



Predicting prey capture rates of southern elephant seals from track and dive parameters

Jade Vacquié-Garcia^{*,1}, Christophe Guinet¹, Anne-Cécile Dragon²,
Morgane Viviant¹, Nory El Ksabi¹, Frédéric Bailleul¹

¹Centre d'Etudes Biologiques de Chizé (CEBC), CNRS UPR 1934, 79360 Villiers-en-bois, France

²Collecte Localisation Satellites (CLS Argos), 8–10 rue Hermès, 31520 Ramonville-Saint-Agne, France

ABSTRACT: In the marine environment, track and dive parameter data (obtained using Argos or GPS tags and time–depth recorders) are commonly used to provide proxies for foraging behaviour of marine predators. However, their accuracy is rarely assessed. Recently, the addition of head-mounted accelerometers has allowed for detection of prey capture attempts (PCAs) at sea, allowing for more accurate estimations of foraging behaviour. Despite increased numbers of such devices being deployed, their use is still marginal compared with other tools which measure track and dive parameters. The objectives of our study were (1) to identify the most relevant combination of tracking and diving metrics in predicting the frequency of PCAs in female southern elephant seals *Mirounga leonina* from the Kerguelen Islands, and (2) to apply it to a broader range of individuals for which only tracking and diving data were available. The results of our models were consistent with the optimal foraging theory as well as the optimal diving theory. The model with the best predictive performance was the one that combined both tracking and diving information. However, most of the variability in the number of PCAs could be solely explained by changes in the diving behaviour of seals. Finally, we used the best predictive model on 20 individuals, which had not been fitted with accelerometers, to determine their main foraging zones. The behavioural indicators established in this study constitute a useful ecological tool for population monitoring and conservation purposes.

KEY WORDS: Biologging · Dive parameters · Foraging · Prey capture events · Marine predator · Southern elephant seals · Track parameters

INTRODUCTION

Observations of the spatio–temporal variations in foraging effort or success of marine predators, particularly in those foraging at depth, are almost impossible. Over the last 3 decades, inferring such information from behavioural data, provided by a broad range of loggers deployed on seabirds, mammals and fish, has been one of the main objectives in biologging science. Hence, most variations in foraging behaviour of diving marine predators have been inferred from surface tracking and/or diving records (e.g. Bailleul et al. 2007b, 2008, Jonsen et al. 2007).

In prey-aggregated environments such as the open ocean, predators usually use an area-restricted search (ARS) behaviour when encountering prey, reducing swimming speed and increasing sinuosity (Charnov 1976, Benhamou & Bovet 1989). Thus, analyses of surface tracks, based on different methodologies—such as time spent in a given location (Bost et al. 1997), first passage time (FPT, Fauchald & Tveraa 2003), or process-based models such as Hidden Markov Models (HMMs, Morales et al. 2004, Jonsen et al. 2007)—usually provide spatio-temporal information on the foraging zones. However, the sole assessment of foraging habitats from surface records is not always relevant, especially for

*Corresponding author: jadevacquiegarcia@gmail.com

diving predators (Weimerskirch et al. 2007, Bailleul et al. 2008, Bastille-Rousseau et al. 2010). Additional information such as diving behaviour is often required to investigate foraging behaviour of such predators.

At depth, diving predators are generally assumed to reduce time spent descending or ascending, while spending more time at the bottom of their dive and increasing 'wiggles' when prey are encountered (Mori 1998). Thus, dive analyses and classifications (e.g. Fedak et al. 2001, Thums et al. 2008) based on their time-depth profiles or the calculation of different metrics (such as dive duration, bottom duration, wiggles, descent and ascent rate) (e.g. Croxall et al. 1985, Fedak et al. 2001, Thums et al. 2008) or first bottom time (Bailleul et al. 2008) have been sometimes used to discriminate between foraging, transiting or resting behaviours. But again, although being pertinent at large spatial scales, the methods derived from diving behaviour records can be inaccurate or misleading regarding the real identification of foraging events.

Therefore, although both tracking and diving data are undeniably useful for identifying foraging behaviour (Dragon et al. 2012) and produce comparable results, they cannot identify 'real' foraging success. Moreover, these proxies generally only provide qualitative information on the foraging activity (i.e. binary information: foraging vs. non-foraging). Despite the fact that the large community of marine ecologists recognizes these points, no study has evaluated the relative contribution of these 2 components (i.e. tracking vs. diving records) in predicting the variations in foraging success.

The recent development of other technologies, particularly oesophageal and stomach temperature sensors (Wilson et al. 1992), Hall sensors or accelerometers (Wilson et al. 2002, Suzuki et al. 2009, Viviant et al. 2010, Guinet et al. 2014), as well as video cameras (Bowen et al. 2002, Davis et al. 2003), is leading to a new stage in the understanding of successful foraging behaviour of marine predators. Indeed, these loggers are focused on measuring prey capture attempts (PCAs), which is currently considered as the best proxy for foraging success (see Guinet et al. 2014 where prey encounter events [PEE] correspond to PCA). However, the aforementioned devices may also have some restrictions. They cannot be used to distinguish between real prey captures and missed attempts, are generally deployed on a limited number of individuals in the field due to high costs, and the large amounts of data may be difficult to record due to limitations in memory as well as battery life.

Nevertheless, they provide the possibility to investigate how variations in movement and diving behaviour can be used to predict variations in foraging behaviour of a diving marine predator.

