

Assessment of scale-dependent foraging behaviour in southern elephant seals incorporating the vertical dimension: a development of the First Passage Time method

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Summary

1. Identifying the spatial scales at which top marine predators forage is important for understanding oceanic ecosystems. Several methods quantify how individuals concentrate their search effort along a given path. Among these, First-Passage Time (FPT) analysis is particularly useful to identify transitions in movement patterns (e.g. between searching and feeding). This method has mainly been applied to terrestrial animals or flying seabirds that have little or no vertical component to their foraging, so we examined the differences between classic FPT and a modification of this approach using the time spent at the bottom of a dive for characterizing the foraging activity of a diving predator: the southern elephant seal.

2. Satellite relayed data loggers were deployed on 20 individuals during three successive summers at the Kerguelen Islands, providing a total of 72 978 dives from eight juvenile males and nine adult females.

3. Spatial scales identified using the time spent at the bottom of a dive ($\bar{\omega} = 68.2 \pm 42.1$ km) were smaller than those obtained by the classic FPT analysis ($\bar{\omega} = 104.7 \pm 67.3$ km). Moreover, foraging areas identified using the new approach clearly overlapped areas where individuals increased their body condition, indicating that it accurately reflected the foraging activity of the seals.

4. These results suggest that incorporating the vertical dimension into FPT provides a different result to the surface path alone. Close to the Antarctic continent, within the pack-ice, sinuosity of the path could be explained by a high sea-ice concentration (restricting elephant seal movements), and was not necessarily related to foraging activity.

5. Our approach distinguished between actual foraging activity and changes in behaviour induced by the physical environment like sea ice, and could be applied to other diving predators. Inclusion of diving parameters appears to be essential to identify the spatial scale of foraging areas of diving animals.

Key-words: bio-logging, diving behaviour, foraging ecology, marine mammals, spatial scale

Introduction

Habitat use can be defined as the manner in which a species uses a collection of environmental components to meet life requisites (Block & Brennan 1993). Of all the activities included in the habitat use concept, foraging activity is one of the most important because obtaining an adequate food

supply is a basic determinant of all other life-history traits (Stevick, McConnell & Hammond 2002). Prey availability to predators in the marine environment is heterogeneous in both time and space. The heterogeneity in the spatial distribution of prey is driven by the physical structuring of the marine environment at different spatial scales, varying from metres to hundreds of kilometres. In such a heterogeneous environment, animals have to adjust their foraging behaviour according to the variation in distribution and availability of their prey to maximize food acquisition (Schneider & Piatt 1986;

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Heinemann, Hunt & Everson 1989; Fauchald, Erikstad & Skarsfjord 2000; Guinet *et al.* 2001).

To maximize the utilization of a high-density prey patch, predators increase their turning rate and reduce their speed, known as an area-restricted search (ARS) (Fauchald & Tveraa 2003). Changes in movement patterns within a foraging path can therefore be viewed as the predators response to spatial structured food resources. Recently, several methods have been developed to quantify how individuals concentrate their search effort along a given path (Fauchald *et al.* 2000; Johnson *et al.* 2002; Fauchald & Tveraa 2003; Fritz, Said & Weimerskirch 2003). First-Passage Time (FPT), defined as the time required for an animal to cross a circle with a given radius, is a scale-dependent measure of search effort (Fauchald & Tveraa 2003), which identifies the spatial scale and position of the shifts in movement pattern. While FPT analysis has been reported to be applicable to many species, most of the studies using this method have concerned terrestrial animals or flying seabirds, and focus on foraging movements in two horizontal dimensions (Frere, Quintana & Gandini 2002; Fauchald & Tveraa 2003; Pinaud & Weimerskirch 2005). The diving behaviour of marine animals makes their approach to using space fundamentally different. Search activity for these species occurs principally under the surface and is therefore inadequately represented by a two-dimensional pathway. The diving (vertical) dimension should also be considered as it contains additional information about search effort. However, no studies have yet considered the vertical dimension in spatial analyses of foraging behaviour.

