, the feeding behaviour of most marine mammals is poorly understood because it usually occurs at great depth, over large spatial scales and in a particularly challenging environment. Bio-logging technology can overcome these problems by enabling the remote measurement of data for free-ranging animals (Cooke et al., 2004; Ropert-Coudert and Wilson, 2005; Rutz and Hays, 2009). Animal-borne video recorders and acoustic tags have provided new insights into the functionality of dive types and the detail of fine-scale foraging behaviour (Arranz et al., 2011; Davis et al., 2003; Fuiman et al., 2002; Hooker et al., 2002; Johnson et al., 2004; Madsen et al., 2005; Marshall et al., 2007; Watanabe et al., 2003). Due to restrictions in the amount of digital memory, however, the data cover a relatively short periods of time when recording continuously (Watanabe et al., 2003). More recently accelerometer tags have emerged as a powerful tool for investigating the foraging behaviour of marine predators. For example, some of the first evidence of the relationship between prey capture attempts and increases in dynamic acceleration were observed in toothed whales by relating acoustic indicators of feeding (buzzes) with body movements (Johnson et al., 2004; Miller et al., 2004). Accelerometer tags can measure body acceleration in up to three dimensions (i.e. surge, stroke and rolling). Using measurements in these three dimensions, prey capture and biting motions associated with biting are used to quantify feeding events (Aguilar Soto et al., 2008; Kokubun et al., 2011; Naito, 2007; Naito et al., 2010; Ropert-Coudert et al., 2004; Sato et al., 2008; Suzuki et al., 2009; Viviant et al., 2010). Accelerometer tags have the advantage of being externally mounted, providing a simple and practical field technique, compared with previously used internal data loggers (i.e. stomach and oesophageal temperature sensors) (Ancel et al., 1997; Charrassin et al., 2001; Kuhn et al., 2009; Wilson et al., 1992) or intra-mandibular angle sensor methods (Fossette et al., 2008; Liebsch et al., 2007; Wilson et al., 2002).

Several studies have shown that for seals, feeding and capture motions are especially visible in the surging axis when using jaw- or head-deployed acceleration data-loggers (Naito et al., 2010; Skinner et al., 2009; Suzuki et al., 2009; Viviant et al., 2010). Seals have a high propulsive efficiency which is due to the maintenance of nearly continuous thrust production during the stroke cycle and a hydrofoil morphology which enhances high thrust with reduced drag (Fish, 1994). Any stroking movements will increase drag and the cost of locomotion; thus swimming with discrete stroke and glide phases, as seals do, has been identified as a particularly efficient way of travelling (Williams and Kooyman, 1985). As deep divers, southern elephant seals are expected to adopt the most energetically efficient mode of locomotion and thus should avoid any unnecessary movements that would increase their drag and therefore their cost of swimming when diving. In this study, we used rapid head movements that are not associated with the propulsive activity of southern elephant seals to identify prey encounter events. More specifically, the aims of the study were to (1) identify prey capture attempts using 2-D accelerometer tags deployed on the head of southern elephant seals, (2) compare the number of foraging dives identified by dive depth profiles and accelerometer profiles and finally (3) compare dive characteristics between prey encounter and non-prey encounter dives.

2. Materials and methods

2.1. Study sites and animals

Three pre-moulting adult female southern elephant seals (T3, T4 and T5) were equipped with data loggers during a translocation study in 2005 on the Kerguelen Plateau (49 35S 70 26E). All seals were caught with a canvas head-bag and anaesthetized with a 1:1 combination of tiletamine and zolazepam (Zoletil 100) injected intra-venously (Field et al., 2002; McMahon et al., 2000). Individuals were equipped with Relayed Data Logger tags (SRDL) (SMRU, St. Andrews, UK) and 2D acceleration data loggers (Loggend, CNRS, France). The accelerometers were positioned on the head (T4 and T5) and the neck (T3) of the animals. The position of the accelerometer was lower on seal T3 as this individual was also equipped with an intra-mandibular angle sensor placed on the head and jaws of the animal to record mouth opening movements that unfortunately did not function. Tags were glued onto the seal fur using a two-component quickset epoxy. Individuals were then placed in specially designed wooden boxes, and then transported by R/V 'La Curieuse' approximately 240 km away from the Island (approximately 24 h journey time) to be released. As seals had already come ashore to moult they were likely to return to land, thereby increasing the likelihood of recovering the tags. Table 1 provides descriptive information on the study animals.

2.2. Instruments

We used accelerometer tags: 2-D loggers (0.009 m length, 0.003 m width, 0.002 m height, 0.063 kg in air, Loggend, CNRS, France). The accelerometer tags recorded pressure at 1 s intervals and 2-D accelerations to detect head movements at 8 Hz for individuals T4 and T5 and at 16 Hz for individual T3 with a memory of 16 Mb. Seals were also equipped with SRDL satellite tags to provide an estimate of the location of the animals at sea and on land.

The 2-D loggers require physical recovery for data retrieval. We used the Argos positions received through the satellite tags to

Table 1
Descriptive information about the three adult female southern elephant seals.

Seal	Body mass[a](kg)	Capture date (dd/mm/yyyy) and location	Release date (dd/mm/yyyy) and location	Recapture date (dd/mm/yyyy)[b]	Accelerometers' recording duration (h)
T3	407	24/01/2005 49°20.900S/70°13.683E	25/01/2005 49°16.812S/73°35.999E	27/01/2005	41.4
T4	317	04/02/2005 49°20.900S/70°13.683E	05/02/2005 49°02.237S/72°24.252E	09/02/2005	73.5
T5	489	04/02/2005 49°20.900S/70°13.683E	05/02/2005 49°02.237S/72°24.252E	09/02/2005	21.7

[a] Body mass at first capture.
[b] The precise location of recapture was not recorded but it was between 49°20.900S/70°13.683E and 49°25.100S/70°17.033E.

determine when and where the animals returned to Kerguelen Island.

2.3. Depth data analysis

Pressure sensor data were used to obtain dive depth profiles. For the purpose of this study and based on the sensor's absolute accuracy, only excursions below a depth of -20 m were analysed. Each dive was divided into a descent phase, a bottom phase (the period between the end of the descent and the beginning of the ascent and during which depth was greater than 80% of maximum depth of a given dive) and an ascent phase. The expression 'Dive depth' hereafter refers to the maximum depth reached during a dive.