In this context, we used head-mounted accelerometers on female elephant seals from the Kerguelen Islands in addition to tracking and diving recorders to develop a model to predict variations in the number of PCAs performed by female seals in the open ocean (>1000 m depth), using track and dive metrics. Then, to illustrate the model, we applied the best predictive model to a broader range of individuals for which only tracking and diving data were available in order to define the main foraging zones of female elephant seals from the Kerguelen Islands. To be able to evaluate the effect of the time scale considered in predictions and applications, we chose to carry out this work on 2 scales, namely the dive scale and the 24 h scale. Kerguelen elephant seals were chosen as study models due to their incredible capacity to dive deeply and almost continuously during their long foraging trips through the Southern Ocean (McConnellet al. 1992). They were also chosen due to the large number of studies carried out on them on the Kerguelen Islands during the last 10 yr, leading to a large dataset on tracking and diving behaviour for this species.

MATERIALS AND METHODS

Deployment of devices and data collection

Thirty-two post-breeding female elephant seals were captured at the Kerguelen Islands (49° 20' S, 70° 20' E) between 2008 and 2012. Individuals were anaesthetised using a 1:1 combination of tiletamine and zolazepam (Zoletil 100), which was injected intravenously (McMahon et al. 2000). Individuals were then equipped with 1 of 4 instrument combinations (Table 1). Seven seals were solely equipped with a SPLASH-10 logger (Wildlife Computers). In these tags, dive depth is collected and archived every second, while locations are estimated by the orbiting Argos satellites and then transmitted to the user. In addition, a GPS onboard system integrated into these tags allows collecting and archiving of animal locations. Thirteen other individuals were equipped with a conductivity-temperature-depth-satellite-related data logger (CTD-SRDL, Sea Mammal Research Unit, University of St Andrews), and an additional time-depth recorder (TDR-MK9, Wildlife Computers). As with the Splash-10 logger, locations are estimated by

Table 1. Combinations of electronic devices deployment on 32 elephant seals. CTD-SRDL: conductivity-temperature-depth-satellite relayed data logger; SPLASH-10: SPLASH-10 tags; TDR-MK9: time–depth recorder; TDR-MK10-X: time–depth recorder combined with an accelerometer

Seal ID	CTD-SRDL	SPLASH-10	TDR-MK9	TDR-MK10-X
2008-8		X		
2009-1	X		X	
2009-10		X		
2009-11		X		
2009-2	X		X	
2009-3	X		X	
2009-4	X		X	
2009-5		X		
2009-6		X		
2009-8	X		X	
2009-9		X		
2010-11	X		X	
2010-13	X		X	
2010-15	X		X	
2010-20		X		
2010-8	X		X	
2010-9	X		X	
2011-13	X		X	
2011-15	X		X	
2011-19	X		X	
2010-18		X		X
2010-19		X		X
2010-21		X		X
2011-14	X			X
2011-16		X		X
2011-17	X			X
2011-18		X		X
2011-21		X		X
2011-22	X			X
2011-26		X		X
2011-27		X		X
2011-28		X		X

the orbiting Argos satellites, and the dive depth is recorded and archived every second in TDR-MK9 tags. Finally, 9 females were equipped with a combination of a SPLASH-10 and a TDR-accelerometer (TDR-MK10-X, Wildlife computers), while 3 individuals were equipped with CTD-SRDLs and TDR-accelerometers. TDR-accelerometers sampled 16 accelerations per second (16 Hz) on 3 axes: longitudinal (surge), vertical (heave) and lateral (roll). The acceleration measured simultaneously on these 3 axes was used to detect prey capture attempts.

Data loggers were glued on the heads of the seals using quick-setting epoxy (Araldite AW 2101, Ciba), after cleaning the fur with acetone. Upon returning from their post-breeding foraging trip after 65 to 80 d, females were located on land via the Argos data, recaptured, and the electronic devices recovered.

Data processing

Tracking and diving data

The time–depth records (SPLASH10, TDR-MK9 or TDR-MK10-X) of the 32 seals were analysed using a custom-written MATLAB code (Matlab v.7.0.1, code available on request) in order to calculate dive metrics to be included into models. A dive was considered as an excursion performed in the open ocean (>1000 m depth) which was deeper than 15 m (Guinet et al. 2014). Then, each of the detected dives was divided into 3 distinct phases based on a cubic polynomial function fitted on their time–depth records. The descent and ascent phases were defined as the time periods when the absolute vertical speed ($\delta z/\delta t$) (obtained every second, calculated from the ratio between the depth [z] difference and the time [t] difference and from the polynomial fit of the dive) exceeded 0.75 m s^{-1} . The bottom phase was defined as the period between the descent and the ascent phases. Eight different dive metrics were then calculated: maximum depth (m), bottom duration (s), post-dive surface duration (s), vertical sinuosity in the bottom phase (no unit), ascent rate (m s^{-1}), descent rate (m s^{-1}) (see Dragon et al. 2012 for details), bottom slope (m s^{-1}), which corresponds to the slope of the bottom phase (i.e. the absolute slope coefficient of the linear regression fitted on the time–depth values in this phase) and depth variability in the bottom phase (m), which is the standard error of the depth values during the bottom phase (Table 2).

Track metrics were also calculated using a custom-written MATLAB code (Matlabv.7.0.1, code available on request) after locations were filtered by manually removing aberrant locations and then by using a switching-state-space model (Jonsen et al. 2007, Dragon et al. 2012). Spatial coordinates (Lon-Lat) were allocated to each dive by linear interpolation between ‘true’ locations provided by the Argos or GPS tags. Two different track metrics were then calculated from dive location: horizontal swimming speed (m s^{-1}) (i.e. ratio of distance to time between 2 successive dives) and turning angles (degrees) (Table 2). Finally, solar elevation (degrees), determined using the ‘suncycle’ function in MATLAB, was calculated as an external metric to each dive based on their location and the time they occurred. This solar elevation provides an indication of the day period (i.e. dawn, day, dusk or night) (Table 2).