Southern elephant seals *Mirounga leonina* are a good species in which to study these types of scale-dependent predator-prey interactions in oceanic habitats. They travel thousands of kilometres during a migration (McConnell, Chambers & Fedak 1992) and dive repeatedly along this path (60 dives per day on average), regularly to depths up to 1500 m and staying submerged for up to 1 h (Stewart & DeLong 1990). Consequently, this species has the potential to use a wide range of habitats throughout the Southern Ocean. A recent study showed that elephant seals from Kerguelen utilized three main habitats (Baillieu *et al.* 2007a). Some seals foraged on the Antarctic shelf in high sea-ice concentrations (up to 98%). Another group foraged at the ice-edge, while a third group remained in open water, mainly within the polar frontal zone.

In Southern elephant seals, different dive types have been identified and characterized by their time-depth profiles (Schreer & Testa 1996; Lesage, Hammill & Kovacs 1999). Dive types with a long bottom time are regarded as foraging activity because the animals are maximizing the proportion of time spent at a particular depth where prey may be encountered (Schreer, Kovacs & O'Hara Hines 2001). In contrast, dives with short bottom times are thought to indicate travelling activity. The proportion of time at the bottom of a dive has been demonstrated to be an indicator of foraging activity in other diving predators (Miller, Johnson & Tyack 2004; Austin *et al.* 2006; Fowler *et al.* 2006), with animals spending more time at depth in favourable foraging conditions. Elephant seals also regularly perform dives during which they stop

swimming and drift passively in the water column (Webb *et al.* 1998; Biuw *et al.* 2003). The vertical movement during these 'drift dives' is largely a result of the body condition (Webb *et al.* 1998), with fat, positively buoyant seals drifting upwards, and lean, negatively buoyant seals sinking. An increase in the drift rate over time is therefore an index of a successful foraging activity (Biuw *et al.* 2003, 2007; Baillieu *et al.* 2007b).

In this study, we test the hypothesis that foraging in elephant seals can be detected not only at the surface (as revealed by tracking locations) but also in their diving behaviour. This approach should provide crucial additional information for the proper identification of the foraging areas of seals and the spatial scale at which they are operating. We then examined the relationships between the foraging behaviour of seals identified in this way with the physical environment, particularly sea-ice concentration.

Materials and methods

STUDY AREA AND DEPLOYMENT OF DEVICES

This study was conducted on the Kerguelen archipelago (49°20'S, 70°20'E) in the Southern Indian Ocean during three consecutive summers (2002/03–2004/05). Twenty Satellite Relayed Data Loggers (SRLDs, 105 × 70 × 40 mm, 545 g, cross-sectional area 28 cm²) from the Sea Mammal Research Unit (University of St Andrews, Scotland), collecting and transmitting locations, pressure, temperature and salinity, were deployed. The devices were pressure-rated to 2000 m. Depth data were sampled every 5 s but the limited Argos bandwidth required that a summary of these data be transmitted. A pseudo-random method to schedule the transmission of an unbiased data sample of the stored records was used (Fedak 2004).

This study was approved by the ethics committee of the French Polar Institute (IPEV), and animals were cared for in accordance with its guidelines. Nine juvenile males and 11 adult female elephant seals were equipped before departing for their post-moult foraging trip (March–September). The seals were restrained in a canvas head-bag, and a 1 : 1 combination of Tiletamine and Zolazepam (Zoletil 100) injected intravenously (McMahon *et al.* 2000; Field *et al.* 2002). The SLDRs were glued on the head of the seals, using quick-setting epoxy (Araldite AW 2101), once the hair had been cleaned with acetone.

DATA ANALYSIS

Seal locations

Locations on the surface were determined by the Argos System, and subsequently filtered using a forward/backward averaging filter (McConnell *et al.* 1992), based on the assumption that elephant seals rarely travel at speeds higher than 3 m s⁻¹. The 17 individual paths were described by 4415 ± 1623 locations, corresponding to 10–20 locations per day. The locations of individual dives along these paths were estimated based on a simple linear interpolation of the distance between locations.

Diving behaviour

A seal was taken to be at the bottom of a dive whenever the depth exceeded 80% of the maximum depth reading for that dive (Lesage *et al.* 1999; Schreer *et al.* 2001). The deeper the dive is, the greater

the transit time to and from the bottom, and therefore the lower the amount of time available to spend at the bottom. Thus, for a dive of a given depth and a given dive duration there is a average bottom time, determined by the multivariate linear regression between these three parameters. Positive residuals from these regressions indicate dives with a longer bottom time than average for a given depth and duration, suggesting an increased foraging effort, while the negative residuals indicate a shorter bottom time than average.