Dive profiles were allocated to two discrete groups based on analysis of the dive shape at the bottom of the dive, as described by Hindell et al. (1991). Dives with a bottom phase were classified as 'foraging' dives (i.e. 'U-shaped' dives) and dives without a bottom phase were classified as 'non-foraging' (i.e. 'V-shaped' dives, bottom duration < 0.1 min). The presence or absence of wiggles (i.e. vertical excursions during the bottom phase) in 'U-shaped' dives was recorded. In order to take into account both the number of wiggles and the vertical distance of each wiggle, we calculated the standard deviation for depth at the bottom of

the dive, hereafter referred as an index of 'wiggle activity'. These labels do not indicate that seals were feeding in any of these dives but are an indicator of foraging effort. This is based on the assumption that if a seal is spending some time at a particular depth and travelling up and down while there, it indicates some degree of foraging (Hindell et al., 1991).

2.4. Acceleration data analysis

Acceleration data processing was performed using Matlab 7.0.1 (Mathworks) to identify rapid head movements that may be associated with prey encounter events. The 2-D loggers used two axes (surge and heave) acceleration sensors that measured both dynamic accelerations (resulting from propulsive activity) and gravitational acceleration. Dynamic accelerations resulting from stroking and rapid head movements were identifiable as regular deviations from the gravitational signal (Fig. 1). Low frequency variations were assumed to be the result of various turning and rolling movements of the seal (Sato et al., 2003; Watanabe et al., 2006). These were separated using a low-pass filter (0.4–0.8 Hz) (Matlab software, version 7.0.1) to extract the information on dynamic accelerations.

We used rapid head movements visible as spikes in the filtered acceleration profiles to identify possible prey capture attempts.
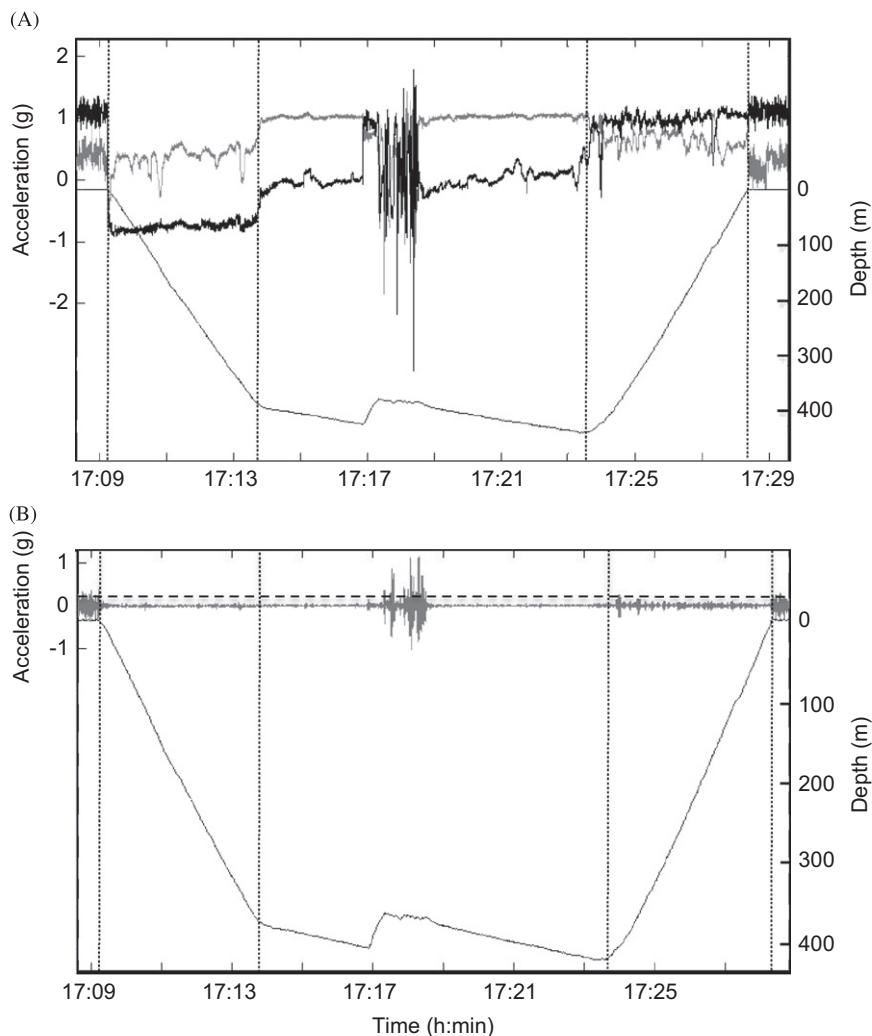
Fig. 1. Dive depth profile and (A) raw acceleration signal, (B) filtered acceleration signal for a 20.01 min dive by seal T5 on January 25, 2005. Different phases (surface, descent, bottom and ascent) of the dive are demarcated by vertical dotted lines. Surge values in the raw acceleration signal are in black; heave values in the raw acceleration signal are in grey. The threshold used in the filtered signal to detect prey encounter event is depicted by a dashed line in (B).

Acceleration profiles with more than one spike above a threshold (in m s^{-2}) visible both in the surge and heave axes were considered to be related to prey encounter events (i.e. prey encounter dives, 'p-e' dives) (Fig. 1). Acceleration profiles with spikes lower than the threshold, however, were considered to be related to dives where animals did not alter their swimming behaviour whilst travelling underwater and therefore we hypothesised that animals did not encountered any prey in these dives (i.e. non-prey encounter dives or 'n-p-e' dives). Acceleration thresholds (in m s^{-2}) were determined for each individual using survival curves showing the number of spikes (i.e. rapid head movements) detected versus a range of thresholds. For each seal, the breaking point in the curve was selected as the threshold (Fig. 2).

Series of spikes above the threshold constituted a prey capture attempt. Prey capture attempts were separated by period of time (≥ 30 s) with no spikes in both the surge and heave acceleration signals. The 30 s threshold used to separate prey capture attempts was selected based on the analyses of a subset of 20 dives for each seals where rapid head movements were detected in the acceleration signal. The 30 s threshold was the breaking point in the survival curve showing the mean number of prey capture attempts visually recorded for the 60 dives versus a range of possible intervals (every 10 s between 0 and 3 min) between prey capture attempts (Fig. 3). Detection algorithms (Matlab software, version 7.0.1) were used to calculate the number of prey capture attempts for each 'p-e' dive. When rapid head movements were detected in the acceleration signal, we visually inspected the dive profiles to determine if animals were swimming upward or downward during prey capture attempts. We also manually recorded if prey capture attempts were isolated or were identified in successive dives. Isolated prey capture attempts were separated by three or more dives where no rapid head movements were detected in the acceleration signal.