At the 24 h scale, all dive and track metrics were either averaged (horizontal swimming speed, turning angles, vertical sinuosity, ascent rate, descent rate,

Table 2. Description of the calculation of track, dive and external metrics at the dive and 24 h scales

Metrics	Description at the dive scale	Unit	Description at the 24 h scale
Dive metrics			
Maximum depth	Maximum depth of the dive	m	Summed over 24 h
Bottom duration	Duration of the bottom phase of the dive	s	Summed
Post-dive surface duration	Duration of the following surface phase of the dive	s	Summed
Vertical sinuosity during bottom phase	Ratio between the total distance swum at the bottom and the sum of the Euclidian distances from the depth at the beginning of the bottom phase to the max. depth and from the max. depth to the depth at the end of the bottom phase	no unit	Averaged over 24 h
Ascent rate	$ \Delta z/\Delta t $ during the ascent phase of the dive (z : depth, t : time)	m s^{-1}	Averaged
Descent rate	$ \Delta z/\Delta t $ during the descent phase of the dive (z : depth, t : time)	m s^{-1}	Averaged
Bottom slope	Absolute slope coefficient of the linear regression fitted to the time–depth values during bottom phase	m s^{-1}	Averaged
Depth variability during bottom phase	Standard error of the depth values during bottom phase	m	Averaged
Track metrics			
Horizontal swimming speed	Speed between the previous and the current dives	m s^{-1}	Averaged
Turning angle	Turning angle between the previous, the current and the following dives	degrees	Averaged
External metrics			
Solar elevation	Angle of the sun with the skyline	degrees	–
Number of dives	–	No unit	Summed

bottom slope, variability in the bottom) or summed (maximum depth, bottom duration, post-dive surface duration), with the exception of solar elevation. The total number of dives over 24 h was also calculated as an additional metric (Table 2).

Acceleration data

Acceleration data from the 12 individuals equipped with a TDR-MK10-X tag were processed following Viviant et al. (2010) and Gallon et al. (2012) (custom-written MATLAB code, available on request). The procedure is described in detail in Guinet et al. (2014). Regardless of the axis, the recorded acceleration is composed of 2 types of acceleration: static and dynamic. The static acceleration is caused by the position of the gravity center of the animal compared with the gravity vector. The static acceleration corresponds to the low-frequency signals whereas dynamic acceleration is the acceleration generated by short movements of the body and/or the head of the animal. This acceleration is represented in the acceleration signal as high-frequency signals. Specifically, the acceleration records were processed firstly by filtering them on the 3 axes to remove 'noise' in the signal induced by swimming movement (static acceleration). Then, for each axis, significant peaks in acceleration were detected when standard deviation of acceleration values

within a 5 s moving window surpassed a threshold. Such a threshold was determined for each axis using the function 'k-means' (tool box statistics, Matlab). Only significant peaks simultaneously detected on the 3 axes were considered as a PCA. A total number of PCAs was calculated per dive and over 24 h.

Data analyses and modelling process

General approach

To develop a general model, at each scale, for predicting the variations in the number of PCAs of female seals using track and dive metrics, we first investigated, using the individuals equipped with accelerometers ($n = 12$), how accurately the number of PCAs can be assessed by the combined use of track and dive data (explanatory models) (Fig. 1). Then, to identify the relative contribution of changes in track and dive behaviour to predict the variations in foraging performance, we tested and compared, on the same individuals, different models with either tracking data or diving data, and then the 2 metrics combined (predictive models). We did this at the 2 scales and then selected the best models to predict the number of PCAs per dive and per 24 h period (Fig. 1). Then, to illustrate the models, we applied the best predictive models to the broader range of individuals for which only track-