First-passage time analysis on tracks

All the surface locations describing the path were associated with a circle of a given radius (r). FPT is defined as time required to cross the circle, and the relative variance [obtained from FPT log-transformed to make the variance independent of the magnitude of the mean FPT (Fauchald & Tveraa 2003)] was calculated as a function of r . This process was repeated for each location at a range of circle sizes. The maximum peak in relative variance across a range of values of r indicated the scale at which the most intensive area-restricted search occurred. Then, the FPT corresponding to that scale was plotted against time from departure. The intensive search areas along each path were those with the longest FPT.

Applying First-Passage Time to the variability of time spent at the bottom of the dive

We calculated the residuals of the multiple regression (bottom time vs. maximum dive depth + dive duration) for each dive within a path. Then, rather than using the time required to cross the circle, we calculated the sum of absolute values of these residuals within each circle. This value represented the variation of the relative bottom time of dives between the first passage of the circle, backward and forward along the path at surface. As for FPT, this value will increase for increasing radius of the circle. However, the increase will be especially large when the individuals significantly change their behaviour (e.g. when they adopt an area-restricted search behaviour). Thus, the relative variance for all points along the path will increase with increasing r . This variance is calculated similarly to the FPT (Fauchald & Tveraa 2003) by $\text{Var}[\log(t(r))]$, where r is the radius of the circle, and $t(r)$ is the sum of absolute value of residuals within a circle. As for FPT, $t(r)$ is log-transformed to make the variance independent of the magnitude of the mean residuals. If search behaviour is concentrated within a certain area, we expect a maximum variance, with the radius (r) corresponding to the spatial scale of the most intensive searched area. For both analyses we used values of r varying from 2 to 800 km.

Once the spatial scale was identified in this way, we calculated the sum of residuals (not the absolute value this time) within each circle. Thus, we obtained a measure of change in behaviour at depth, called residual first bottom time (rFBT). As for FPT, the rFBT corresponding to the scale of the maximum variance was plotted against time from departure for each individual and we identified the zones where the animals spent a longer (positive sum of residuals) or a shorter than average time (negative sum of residuals) at the bottom of dives.

Successful foraging areas

We assigned each dive to one of six distinct dive types (see details in Bailleul *et al.* 2007a), and isolated the drift dives. From the time-depth profiles of these dives, we identified the putative drift segment

by fitting different regression lines through the inflection points (see fig. 1 in Biuw *et al.* 2003). The drift rate (m s^{-1}) was calculated as the slope coefficient (positive or negative) of the best-fitting regression line. Only dives where the depth of the shallowest inflection point was at least 10 m and where the drift phase represented more than 40% of the total duration were used (Biuw *et al.* 2003). The daily average of drift rate was then calculated, and the changes in this daily drift rate derived over successive days.

These data were mapped on to a 0.5° grid (as determined in Bailleul *et al.* 2007b), providing spatially explicit indication of changes in the seals body condition (Crocker, Le Boeuf & Costa 1997; Biuw *et al.* 2003). The correspondence between areas where body condition increased and the areas identified by FPT analysis and those identified by rFBT gave an index of success in foraging activity and its location. The higher the overlap between those various measures, the more precise the success foraging area identification.

Sea ice data

Daily maps of ice concentration, expressed as percentage of the sea covered by sea ice, were obtained from the University of Bremen (Germany). Ice concentration maps had a ground resolution of 6.25 km × 6.25 km. Ice concentration was then extracted for each location along each surface path.

Statistical analysis

Given the small sample sizes and in accordance with statistical assumptions, we used nonparametric statistics. Results are presented as means (\pm SD), and significance was assumed for $P < 0.05$.

