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

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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 ± 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 (Otomycteris 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 (Kooymann 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, Hibi & 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.
ever, all female Antarctic fur seals breeding at Pointe Suzanne, diving behaviour, we did not include the spatial component. How-
females were equipped simultaneously with head-mounted fur just under the glued logger after a single foraging trip. Not all

gers and sampled at 1 Hz. Devices were recovered by cutting the

of 16 Hz. Depth sensors ([\textit{Gymnoscopelus} sp. and \textit{Electrona subsaspera} representing 60\% and 20\% of the diet, respec-
tively (Cherel, Guinet & Tremblay 1997; Lea et al. 2002b). These
prey species are only accessible to diving fur seals at night when

acceleration changes (Suzuki 2002). The accelerometers attached to the fur under the ani-
field that were recorded by the main recording unit connected to

with accelerometers and four with Hall sensor units mounted on

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 Infor-
mation). Mouth-openings induce variations in the electromagnetic
reading when seals are at the surface which was cor-
rected according to the interide 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 off-
set corrected to 0 ± 0.2 (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 for-
aging time adjustments at bottom appear meaningful only for
dives deeper than 15 m. For each dive deeper than 15 m, the fol-

owing 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 ascent 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 des-
cent 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

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 (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 cus-
tom-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 cor-
rected according to the interide and interdiving bout surface
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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.

**AEROCIC 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 56.2 ± 0.85 m, with an increase in post-dive intervals past this threshold (slope estimate ± SE for dives less than and >56 m are 1.43 ± 0.03 and 1.26 ± 0.02, respectively; P < 0.0001; 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 ± 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 2.5 ± 0.5 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: 9.0 ± 2.3 days, n = 13, non-equipped: 8.3 ± 3.3 days, n = 22, t-test = 0.72, P = 0.48) 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 97.4 ± 41.5 s and 50.4 ± 22.4 m, respectively. Bottom duration and diving efficiency were 42.9 ± 30 s and 0.3 ± 0.16, 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...
We detected 196 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).

**MOUTH-OPENING EVENTS**

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

![Graph](image_url)
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; ADL Cost, 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 intersite 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.

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Data accessibility

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

References


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.