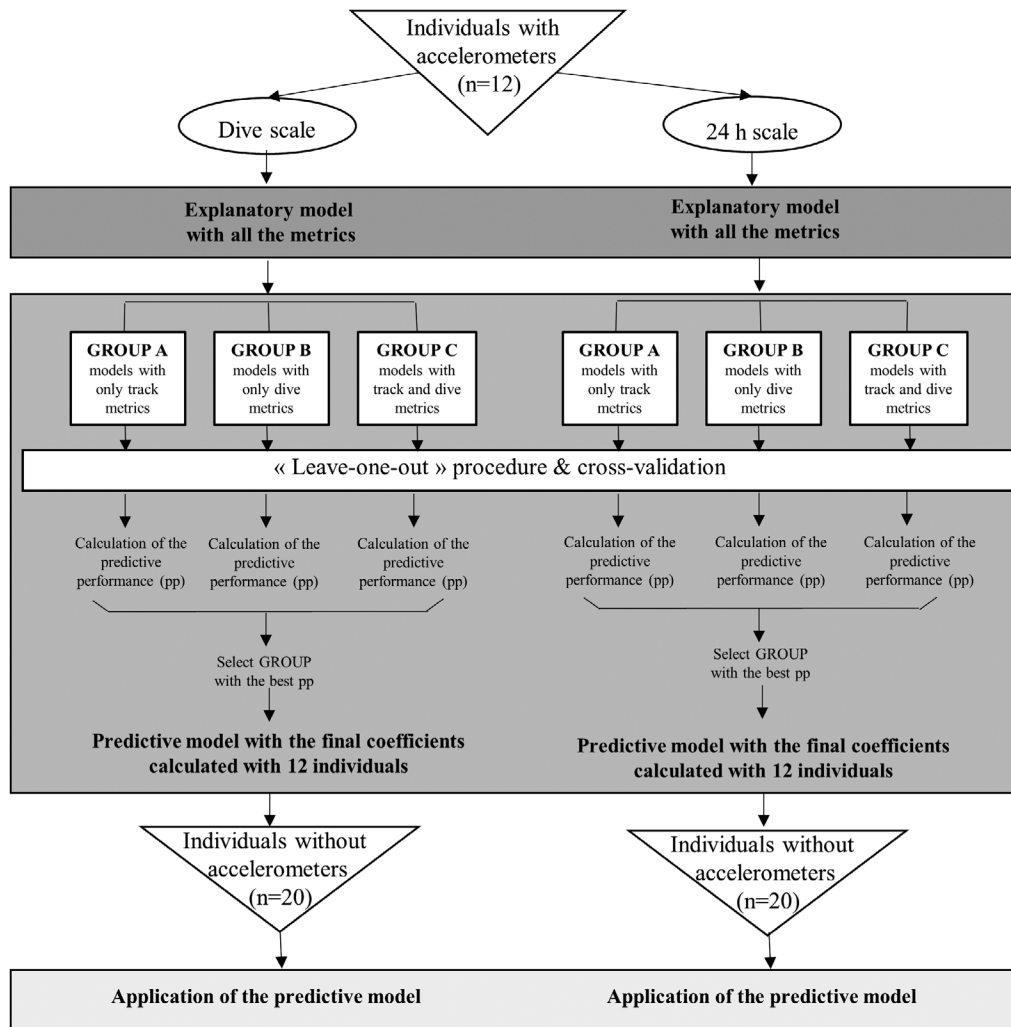


Fig. 1. Modelling process: creation of explanatory and predictive models at the dive and 24 h scale and their application

ing and diving data were available ($n = 20$) in order to define the main foraging zones of the elephant seals from the Kerguelen Islands (Fig. 1).

Relationship between PCAs and other foraging metrics (explanatory models)

The relationship between the number of PCAs and track, dive and external metrics were investigated per dive and over 24 h on all the individuals equipped with an accelerometer ($n = 12$) using generalized linear mixed models (GLMM) (package 'lme4' in R 2.10.1; R Development Core Team 2010). Metrics were first standardized (Zuuret et al. 2007) after verifying that no correlation values between metrics exceeded a value of 0.8. Models were fitted with a Poisson family distribution with individuals included

as random intercepts to avoid the effects of the hierarchical structure of the data. All the combinations of metrics were tested and the models, at each scale, were ranked according to the corrected Akaike's information criterion, AICc (Burnham & Anderson 2004); all models are listed in the Supplement at www.int-res.com/articles/suppl/m541p265_supp.xls. The AICc weight of each model was calculated to represent the relative likelihood of the candidate models. The candidate models selected were those for which the cumulative sum of the AICc weight was greater than 0.95. If the analyses indicated more than 1 candidate model, a model-averaging procedure was conducted. This procedure takes into account all of the coefficients obtained by the selected models at each scale and calculates averaged coefficients in function of the AICc weight of each model (Burnham & Anderson 2002).

Predicting PCAs from other foraging metrics (predictive models)

In order to identify the most relevant metrics to predict the number of PCAs per dive or over 24 h, we considered 3 different groups of models—Group A: track and external metrics selected in explanatory models; Group B: dive and external metrics selected in explanatory models; Group C: all the metrics selected in explanatory models.

Using the modelling process previously described, for each group of the per dive and over 24 h scales, we tested all the possible combinations of metrics on all of the individuals equipped with accelerometers ($n = 12$) minus one individual ('leave-one-out' procedure). Models were then selected according to their AICc weight as previously described. If the analyses indicated more than 1 candidate model, a model-averaging procedure was conducted to obtain averaged coefficients. The coefficients obtained for each group of the per dive and over 24 h scales were applied to the remaining individual to compare observed and predicted number of PCAs. The procedure was repeated in such a way that all the individuals were left out once (cross-validation). The predictive performance (pp) of the 6 groups (3 groups per scale) was assessed, using the following equation to compare all the observed and predicted number of PCA obtained for each individual left out:

$$pp = 1 - \frac{(\loglik(m) - \loglik(c))}{(\loglik(mn) - \loglik(c))} \quad (1)$$

where m represents the tested group, mn corresponds to null models and c to perfect models where the predicted number of PCAs of all the individuals left out are equal to the observed number of PCAs. 'Loglik' means log of likelihood. The closer to 1 the result is, the higher is the predictive performance of the group.

Model groups with the best predictive performance were selected at the dive and 24 h scales. Then they were fitted, with a model-averaging procedure, to the 12 individuals with accelerometers to obtain final coefficients required for a future application.

Application

The final coefficients were applied to all individuals that had not been equipped with an accelerometer ($n = 20$) to predict the number of PCAs per dive

Table 3. Coefficients of the explanatory models developed at the dive and 24 h scales. Variables in **bold** correspond to the variables which most affected the number of PCAs. Explanatory variables are raw values at the dive scale and summed or averaged at the 24 h scale. na: not applicable

	Dive scale		24 h scale	
	Estimate	SE	Estimate	SE
Intercept	1.57	0.240	5.95	0.0084
Horizontal swimming speed	-0.081	0.003	-0.179	0.006
Turning angle	0.035	0.002	0.080	0.004
Maximum depth	-0.113	0.004	0.452	0.012
Bottom duration	0.028	0.003	0.495	0.010
Post-dive surface duration	-0.126	0.004	0.406	0.038
Descent rate	0.180	0.003	-0.068	0.006
Ascent rate	0.220	0.003	0.034	0.008
Vertical bottom sinuosity	0.083	0.002	0.202	0.004
Trend in the bottom	-0.003	0.003	7.59×10^{-5}	0.001
Variability in the bottom	-0.052	0.003	9.11×10^{-6}	0.001
Solar elevation	0.029	0.003	na	na
Number of dives	na	na	0.099	0.006

or over 24 h for female elephant seals from the Kerguelen Islands. To obtain a PCA rate (i.e. the number of PCAs per unit of time), this number was corrected by the dive duration or the summed dive duration at the dive or 24 h scale, respectively.