Results

DISTRIBUTION AT SEA

Three individuals for which there were < 30 days of data were removed from the analysis. Therefore, the analyses were conducted on 17 animals (eight males and nine females) that had an average path duration of 159.3 ± 45.1 days. During this time, each seal covered an average distance of 7086 ± 2568 km, with a range of 3681–14 661 km. During the course of this study, nine seals foraged mainly within the pack-ice, five individuals foraged mainly at the edge of the pack-ice, while three animals foraged exclusively in open water, within the polar frontal zone (ice-free zone).

DIVING BEHAVIOUR

A total of 72 978 individual dive records were collected. The linear relationship between the three diving parameters, z = bottom time, x = maximum dive depth and y = dive duration, was significant ($z = -0.21x + 0.54y + 5.77$; $R^2 = 0.62$; $P < 0.001$). From this relationship, 38 646 positive residual bottom times were obtained with an overall range of 22.9 min against 38 701 negative ones with an overall range of 28.9 min. Of all the dives, 4006 were identified as drift dives. A total of 2087 drift dives had a positive slope (i.e. indicating positive buoyancy) during the drift segment and were referred to as positive drift dives.

AREA-RESTRICTED SEARCH BEHAVIOUR

All individuals adopted an area-restricted search pattern, indicated by the maximum peaks of variance plotted as a function of r (Fig. 1). The range of individual spatial scales determined by the FPT was relatively large (from 40 km to 280 km). Variance in rFBT showed individual maximum peaks ranging from 25 km to 180 km (Fig. 1).

COMPARISON BETWEEN THE TWO METHODS

A difference between the spatial scales obtained

Although every peak in variance potentially indicates a search area, we focused only on the maximum in relative variance that indicates the most intensive area-restricted search. While the spatial scales obtained by FPT analysis were 104.7 ± 67.3 km, spatial scales determined by the rFBT method were significantly lower on average (68.2 ± 42.1 km; Wilcoxon paired test: $W = 83$, $P = 0.009$). Year, sex or geographical areas did not influence the difference between the two methods (Kruskal–Wallis tests: $F = 0.280$, d.f. = 2, $P = 0.869$; $U = 36.5$, d.f. = 1, $P = 0.961$; $F = 0.468$, d.f. = 2, $P = 0.792$, respectively). Also, no effect of these parameters was observed on the spatial scales obtained with FPT (year: $F = 0.795$, d.f. = 2, $P = 0.672$; sex: $U = 41$, $P = 0.629$; geographical areas: $F = 0.197$, d.f. = 2, $P = 0.906$) or obtained with the rFBT method (year: $F = 0.006$, d.f. = 2, $P = 0.997$; sex: $U = 44.5$, $P = 0.412$; geographical areas: $F = 0.486$, d.f. = 2, $P = 0.784$).

A difference in the intensive search areas location

The longest FPT indicates an important increase in sinuosity at the surface, while the greatest positive rFBT indicates areas where the bottom time was the longest. An increase in sinuosity did not always correspond to an increase in time spent at the bottom of dives (Fig. 2). Therefore, the areas identified by rFBT (and calculated from the radii showing maximum peaks) were 35% smaller on average than those obtained by the FPT analysis. Moreover, high FPT values sometimes corresponded to negative rFBT values (Fig. 2). Therefore, while some individuals appeared, at surface, to spend a long time within an area, they spent actually a relatively short time at the bottom of their dives.

A difference in the successful foraging areas location

The areas, where the most important positive changes in drift rates were observed (suggesting that individuals improved their body condition), were identified. Regions where there is overlap between these areas and the most intensive search areas give an index of successful foraging activity. Nineteen of 23 intensive search areas identified (82%) corresponded to a successful foraging activity. This correspondence was twice as pronounced using the areas identified by rFBT (overlap of $31.8\% \pm 26.5$ on average) rather than those obtained by FPT analysis (overlap of $14.7\% \pm 13.7$ on average).

EFFECT OF MAXIMUM SEA-ICE CONCENTRATION

Except for three seals (numbers 2848, 10 029 and 10 035), which left the sea-ice zone very early, the residual bottom times were negatively related to the sea-ice concentration (Table 1), indicating that the higher the sea-ice concentration, the shorter the time spent at the bottom of dives, while no such relationship was observed for those individuals that foraged along the ice edge. This short bottom time is related to shallow depth of the dives and their short dive duration. Moreover, no positive drift dives were recorded when sea-ice concentration was very high.