2.5. Dive parameters in relation to foraging behaviour and prey encounters.

Binomial generalised mixed effect models were used to investigate the relationship between diving parameters and foraging behaviour, and between diving parameters and prey encounters. The first model compared diving parameters between foraging
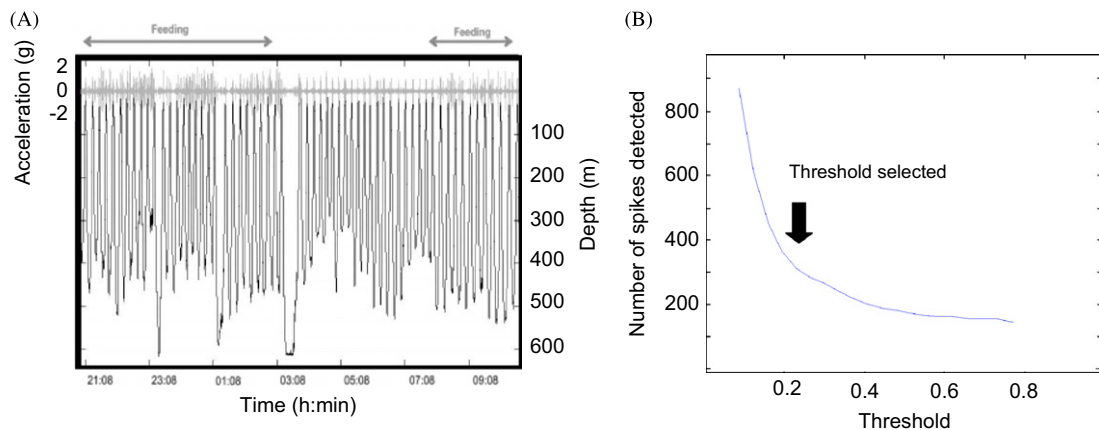
Fig. 2. (A) Filtered surge acceleration (grey) and depth (black) recorded by seal T3 over a 12 h period on January 26, 2005 and (B) associated survival graph used to select the threshold for detecting prey encounter events.
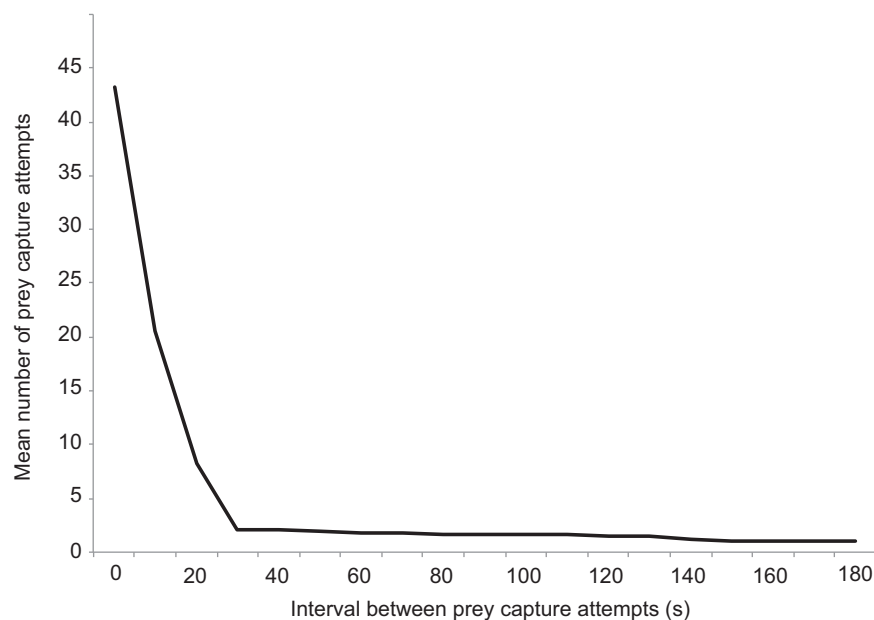
Fig. 3. Survival graph showing the mean number of prey capture attempts recorded versus a range of 10 s intervals between prey capture attempts obtained by visually analysing a sub-sample of 20 dives for each seal.

and non-foraging dives based on the depth profiles analyses. The second model compared diving parameters between 'p-e' and 'n-p-e' dives identified by the acceleration signal analyses.

The models were developed with *R* software (version 2.12.2) package lme4 (Bates, 2007). Individual seals were included as random effects and diving parameters as fixed effects. Deletion tests were used to assess the significance of each parameter in the models using likelihood ratio tests. For each dive, key diving parameters (*i.e.* dive duration, bottom duration, dive depth, post-dive surface duration, 'wiggle activity' and ascent rate) were calculated. We expected that seals would alter their ascent rate in response to the prey encountered during a dive, but their descent rates were expected to vary in response to the prey encountered during the preceding dive (Gallon et al., 2007). We therefore included in the diving parameters of each dive the descent rate of the following dive.

3. Results

3.1. Overall diving behaviour

Recording periods for individuals T3, T4 and T5 lasted 41.4, 73.5 and 21.7 h respectively. Mean dive duration was 15.5 ± 6.1 min for the 462 dives recorded from the three seals and the maximum dive duration was 64.7 min recorded by seal T3 (Table 2). Within a dive, the time spent at the bottom lasted 3.4 ± 4.4 min ($21.9 \pm 28.4\%$ of the total dive duration). The overall mean dive depth was 371 ± 152 m and the maximum dive depth was 903 m recorded by seal T4. Among the 462 dives, dives between 67.2% and 80.3% were classified as U-shaped dives (*i.e.* foraging dives).

Table 2
Main dive characteristics obtained for the three translocated female southern elephant seals. Mean values are given with $\pm$ s.d.