RESULTS

General results

The 12 female elephant seals equipped with accelerometers spent (mean \pm SD) 71 ± 23 d at sea. However, 6 devices failed after 10 ± 4 d. A total of 27 877 dives (data collected by the 6 devices that prematurely failed included) were analysed. Of this total, 23 597 (85%) contained at least 1 PCA. The mean number of PCAs per dive was 8 ± 7 (range 0 to 55). For all individuals, a total of 442 d were analysed. The cumulative number of PCAs over 24 h was 500 ± 259 (range 0 to 1771). Female elephant seals performed 63 ± 13 dives over 24 h.

Relationship between PCAs and other foraging metrics (explanatory models)

At both time scales, a model-averaging procedure was conducted. All metrics tested were found to correlate with the number of PCAs and defined as candidates for the predictive models (Table 3).

At the dive scale, the relationship was positive for the following metrics in order of importance: ascent

Table 4. Predictive performances (see Eq. 1) of the 3 groups of models at each scale. Group A: models composed using track and external metrics; Group B models composed using dive and external metrics; Group C models composed using all the metrics combined. The predictive performances of the best groups at each scale are in **bold**

	Group A	Group B	Group C
Dive scale	0.018	0.215	0.217
24 h scale	0.194	0.751	0.764

rate, descent rate, vertical sinuosity during the bottom phase, turning angles, solar elevation and bottom duration. The relationship was negative, in order of importance, for post-dive surface duration, maximum depth, horizontal swimming speed, depth variability at the bottom and bottom slope.

At the 24 h scale, the relationship was positive for the following metrics in order of importance: bottom duration, maximum depth, post-dive surface duration, vertical sinuosity during the bottom phase, the total

number of dives, turning angles, ascent rate, depth variability in the bottom phase and bottom slope. The relationship was negative, in order of importance, for horizontal swimming speed and descent rate.

Predicting PCAs from other foraging metrics (predictive models)

The predictive performances of the groups (A, B and C) are summarised in Table 4 and detailed in Fig. 2 for both scales. In each case, the group of models that included all metrics (i.e. Group C) had the best predictive performance. Dive metrics contributed more to predictive performance than track metrics.

Application

Measured and predicted foraging zones of southern elephant seals are shown in Fig. 3. Fig. 3A,C show the measured rate of PCAs and tracks of the

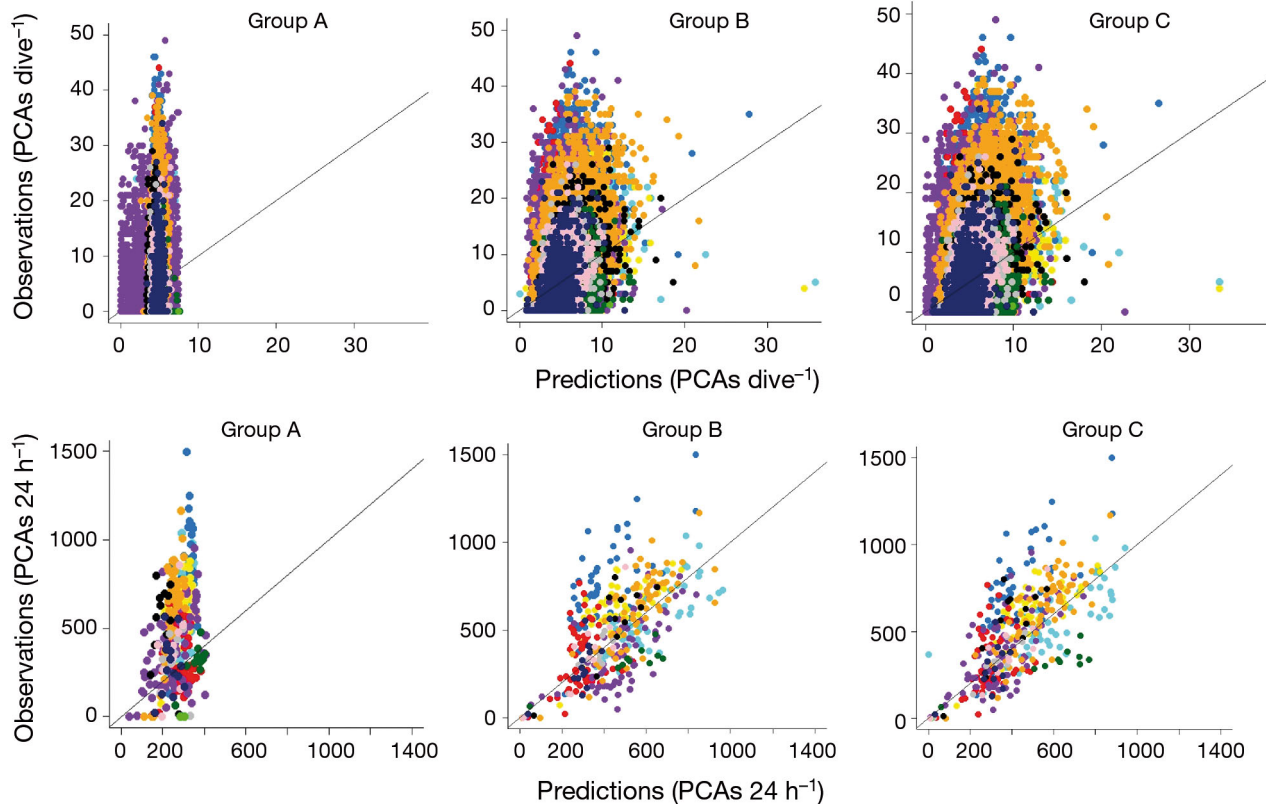


Fig. 2. Observed number of prey catch attempts (PCAs) versus the predicted number of PCAs at both time scales female southern elephant seals, obtained from the 12 individuals equipped with accelerometers and using the 'leave-one-out' procedure. At the dive scale, each dot represents a dive. At the 24 h scale, each dot corresponds to a 24 h period. Each colour corresponds to a different individual. Group A: models composed using track and external metrics; Group B models composed using dive and external metrics; Group C models composed using all the metrics combined