Discussion

This study combines, for the first time, horizontal movement patterns, to infer search behaviour and the spatial scale of foraging, and diving behaviour to better identify foraging areas. These areas were then contrasted with those where elephant seals were known to forage successfully (or unsuccessfully) using relative body composition data from drift dives. Theoretical studies of foraging behaviour of diving animals often assume that the number of prey encountered is a linear function of time spent searching, so that the rate of energy acquisition increases with the time at depth (Kramer 1988; Houston & Carbone 1992). The foraging tactics of elephant seals are not well known, but if we assume that they either search for and actively pursue prey, or they wait for and ambush prey in the water column, then the time spent at the bottom of dive is an indirect index of foraging effort. The correspondence found between locations of higher than average bottom time and areas of increasing body conditions confirm this. Our results showed that the obtained foraging spatial scales, incorporating this parameter, were finer than the ones obtained using solely surface location data. We suggest that this is due to the information quantity used by each method. In the case of the FPT, the time spent measurement in a sector comprises several different activities (moving, diving, etc.), while only

Table 1. Correlation between bottom time (residuals) and sea-ice concentration. Significant results are indicated in **bold**.

Seal	Sex	Year	Pearson correlation coefficient (r_s)	P -value	Foraging areas
2845	M	2002	-0.31	0.01	PI
2848	M	2002	-0.13	0.23	PI
9926	M	2004	-0.35	< 0.001	PI
9929	M	2004	-0.30	< 0.001	PI
9934	M	2004	-0.46	< 0.001	PI
9938	F	2004	-0.26	0.004	PI
10028	M	2005	-0.32	< 0.001	PI
10029	M	2005	0.10	0.36	PI
10035	M	2005	0.04	0.82	PI
9927	F	2004	0.0618	0.55	Ed
9931	F	2004	0.0896	0.46	Ed
9932	F	2004	-0.32	0.12	Ed