Seal	T3	T4	T5
Number of dives	132	262	71
Mean dive duration (min)	15.27 ± 8.69	15.44 ± 4.94	16.26 ± 4.02
Maximum dive duration (min)	64.68	30.55	27.67
Mean bottom duration (min)	2.64 ± 4.83	3.60 ± 4.14	4.34 ± 4.46
Mean surface duration (min)	3.63 ± 9.16	1.43 ± 1.44	1.99 ± 0.43
Mean descent rate (m s^{-1})	1.37 ± 0.42	0.96 ± 0.22	1.10 ± 0.29
Mean ascent rate (m s^{-1})	1.44 ± 0.51	0.87 ± 0.38	1.17 ± 0.36
Mean dive depth (m)	475 ± 82	310 ± 151	402 ± 138
Maximum dive depth (m)	751	903	780

3.2. Head accelerations

Acceleration profiles showed clear differences between the phases of the dive in both the raw and filtered acceleration signals (Figs. 1 and 4). The acceleration threshold used to identify spikes associated with probable prey encounter event was 2.45 m s^{-2} and was the same for all three seals (Fig. 2). Small spikes associated with propulsive activity (*i.e.* stroke and glide) were visible in both the heave and surge axes during the descent and ascent phases whilst large spikes associated with possible prey encounter events (*i.e.* spikes above the threshold) occurred during the bottom phase of the dives in 79.6% of the prey capture attempts among the three seals (Table 3).

3.3. Occurrence of prey capture attempt during the dive

Between 39.4% and 53.5% of the acceleration profiles presented spikes above the threshold (see example Fig. 4). Prey capture attempts were detected in 0.0%, 7.0% and 21.1% of the non-foraging dives (*i.e.* 'V-shaped' dives) and in 49.1%, 68.2% and 73.1% of the foraging dives (*i.e.* 'U-shaped' dives) for individuals T3, T4 and T5, respectively. Overall, 426 prey capture attempts were identified in 209 'p-e' dives (Table 3). Prey capture attempts lasted between less than 1 s and up to 7.6 min. Between 1 and 5 prey capture attempts occurred in 'p-e' dives with an overall mean of 2.04 prey capture attempts per 'p-e' dive. When encountering prey, seals swam deeper in 76.8% of the prey capture attempts (see 'Angle of attack' in Table 3). Prey capture attempts were distributed in successive dives rather than isolated throughout time (see Fig. 2). The percentage of grouped feeding dives were 96, 95 and 92 for seals T3, T4 and T5, respectively.
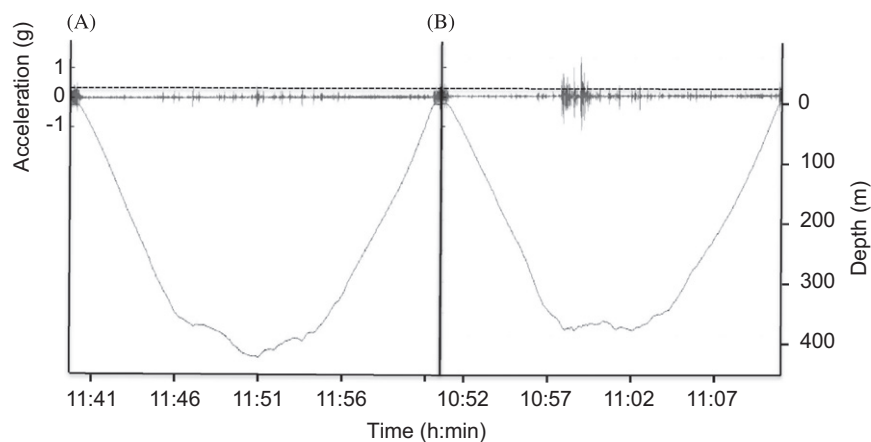
3.4. Dives associated with foraging and prey encounter events

There was significant variation between individual seals in both models used (Table 4). The first model found that dive and

Table 3
Summary of the characteristics of the prey encounter dives.

Seal	Number of prey capture attempt during			Mean number of prey capture attempt per 'p-e' dive	Angle of attack	
	Descent	Bottom	Ascent		Downward	Upward
T3	24	65	16	2.02	78	27
T4	9	220	26	2.13	203	52
T5	7	54	5	1.78	46	20

Fig. 4. Surge acceleration (grey) and depth (black) recorded by seal T4 over two dives on February 2, 2005 showing a change in dive profile (A) not associated with a change in acceleration and (B) associated with a change in acceleration.

Table 4
Summary of the parameters obtained from binomial linear mixed effect models in R (v2.12.2) for the dive profiles analyses ('foraging') and for the accelerometry signal analyses ('Prey encounter'). Seal ID (see text) was included as random effect; dive duration, bottom duration, surface duration, descent and ascent rates, dive depth and bottom activity as fixed effects. The significance of a parameter was tested by removing each parameter from the full model and looking at the effect of the deletion on the fit of the model using likelihood ratio tests (L.Ratio).

Model	Parameter	AIC	X^2	Slope	P
Foraging	Full model	418.38			
	Term removed:				
	Dive duration	**427.24**	**10.86**	**0.217 ± 0.071**	**< 0.001**
	Bottom duration	**426.72**	**10.34**	**0.246 ± 0.080**	**< 0.001**
	Surface duration	416.90	0.51		0.47
	Descent rate ($n+1$)	**429.60**	**13.22**	**1.934 ± 0.544**	**< 0.001**
	Ascent rate	416.49	0.10		0.75
	Dive depth	417.18	0.79		0.37
	Individual			**−5.226 ± 0.991**	**< 0.001**
Prey encounter	Full model	444.99			
	Term removed:				
	Dive duration	443.01	0.02		0.90
	Bottom duration	**451.49**	**8.49**	**0.174 ± 0.061**	**< 0.01**
	Surface duration	**447.19**	**4.20**	**−0.092 ± 0.055**	**0.04**
	Descent rate ($n+1$)	**451.78**	**8.79**	**1.484 ± 0.502**	**< 0.01**
	Ascent rate	445.95	2.96		0.09
	Dive depth	**480.21**	**37.21**	**0.010 ± 0.002**	**< 0.0001**
	Bottom activity	443.01	0.02		0.90
	Individual			**−7.253 ± 1.153**	**< 0.0001**

The slopes values ± s.e.m. are given for significant terms (in bold). AIC: Akaike information criterium.

bottom durations were longer and descent rate higher during foraging dives than during non-foraging dives ($p < 0.001$ for all). The second model that compared 'p-e' and 'n-p-e' dives found that bottom duration, descent rate and dive depth significantly increased whilst surface duration significantly decreased ($p < 0.05$ for all). Wiggle activity, however, did not significantly vary between 'p-e' and 'n-p-e' dives ($p=0.9$).