individuals equipped with accelerometers ($n = 12$). Final coefficients obtained from the predictive models at both scales were then applied to the individuals that had not been equipped with accelerometers ($n = 20$), to predict the number of PCAs that occurred along their tracks. Fig. 3B,D show the rate of predicted PCAs and tracks of these individuals. These individuals spent on average (\pm SD) 74.8 ± 15.3 d at sea and performed 64 ± 14 dives per 24 h. A total of 99 228 dives of the 20 seals with accelerometers were analysed. The mean predicted number of PCAs per dive was 5 ± 11 (range 0 to 50 with 12 extreme values). For all individuals, a total of 1476 periods of 24 h were identified and analysed. The cumulative predicted number of PCAs over 24 h was 446 ± 576

(range 6 to 4735). One 24 h period of a single track with over 20000 predicted PCAs was removed from the analysis.

DISCUSSION

In agreement with previous studies, we found that track information such as travelling speed and track sinuosity provide insight into variation of prey capture attempts rate (Knoppien & Reddingius 1985, Kareiva & Odell 1987, Benhamou & Bovet 1989, Fauchald & Tveraa 2003). However, the main finding of our study was that, in female southern elephant seals, most of the variability in prey capture attempts

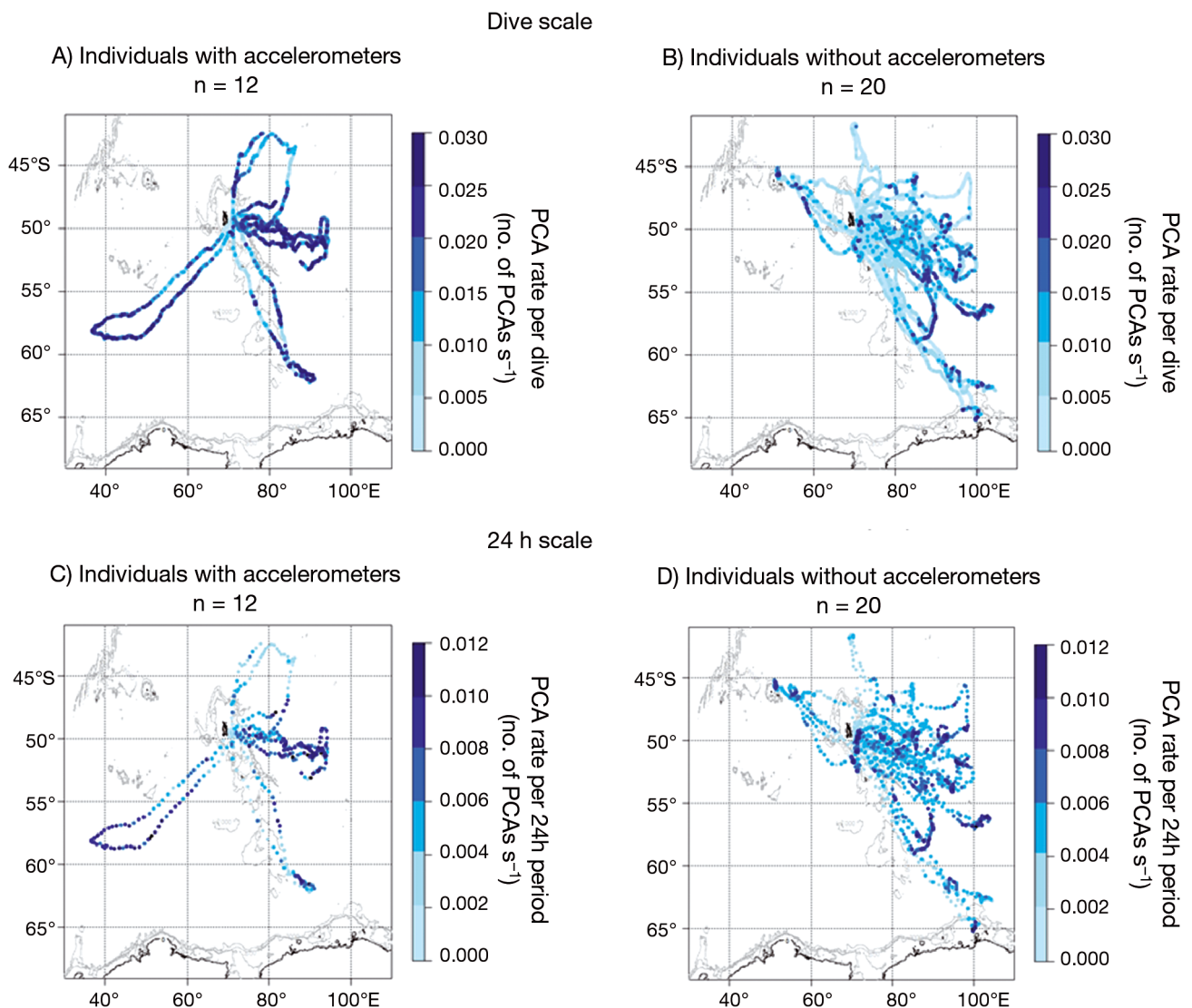


Fig. 3. Foraging behaviour (prey capture attempt [PCA] rate) of southern elephant seals. Each dot corresponds to (A,B) a dive or (C,D) a 24 h period. (A,C) Foraging behaviour measured on the 12 individuals with accelerometers. (B,D) Predicted foraging behaviour (estimated for the 20 individuals that had not been equipped with accelerometers) using Group C models

rate is best explained by changes in diving behaviour. As a consequence, the predictive models of PCA containing diving information (derived from Group B) were nearly as powerful as those combining both tracking and diving data (derived from Group C) while predictive performances of models built using only tracking data (derived from Group A) were comparatively poor. Predictive models built from diving data had a predictive value nearly 4 times as high as those based on tracking data alone.