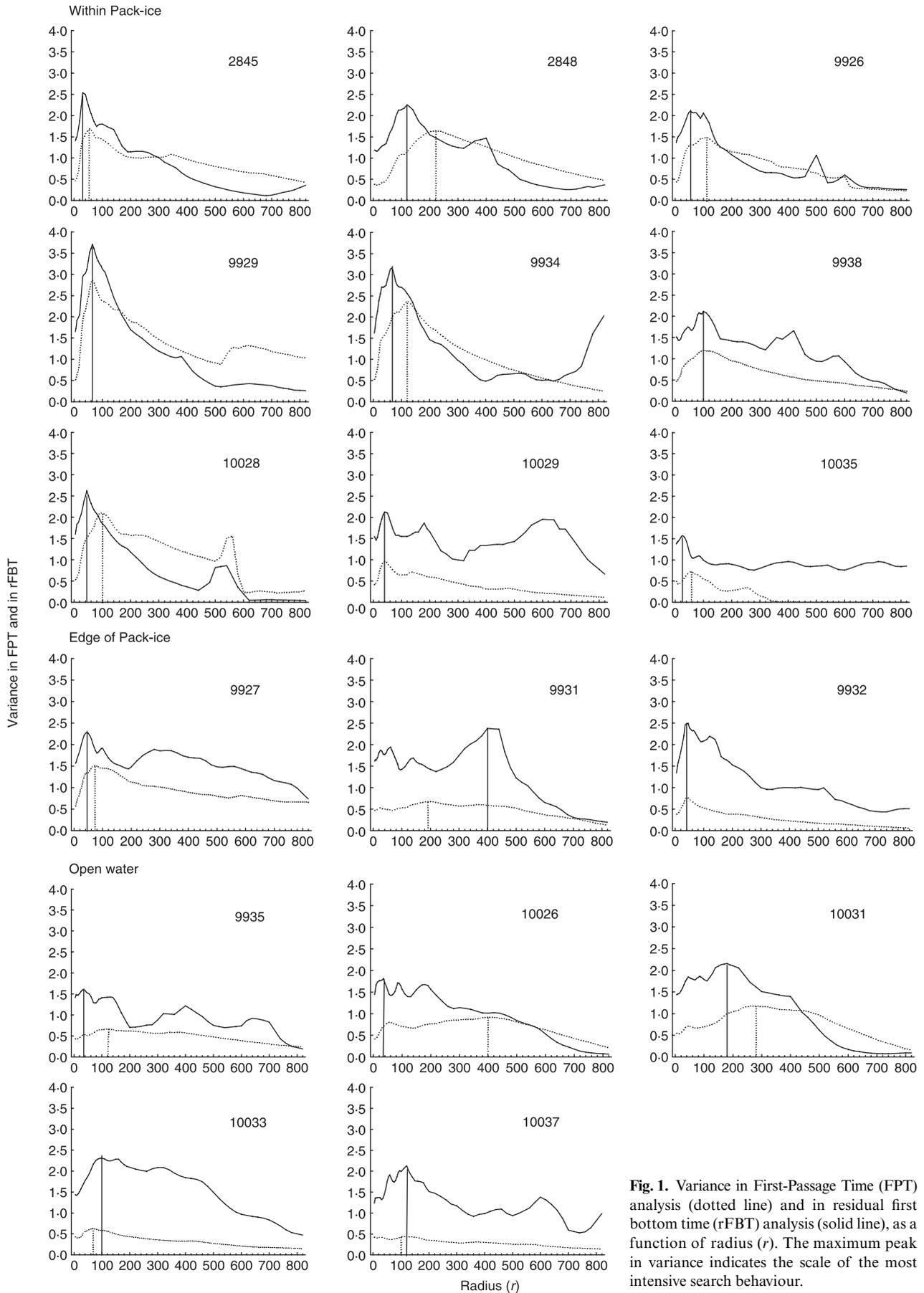


Fig. 1. Variance in First-Passage Time (FPT) analysis (dotted line) and in residual first bottom time (rFBT) analysis (solid line), as a function of radius (r). The maximum peak in variance indicates the scale of the most intensive search behaviour.