Because data from seal T4 comprised 56% of all data, results observed were potentially driven by the behaviour of this animal. We re-ran both models without these data to determine if this was the case but the model output when the data from seal T4 was excluded was similar to that when it was included. Dive and bottom durations and descent rate were all significant parameters in the 'foraging' model without seal T4 (L.Ratio tests, $X^2=15.79$, 12.44 and 6.34; $p < 0.001$, $p < 0.001$ and $p=0.012$, respectively). Bottom duration, descent rate, ascent rate and dive depth were all significant parameters in the 'p-e' model without seal T4 (L.Ratio tests, $X^2=4.39$, 6.04, 4.59 and 4.56; $p=0.036$, 0.014, 0.032 and 0.0033, respectively). The only difference between models run with and without seal T4 was that surface duration was a non-significant parameter in the 'p-e' model (L.Ratio tests, $X^2=1.09$; $p=0.297$).

4. Discussion

This study is the first to present data obtained from accelerometer tags deployed on the head and neck of southern elephant seals. Whilst it is impossible to directly infer prey encounter and/or successful prey capture from these data, studying acceleration profiles has provided a better understanding of where and when these deep-divers may have encountered prey. Direct calibration would be necessary to fully identify successful individual prey capture, however the sampling rates used in this study (8 and 16 Hz) were sufficient to detect rapid head movements. Acceleration and depth profiles showed clear differences between propulsive activity (*i.e.* stroke and glide) and rapid head movements that could be associated with prey encounter events in the filtered signal at both frequencies. This is because acceleration of the head during a prey encounter event is likely to be far greater in amplitude and much shorter in duration than acceleration signals produced during continuous swimming (Skinner et al., 2009). We acknowledge, however, that other behaviour might also be associated with rapid head movements. One such behaviour could be predator detection and/or avoidance but for southern elephant seals this normally operates at greater time and space scales than the head movements reported here and is considered to be characterised by a V-shaped dive where seals swim deeper to avoid their predator (Hindell et al., 1991). In this study, the majority of rapid head movements occurred in U-shaped dives, at the bottom of the dive, which suggests that seals were not escaping from a predator. Moreover, probable prey capture attempts were detected in successive dives (> 92%) suggesting seals were feeding on patches of prey at a particular depth. This is consistent with numerous studies that use dive bouts to infer instances of a forager exploiting discrete prey patches (*e.g.* Boyd, 1996; Harcourt et al., 2002; Lea et al., 2002; Mori et al., 2002, 2005). Consequently, we are confident that the majority of the rapid head movements detected in the acceleration signals in this study are associated with prey encounter events.

4.1. Dive profile and prey encounter events

Dive profile analysis is a widespread approach for inferring behaviour associated with individual dives in pinnipeds (*e.g.* Hindell et al., 1991; Le Boeuf et al., 1988). However, the role of the different categories of dives remains poorly understood (Austin et al., 2006; Davis et al., 2003; Kuhn et al., 2009; Lesage et al., 1999; Mori et al., 2005), especially for southern elephant seals (Horsburgh et al., 2008). Dives with long bottom durations and/or with a significant wiggle activity are commonly considered to be associated with foraging, the undulations representing the search and pursuit of prey. Conversely, V-shaped dives are considered as travelling, predator avoidance or explorations of the water column (*e.g.* Dragon et al., 2012a; Hindell et al., 1991; Le Boeuf et al., 1992; Lesage et al., 1999; Schreer and Testa, 1996). In the present study there were only a few rapid head movements detected in V-shaped dives suggesting that seals did not encounter prey in these dives and thus confirming that dive shape alone

is a reliable indicator of seals' behaviour. During the descent period of one V-shaped dive recorded by seal T5, however, rapid head movements were detected across a 7 min period during which the seal descended from 400 m to 800 m at a mean vertical travel speed of 0.95 m s^{-1}. This is substantially slower than vertical velocities recorded previously in northern elephant seals (3 m s^{-1}; Le Boeuf et al., 1992) and the estimated maximum swimming speed for southern elephant seals (5.4–6.7 m s^{-1}; Laws, 1956). This is therefore unlikely to indicate predator avoidance as a seal attempting to evade danger would be expected to swim as quickly as possible and is more likely to suggest potential prey–predator interaction.

4.2. Foraging strategy

The diving parameters (*i.e.* dive duration, bottom duration, surface duration, dive depth) obtained for the translocated seals in this study were similar to those reported previously for southern elephant seals (Bailleul et al., 2007; Campagna et al., 2000; Dragon et al., 2012a; Hindell et al., 1991) which suggests that the data collected from translocated seals are representative of foraging behaviour in elephant seals. The acceleration analysis detected rapid head movements in half of the dives, with prey capture attempts occurring predominantly during the bottom phase of the dives. Prey encounter dives occurred in succession and seals generally swam downward during prey capture attempts suggesting they were following a patch of prey from above. Unfortunately, deployments were too short to test for diurnal variation in diving (Biuw et al., 2007, 2010; Slip et al., 1994), which may also account for the fact that 'p-e' dives were deeper than 'n-p-e' dives in this study. Contrary to bottom duration that did increase in 'p-e' dives, wiggle activity did not differ between 'p-e' and 'n-p-e' dives. This suggests that bottom duration was a more reliable indicator of prey encounter event compared to the distance and/or number of vertical excursions (*i.e.* wiggle activity) that seals performed at the bottom of a dive. Thus, wiggles performed at the bottom of a dive by southern elephant seals might be a searching technique to locate prey by scanning the water column contrary to other species where wiggles have been associated with the pursuit of prey (Hanuise et al., 2010; Simeone and Wilson, 2003; Takahashi et al., 2008).