Relationship between PCAs and other foraging metrics (explanatory models)

The number of PCAs was found to be related to all track and dive metrics tested, at both scales. These findings are consistent with previous studies on elephant seals, which suggested that changes in movement (sinuosity and horizontal speed) and diving behaviour could be related to a change in body condition (Thums et al. 2011, Dragon et al. 2012), and therefore potential food intake.

Elephant seals were found to reduce their traveling speed and increase their track sinuosity when encountering more prey items at the 2 time-scales. This result is in accordance with the predictions stating that, in a prey-aggregated environment such as the open ocean, a predator should intensify its foraging activity in a productive patch (Kareiva & Odell 1987), decreasing horizontal speed and increasing horizontal sinuosity (Benhamou & Bovet 1989).

At the dive scale, the number of PCAs increased when seals increased their bottom time, which is in accordance with the Optimal Diving Theory (Gentry & Kooyman 1986, Houston & Carbone 1992, Thompson et al. 1993, Carbone & Houston 1996) and consistent with the fact that diving predators mainly forage during the bottom phase of a dive (Wilson et al. 2002, Fossette et al. 2008, Guinet et al. 2014). The number of PCAs also increased when seals increased their bottom vertical sinuosity. This last finding reveals that when encountering prey during the bottom phase of pelagic dives, elephant seals do not swim at a constant depth, but continuously zig-zag up and down, suggesting that they are actively foraging within the patch of prey (Thompson et al. 1993). Elephant seals were also more successful when remaining at the same general depth and exhibiting lower depth variability during the bottom phase of their dive. This relationship, obtained at the dive scale, suggests that seals are more successful when encountering prey structured in a discrete patch over a narrow

depth thickness. These discrete patches could be related to changes in oceanographic conditions down the water column, creating marked prey habitat boundaries, as discussed in McIntyre et al. (2014). Many fish species, including myctophids (which are a major prey item for elephant seals (Slip 1995, Daneri & Carlini 2002, Cherel et al. 2008) are particularly sensitive to temperature regimes and are limited to a surprisingly narrow thermal niche (Beitinger & Fitzpatrick 1979, Hulley 1990).

The number of PCAs decreased with increasing diving depth at the dive scale. This result suggests that prey density decreases with increasing depth, consistent with a decrease in biomass with depth (Williams & Koslow 1997). A decrease in bioluminescence events (considered as an indicator of prey) with increasing depth (Vacquié-Garcia et al. 2012) also supports this theory. Given the results of our model, shallow dives lead more often to several PCAs. In contrast, deep dives may lead to a low number of PCAs. It is possible that the nutritional value of prey captured at depth may be significantly higher than that of prey captured in shallow areas (Thumset al. 2011).

Both descent and ascent rates were found to increase in dives where we detected PCAs. These results suggest that seals adjust their transit rates (by modifying their dive pitch [diving at steeper angle] and/or their swimming activity) according to their foraging success: they rise to the surface and anticipate their future foraging success by increasing their descent rate in order to return rapidly to the prey patch, as found in other species such as the fur seal *Arctocephalus gazella* (Viviant et al. 2014).

Surface duration following a dive was negatively related to increasing numbers of PCAs. This finding is counter-intuitive as seals foraging successfully during a dive exhibit a higher swimming effort (J. Joffrey pers. comm.) and should, therefore, spend more time at the surface to recover. Our results suggest that after a successful dive, seals tend to decrease their surface time to return to depth more rapidly and maximize foraging opportunities. This type of finding is consistent with those reported for king penguins (Hanuise et al. 2010).

A change in sign of the relationships between the models at the dive scale and the 24 h scale was observed for 5 parameters: maximum depth, post-dive surface duration, descent rate, bottom slope and depth variability at the bottom. Maximum depth was found to have a negative effect at the dive scale, but cumulative depth over a 24 h period was found to be positively related to the number of PCAs performed.

A negative relationship between surface interval and the number of PCAs was detected at the dive scale, but a positive relationship was detected between the number of PCAs and the cumulative surface duration at the 24 h scale. Furthermore, while descent rate was found to have a positive effect on the number of PCAs at the dive scale, a negative effect was detected at the 24 h scale. These changes in sign suggest that on a 24 h scale, elephant seals are more successful when they perform a greater number of shallower and shorter dives compared to longer and deeper dives. Indeed, an increase in dive duration with diving depth is a common trait found in all diving predators. As a consequence, when performing a greater number of shallower and shorter dives over 24 h, the cumulative depth (i.e. the total vertical distance covered) as well as the total amount of time spent at surface, increased compared to when seals were performing deeper and longer dives. Consistently, mean descent rate tended to increase with increasing diving depth in king penguins (Hanuise et al. 2010) but also elephant seals (L. Yves pers. comm.). Therefore, when performing shallower dives, seals should on average exhibit a lower mean descent rate compared with times when they dive deeper to reach prey. The relationships of bottom slope and depth variability at the bottom with the number of PCAs were negative at the dive scale but became positive and marginally significant at the 24 h scale. This change in sign remains difficult to interpret. Interestingly, when considering the cumulative dive depth and its variability, seals performed a greater number of PCAs when diving shallower with a lower variability of their diving depth, indicating that elephant seals were more successful when encountering prey closer to the surface, and over a limited range of depths.