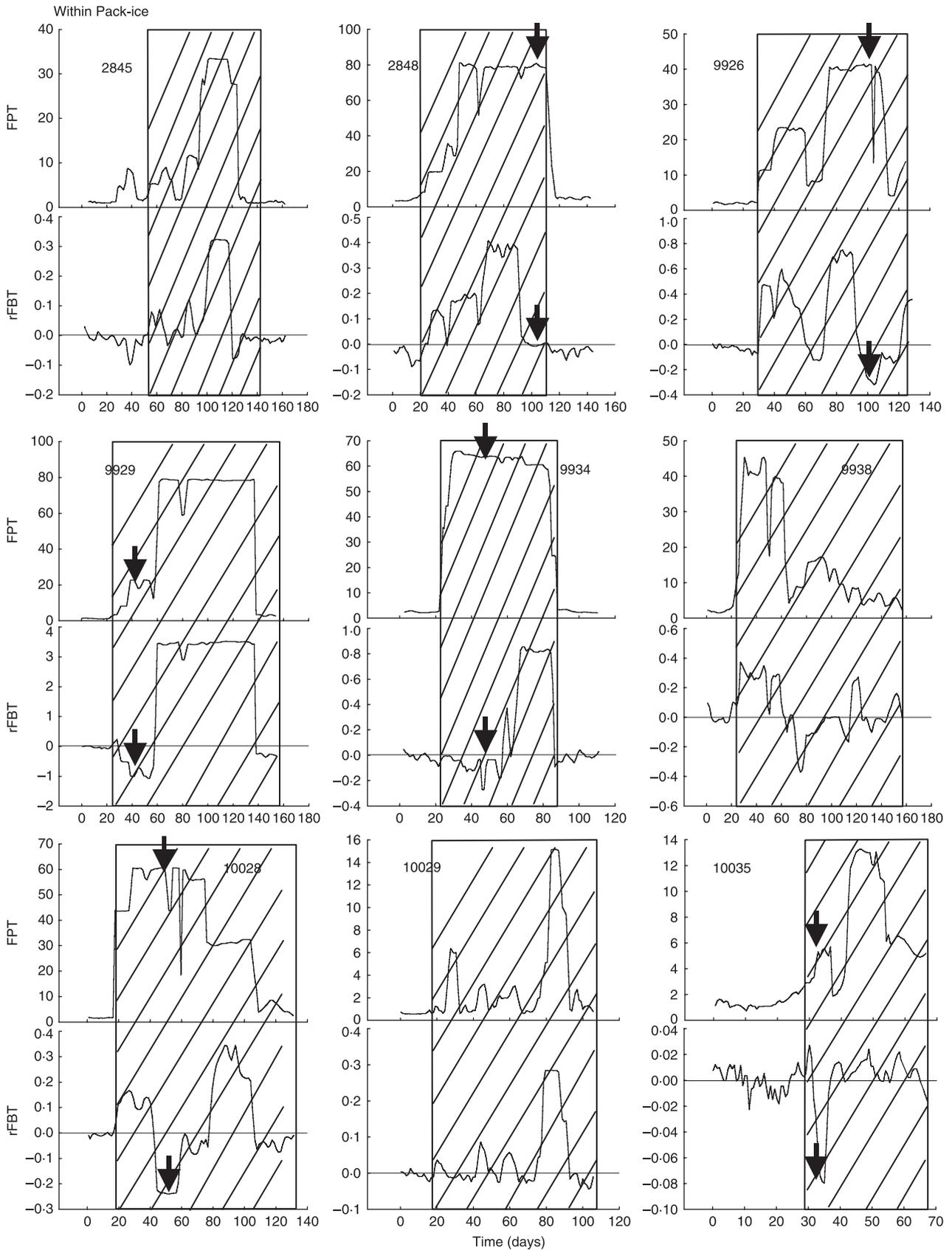


Fig. 2. The First-Passage Time (FPT) and residual first bottom time (rFBT) at the scale of the maximum variance plotted against time from departure. Search areas were defined as those with the longest FPT. With rFBT, the greatest positive residuals indicate that seals spent longer than average at the bottom of dives; therefore, identifying foraging areas. Negative residuals indicate relatively short bottom times. Black arrows indicate the noncorrespondence between sinuosity and time spent at the bottom of dives. The streaked section indicates the presence of sea ice.