Our statistical models showed that for all seals 'p-e' dives were characterised by longer bottom duration, higher transit rate and deeper dive depth than for 'n-p-e' dives, with one of the seals also shortening surface duration. In most species of pinnipeds and diving seabirds, dives with long bottom durations are thought to be associated with feeding (Schreer et al., 2001). The marginal value theorem proposed by Charnov (1976) does predict that an individual will stay longer in a more profitable patch, which has since been directly validated in both captive and wild studies involving pinnipeds species (Austin et al., 2006; Sparling et al., 2007). Seals can facilitate the relocation of a prey patch and reduce travel time by reducing surface duration and increasing descent rates. This allows seals to spend more time at depth where prey is more likely to be encountered, as predicted by optimal foraging theory (Mori and Boyd, 2004). Dragon et al. (2012a), however, found that bottom duration decreased in deep foraging dives (~650 m) performed by southern elephant seals, even in profitable patches, while seals that were diving to moderate depths (~350 m) were able to maximise their time spent foraging at the bottom of the dive. This suggests that deep divers may have to shorten bottom duration in profitable patches in deep dives because of the high energetic demand of this dive class. The translocated seals in this study, however, made fewer deep dives because they were limited by the bathymetry of the Kerguelen plateau where they were released and which represents the last section of their migration back to the colony. Further studies

deploying accelerometers for longer periods of time on southern elephant seals will allow a more detailed investigation of the differences in foraging strategies between shallow, moderate and deep dives.

Dive duration, however, did not significantly differ between feeding and non-feeding dives. This suggests that seals were modifying the shape of their dives and/or that they were increasing their transit rate in 'p-e' dives. Sato et al. (2004) found that macaroni penguins adopted shallow body angles after they had short or no bottom phase whilst they travel to the surface at steep body angle after encountering a good patch of prey. Shallow angles during descent and ascent might help predators to scan the water column to locate a new patch of prey (Wilson et al., 1996) and might also contribute towards increased horizontal distances travelled (Sato et al., 2004).

4.3. Accelerometry protocols and perspectives

Whilst further validation by video recording is required to identify precisely the actual function of rapid head movements for southern elephant seals, this pilot study provides valuable information for the development of future tags and sampling protocols. A key challenge is finding the right balance between increasing the tag's recording duration and detecting signal motions associated with foraging (Halsey et al., 2009). Kokubun et al. (2011) used small accelerometers and cameras to successfully associate penguin head movements with prey encounter. They found that improvements could be made to the recording duration, extending it by at least three times, by recording only one axis (*i.e.* surge) and reducing the sampling rate from 32 Hz to 16 Hz for accelerometers deployed on chinstrap and gentoo penguins. Similarly, the present study suggests that deploying accelerometers that record the surge and heave axes at 8 Hz is appropriate for the detections of rapid head movements that could be associated with prey encounter in southern elephant seals. Our study also suggests that the position of the tag, more than the sampling rate, may have affected the detection of movements associated with prey encounter. Seals' heads accelerate at a greater rate and amplitude than the rest of the body during prey capture attempts (Skinner et al., 2009) and higher sampling rates may be necessary to detect neck accelerations associated with head movements. The tag that recorded accelerations at 16 Hz was placed on the neck of seal T3, and this could explain the lower rate of feeding events found in this seal in spite of the higher sampling rate (39.4% compared with 46% and 52.1% for seals T4 and T5, respectively). Another challenge is selecting the appropriate filtering frequency and threshold amplitude as they may vary between individuals, prey species and/or foraging tactics. In the present study, the filters and thresholds were individually determined for each seal, and were similar among individuals. This was not unexpected as the three seals were all females, similar in size and were foraging in the same area over a short period of time. More deployments, over longer periods, on different genders and age classes are needed to test how constant the filtering frequency and threshold amplitude are between individuals of this species. This information could then be used to build a 'clever tag' that would filter and identify prey capture attempts in real time, reducing the amount of data so it could be sent directly via a Satellite Relay Data Logger (SRDL) avoiding the need to recover the tag.

Acknowledgments

References

Aguilar Soto, N., Johnson, M.P., Madsen, P.T., Diaz, F., Dominguez, I., Brito, A., Tyack, P.L., 2008. Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Island). J. Anim. Ecol. 77, 936–947.

Ancel, A., Horning, M., Kooyman, G.L., 1997. Prey ingestion revealed by oesophagus and stomach temperature recordings in cormorants. J. Exp. Biol. 200, 149–154.

Arranz, P., Aguilar de Soto, N., Madsen, P.T., Brito, A., Bordes, F., Johnson, M.P., 2011. Following a foraging fish-finder: diel habitat use of Blainville's beaked whales revealed by echolocation. PLoS One 6 (12), e28353.

Austin, D., Bowen, D.W., McMillan, J.I., Iverson, S.J., 2006. Linking movement, diving and habitat to foraging success in a large marine predator. Ecology 87 (12), 3095–3108.

Bailleul, F., Authier, M., Ducatez, S., Roquet, F., Charrassin, J.-B., Cherel, Y., Guinet, C, 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, 1–11.

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. J. Anim. Ecol. 77, 948–957.

Bailleul, F., Charrassin, J.-B., Ezraty, R., Girard-Ardhuin, F., McMahon, C., Field, I., Guinet, C., 2007. Southern elephant seals from Kerguelen Islands confronted by Antarctic sea ice. Changes in movements and in diving behaviour. Deep-Sea Res. II 54, 343–355.

Bates, D., 2007. lme4: Linear Mixed-effects Models Using S4 Classes. R package Version 0.99875-6. 〈http://CRAN.R-project.org/package.lme4〉.

Biuw, M., Nost, O.A., Stien, A., Zhou, Q., Lyderson, C., Kovacs, K.M., 2010. Effects of hydrographic variability on the spatial, seasonal and diel diving patterns of southern elephant seals in the Eastern Weddell sea. PLoS One 5 (11), e13816.

Biuw, M., Boehme, L., Guinet, C., Hindell, M., Costa, D., Charrassin, J.B., Roquet, F., Bailleul, F., Meredith, M., Thorpe, S., et al., 2007. Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. Proc. Natl. Acad. Sci. USA 104, 13705–13710.

Boyd, I.L., 1996. Temporal scales of foraging in a marine predator. Ecology 77, 426–434.

Campagna, C., Rivas, A.L., Marin, MR., 2000. Temperature and depth profiles recorded during dives of elephant seals reflect distinct ocean environments. J. Mar. Syst. 24, 299–312.

Charrassin, J.-B., Kato, A., Handrich, Y., Sato, K., Naito, Y., Ancel, A., Bost, C.-A., Gauthier-Clerc, A., Ropert-Coudert, Y., Le Maho, Y., 2001. Feeding behaviour of free-ranging penguins (Aptenodytes patagonicus) determined by oesophageal temperature. Proc. R. Soc. London B 268, 1–7.