Predicting PCAs from other foraging metrics (predictive models)

In recent decades, a growing number of analytical methods have been developed to infer preferred foraging areas from tracking data (Benhamou & Bovet 1989, Fauchald & Tveraa 2003 among others). Our study indicates that the relationships existing between the number of PCAs and tracking data are consistent with the theoretical predictions (Kareiva & Odell 1987). However, the predictive performances of the track-only based models (Group A) tended to be negligent at the dive scale ($pp = 0.018$) and remained poor at the 24 h scale ($pp = 0.194$) (Table 3).

The use of dive metrics improved the predictive power of models (Group B) ($pp = 0.215$ at the dive scale and $pp = 0.751$ at the 24 h scale), indicating that the change in dive behaviour provides a more powerful insight in the variation of the number of PCA of the seals than the horizontal spatial behaviour. Therefore, existing dive data recorded along the track of these predators can be used to assess more precisely the variation in foraging behaviour of seals, compared with analyses of track data alone. Time-depth dive profiles are transmitted at different resolutions by an increasing number of satellite-relayed data loggers, and this information may prove to be highly valuable to better assess the spatio-temporal variation of the foraging behaviour of these predators, and possibly other diving predators such as fur seals or king penguins. As expected, the inclusion of track metrics with the dive metrics at the 2 scales improved the predictive power of both models, but this effect was marginal ($pp = 0.217$ at the dive scale and $pp = 0.764$ at the 24 h scale). This result emphasizes the importance of dive metrics when assessing spatio-temporal variation of foraging behaviour. The fact that the track data alone does not correctly predict the foraging behaviour of animals is not surprising. Indeed, other studies have emphasized the limitations of track data and the usefulness of diving data when measuring variations in foraging performance in deep-diving predators ('first bottom time', Bailleul et al. 2008). Considering the low number of predators used, the predictive performance of the selected groups at each scale (Group C) can be considered as low at the dive scale ($pp = 0.217$) and good ($pp = 0.764$) at the 24 h scale at predicting the number of PCAs (Table 4). We can explain the good predictive performance of the Group C model at the 24 h scale by the fact that all the parameters are averaged or summed over 24 h. In the model derived from Group C at this scale, the results combine day and night foraging strategies, smoothing all dive recovery times and chances of foraging. In contrast, the model derived from Group C at the dive scale exhibits significantly more scatter because it forces integration of day and night foraging patterns, which are mostly different (Hindell et al. 1991, McIntyre et al. 2010). Change of the predictive power according to the time scale considered should, in future, be investigated at different time intervals, separating dives into day and night. All 12 individuals equipped with accelerometers showed low and good predictions for Group C model at each scale (Fig. 2). Models derived from this group, at the 24 h scale, were capable of predicting the foraging activity of new individuals based on

their diving patterns only and the predictions were only marginally improved when adding tracking data. It is important to note that the models derived from Group C at each scale were developed for female elephant seals foraging in pelagic waters of the Southern Ocean and their applicability to other species or regions remains to be tested. Testing models on female northern elephant seals would assist in assessing their generic value, as these animals forage pelagically and some individuals are already equipped with accelerometers detecting PCAs.

Application

When applying the models derived from Group C at the 2 scales to the 20 individuals for which we had only track and dive data, we observed a main foraging zone east of Kerguelen (Fig. 3). The Crozet area and the edges of the Antarctic plateau also emerged as important foraging zones. This coincides with areas where it has been reported that the body condition of seals has improved (Biuw et al. 2007, Bailleul et al. 2007b). The improvement of the predictive performances of foraging behaviour using dive data should allow for more precise assessments of inter-annual variation in the foraging behaviour of elephant seals. Further, improved predictive performance may provide insights into possible relationships between local oceanographic conditions and foraging patterns. However, while this approach can be used to locate areas of favourable foraging, it does not provide information on the quality (size and energetic content) of the prey. A given PCA, in the case where this PCA is associated to a real capture or ingestion, may correspond to very different prey items, since elephant seals are known to take a variety of prey items, from squid to fish (e.g. Rodhouse et al. 1992, Slip 1995, Daneri & Carlini 2002, Cherel et al. 2008, Naito et al. 2013).

CONCLUSIONS

The combination of track and dive behavioural variables enables prediction of the number of PCAs of female southern elephant seals with a reasonable level of confidence, thereby providing quantitative measurements of their foraging behaviour. This approach may therefore constitute a useful ecological tool for population monitoring or conservation purposes (Morris et al. 2009). In addition, the tools used to obtain these variables are less expensive than

accelerometers and can more easily be applied on a large number of individuals. The use of behavioural variables to assess foraging activity allows for a better understanding of foraging ecology of diving marine predators with a new emphasis on prey distribution through the oceans and/or on the relationship between foraging efficiency and environmental conditions. It also provides an unprecedented opportunity to re-examine/re-analyse old datasets leading to new perspectives in long-term studies of foraging ecology of such predators.

Acknowledgements. The authors thank all the colleagues and volunteers involved in the field work on southern elephant seals at the Kerguelen Islands, with special acknowledgement of the invaluable field contribution of G. Bessigneul and A. Chaigne. This work was supported by the ANR Topp-Patches, ANR Mycto-3D-Map, the CNES-TOSCA and the Total Foundation. We are indebted to IPEV (Institut Polaire Français), for financial and logistical support of Antarctic research program 109 (Seabirds and Marine Mammal Ecology led by H. Weimerskirch). Special thanks also go to Pascal Monestiez and Kevin Le Rest (CEBC CNRS) for their helpful advice at the different stages of the manuscript. Finally, the authors also thank Lauren Biermann for her help with English editing.

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*Editorial responsibility: Scott Shaffer,
San Jose, California, USA*

*Submitted: February 10, 2015; Accepted: October 6, 2015
Proofs received from author(s): December 7, 2015*