Charnov, E.L., 1976. Optimal foraging: the marginal value theorem. Theor. Popul. Biol. 9, 129–136.

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. Mar. Ecol. Prog. Ser. 370, 239–247.

Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G., Butler, P.J., 2004. Biotelemetry: a mechanistic approach to ecology. Trends Ecol. Evol. 19, 334–343.

Davis, R.W., Fuiman, L.A., Williams, T.M., Horning, M., Hagey, W., 2003. Classification of Weddell seal dives based on 3-dimensional movements and video-recorded observations. Mar. Ecol. Prog. Ser. 264, 109–122.

Dragon, A.-C., Bar-Hen, A., Monestiez, P., Guinet, C., 2012a. Horizontal and vertical movements as predictors of foraging success in a marine predator. Mar. Ecol. Prog. Ser. 447, 243–257.

Dragon, A.-C., Bar-Hen, A., Monestiez, P., Guinet, C., 2012b. Comparative analysis of methods for inferring successful foraging areas from Argos and GPS tracking data. Mar. Ecol. Prog. Ser. 452, 253–267.

Field, I.C., Hindell, M.A., Slip, D.J., Michael, K.J., 2001. Foraging strategies of southern elephant seals (Mirounga leonina) in relation to frontal zones and water masses. Antarct. Sci. 13, 371–379.

Field, I.C., Bradshaw, C.J.A., McMahon, C.R., Harrington, J., Burton, H.R., 2002. Effects of age, size and condition of elephant seals (Mirounga leonina) on their intravenous anaesthesia with tiletamine and zolazepam. Vet. Rec. 151, 235–240.

Fish, F.E., 1994. Influence of hydrodynamic—design and propulsive mode on mammalian swimming energetics. Aust. J. Zool. 42, 79–101.

Fossette, S., Gaspar, P., Handrich, Y., Le Maho, Y., Georges, J.-Y., 2008. Dive and beak movement patterns in leatherback turtles Dermochelys coriacea during inter-nesting intervals in French Guiana. J. Anim. Ecol. 77, 236–246.

Fuiman, L.A., Davis, R.W., Williams, T.M., 2002. Behavior of midwater fishes under the Antarctic ice: observations by a predator. Mar. Biol. 140, 815–822.

Gallon, S., Georges, J.-Y., Sparling, C., Fedak, M., Biuw, M., Thompson, D., 2007. How fast does a seal swim? Variations in swimming behaviour under differing foraging conditions. J. Exp. Biol. 210 (18), 3285–3294.

Guinet, C., Cherel, Y., Ridoux, V., Jouventin, P., 1996. Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass. Antarct. Sci. 8, 23–30.

Halsey, L.G., Green, J.A., Wilson, R.P., Frappell, P.B., 2009. Accelerometry to estimate energy expenditure during activity: best practice with data loggers. Physiol. Biochem. Zool. 82, 396–404.

Hanuise, N., Bost, C.-A., Huin, W., Auber, A., Halsey, L.G., Handrich, Y., 2010. Measuring foraging activity in a deep-diving bird: comparing wiggles, oeso-phageal temperatures and beak-opening angles as proxy of feeding. J. Exp. Biol. 213, 3874–3880.

Harcourt, R., Bradshaw, C.J.A., Dickson, K., Davis, L.S., 2002. Foraging ecology of a generalist predator, the female New Zealand fur seal. Mar. Ecol. Prog. Ser. 227, 11–24.

Hindell, M.A., Bradshaw, C.J.A., Summer, M.D., Michael, K.J., Burton, H.R., 2003. Dispersal of female southern elephant seals and their prey consumption during the austral summer: relevance to management and oceanographic zones. J. Appl. Ecol. 40, 703–715.

Hindell, M.A., Slip, D.J., Burton, H.R., 1991. The diving behavior of adult male and female southern elephant seals, Mirounga leonina (Pinnipedia, Phocidae). Aust. J. Zool. 39, 595–619.

Hooker, S.K., Boyd, I.L., Jessopp, M., Cox, O., Blackwell, J., Boveng, P.L., Bengtson, J.L., 2002. Monitoring the prey-field of marine predators: combining digital imaging with datalogging tags. Mar. Mamm. Sci. 18, 680–697.

Horsburgh, J.M., Morrice, M., Lea, M.-A., Hindell, M.A., 2008. Determining feeding events and prey encounter rates in a southern elephant seal: a method using swim speed and stomach temperature. Mar. Mamm. Sci. 24 (1), 207–217.

Johnson, M.P., Madsen, P.T., Zimmer, W.M.X., Aguilar de Soto, N., Tyack, P.L., 2004. Beaked whales echolocate on prey. Biol. Lett. 271, 383–386.

Kokubun, N., Kim, J.H., Shin, H.C., Naito, Y., Takahashi, A., 2011. Penguin head movement detected using small accelerometers: a proxy of prey encounter rate. J. Exp. Biol. 214, 3760–3767.

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. J. Anim. Ecol. 78 (3), 513–523.

Laws, R.M., 1956. The elephant seal (Mirounga leonina Linn.). II. General, social and reproductive behaviour. Sci. Rep. Falkland Isl. Depend. Surv. 13, 1–88.

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

Le Boeuf, B.J., Naito, Y., Asaga, T., Crocker, D., Costa, D.P., 1992. Swim speed in a female northern elephant seal: metabolic and foraging implications. Can. J. Zool. 70, 768–795.

Le Boeuf, B.J., Costa, D.P., Huntley, A.C., Feldkamp, S.D., 1988. Continuous, deep diving in female northern elephant seals, Mirounga angustirostris. Can. J. Zool. 66, 446–458.

Lesage, V., Mammill, M.O., Kovacs, K.M., 1999. Functional classification of harbour seal (Phoca vitulina) dives using depth profiles, swimming velocity and an index of foraging success. Can. J. Zool. 77, 74–87.

Liebsch, N., Wilson, R.P., Bornemann, H., Adelung, D., Plotz, J., 2007. Mouthing off about fish capture: jaw movements in pinnipeds reveals the real secret of ingestion. Deep-Sea Res. II 54, 256–269.

Madsen, P.T., Johnson, M.P., Aguilar de Soto, N., Zimmer, W.M.X., Tyack, P.L., 2005. Biosonar performance of foraging beaked whales (Mesoplodon densirostris). J. Exp. Biol. 208, 181–194.

Marshall, G., Bakhtiari, M., Shepard, M., Tweedy, J., Rasch, D., Abernathy, K., Joliff, B., Carrier, J.C., Heithaus, M.R., 2007. An advanced solid-state animal-borne video and environmental data-logging device ("CRITTERCAM") for marine research. Mar. Technol. Soc. J. 41, 31–38.

McConnell, B.J., Chambers, C., Fedak, M.A., 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. Antarct. Sci. 4, 393–398.

McMahon, C.R., Burton, H., McLean, S., Slip, D., Bester, M., 2000. Field immobilisation of southern elephant seals with intravenous tiletamine and zolazepam. Vet. Rec. 146, 251–254.

Miller, P.J.O., Johnson, M.P., Tyack, P.L., Terray, E.A., 2004. Swimming gaits, passive drag and buoyancy of diving sperm whales Physeter macrocephalus. J. Exp. Biol. 207, 1953–1967.

Mori, Y., Watanabe, Y., Mitani, Y., Sato, K., Cameron, M.F., Naito, Y., 2005. A comparison of prey richness estimates for Weddell seals using diving profiles and image data. Mar. Ecol. Prog. Ser. 295, 257–263.

Mori, Y., Boyd, I.L., 2004. The behavioral basis for nonlinear functional responses and optimal foraging in Antarctic fur seals. Ecology 85, 398–410.

Mori, Y., Takahashi, A., Mehlum, F., Watanuki, Y., 2002. An application of optimal diving models to diving behaviour of Brünnich's guillemots. Anim. Behav. 64, 739–745.

Naito, Y., Bornemann, H., Takahashi, A., McIntyre, T., Plotz, J., 2010. Fine-scale feeding behaviour of Weddell seals revealed by mandible accelerometer. Polar Sci. 4, 309–316.

Naito, Y., 2007. How can we observe the underwater feeding behaviour of endotherms? Polar Sci. 1, 101–111.

Newland, C., Field, I.C., Cherel, Y., Guinet, C., Bradshaw, C.J.A., McMahon, C.R., Hindell, M., 2011. Diet of juvenile southern elephant seals reappraised by stable isotopes in whiskers. Mar. Ecol. Prog. Ser. 424, 247–258.

Robinson, P.W., Simmons, S.E., Crocker, D.E., Costa, D.P., 2010. Measurement of foraging success in a highly pelagic marine predator, the northern elephant seal. J. Anim. Ecol. 79, 1146–1156.

Ropert-Coudert, Y., Gremillet, D., Kato, A., Ryan, P.G., Naito, Y., Le Maho, Y., 2004. A fine-scale time budget of Cape gannets provides insights into the foraging strategies of coastal seabirds. Anim. Behav. 67, 985–992.

Ropert-Coudert, Y., Wilson, R.P., 2005. Trends and perspectives in animal-attached remote sensing. Front. Ecol. Environ. 3, 437–444.

Rutz, C., Hays, G.C., 2009. New frontiers in biologging science. Biol. Lett. 5, 289–292.

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. J. Exp. Biol. 211, 58–65.

Sato, K., Charrassin, J.-B., Bost, C-A., Naito, Y., 2004. Why do macaroni penguins choose shallow body angles that result in longer descent and ascent durations? J. Exp. Biol. 207, 4057–4065.

Sato, K., Mitani, Y., Cameron, M.F., Siniff, D.B., Naito, Y., 2003. Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. J. Exp. Biol. 206, 1461–1470.

Schreer, J.F., Kovacs, K.M., O'Hara Hines, R.J., 2001. Comparative diving patterns of pinnipeds and seabirds. Ecol. Monogr. 71, 137–162.

Schreer, J.F., Testa, J.W., 1996. Classification of Weddell seal diving behaviour. Mar. Mamm. Sci. 12, 227–250.

Simeone, A., Wilson, R.P., 2003. In-depth studies of magellanic penguin (*Spheniscus magellanicus*) foraging: can we estimate prey consumption by perturbation in the dive profile? Mar. Biol. 143, 825–831.

Skinner, J.P., Norberg, S.E., Andrews, R.D., 2009. Head striking during fish capture attempts by Steller sea lions and the potential for using head surge acceleration to predict feeding behaviour. Endangered Species Res. 10, 61–69.

Slip, D.J., Hindell, M.A., Burton, H.R., 1994. Diving behaviour of southern elephant seals from Macquarie Island: an overview. In: Le Boeuf, B.J., Laws, R.M. (Eds.), Elephant Seals—Population Ecology, Behaviour and Physiology. University of California Press, Berkeley, pp. 253–270.

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. Anim. Behav. 74, 207–218.

Suzuki, I., Naito, Y., Folklow, L.P., Miyasaki, N., Blix, A.S., 2009. Validation of a device for accurate timing of feeding events in marine animals. Polar Biol. 32, 667–671.

Takahashi, A., Kokuburn, N., Mori, Y., Shin, H.C., 2008. Krill-feeding behaviour of Gentoo penguins as shown by animal-borne camera loggers. Polar Biol. 31, 1291–1294.

Thums, M., Bradshaw, C.J.A., Hindell, M., 2011. In situ measures of foraging success and prey encounter reveal marine habitat-dependent search startegies. Ecology 92 (6), 1258–1270.

Viviant, M., Trites, A.W., Rosen, D.A.S., Monestiez, P., Guinet, C., 2010. Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. Polar Biol. 33, 713–719.

Watanabe, Y., Baranov, E.A., Sato, K., Naito, Y., Miyazaki, N., 2006. Body density affects stroke patterns in Baikal seals. J. Exp. Biol. 209, 3269–3280.

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. Mar. Ecol. Prog. Ser. 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 localisation in free-living animals using penguins as a model. Mar. Biol. 140, 17–27.

Wilson, R.P., Culik, B.M., Peters, G., Bannasch, R., 1996. Diving behaviour of Gentoo penguins, *Pygoscelis papua*; factors keeping dive profiles in shape. Mar. Biol. 126, 153–162.

Wilson, R.P., Cooper, J., Plotz, J., 1992. Can we determine when marine endotherm feed? A case study with seabirds. J. Exp. Biol. 167, 267–275.

Williams, T.M., Kooyman, G.L., 1985. Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. Physiol. Zool. 58, 576–589.