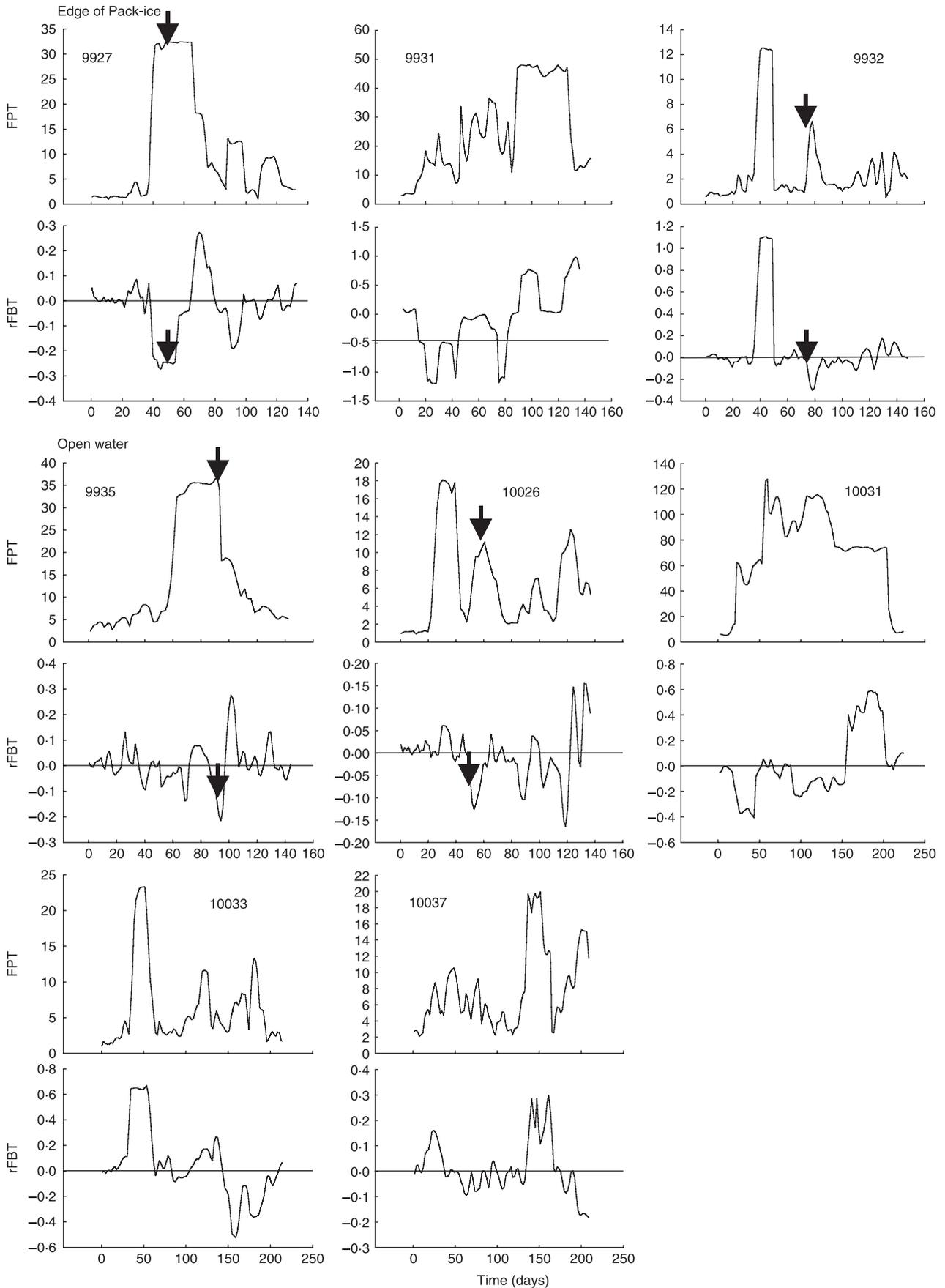


Fig. 2. Continued.

the time spent at depth was used in the rFBT analysis. Therefore FPT could determine how the seals select habitat on a large scale (where do they spend most of their time), while the rFBT is a measure of foraging activity within these habitats.

However, foraging effort can be independent of foraging success and not necessarily related to the presence of prey. Foraging effort and foraging success taken independently provide limited information on the foraging ecology of a predator. On the other hand, quantifying both measures together allows a more precise identification of the feeding zones (Bailleul *et al.* 2007b). The overlap between areas identified with the rFBT method and areas where individuals improved their body condition supports the assumption that the foraging movements change in response to the distribution of food (Fauchald *et al.* 2000; Pinaud & Weimerskirch 2005). Moreover, change of the slope of the drift phase of drift dives can only be detected over several days, and consequently provide information regarding favourable vs. unfavourable foraging zone at medium temporal and spatial scales. However, changes in the time spent at the bottom of dives can be detected within a day providing information on quality and availability of prey at a considerably finer scale.

By studying behaviour of elephant seals in this way, we potentially obtain information on the distribution, abundance and availability of prey, in a large area of the Southern Ocean, where studies of the ecosystem *in situ* remains difficult. We observed that elephant seals from Kerguelen used a wide variety of habitats to forage, principally located on the plateau close to the Antarctic continent, at the edge of pack-ice or along the polar frontal zone. If resources are patchily distributed (e.g. Fauchald 1999), the scales at which foraging activity occur can illustrate the size of patches in these geographical sectors. For example, within the Frontal zone meso-scale structures such as eddies, reflected by sea-level anomalies, are known to drive the accumulation of nutrients and therefore concentrate productivity favourable for all upper trophic levels (review in Rhines 2001). The scale of foraging for individuals using this region (i.e. 170 km diameter on average) corresponds to the size of eddies (diameter of 150–200 km, see Park *et al.* 2002), suggesting a strong relationship between foraging activity and the mesoscale structure of the ocean in this region. However, even if most peaks in the variance plots are quite well defined especially for the animals related to pack-ice, we acknowledge that some are less convincing for many of the open water animals. This could be explained by a less pronounced ARS behaviour for these individuals and may be a weak relationship with striking environmental structures.

Except eddies, other physical processes can also explain the spatial scales used by animals. The Antarctic sea ice is known to be highly productive (Smith & Nelson 1985; Ainley & DeMaster 1990; Bailleul *et al.* 2007a) and this is assumed to explain changes in sinuosity along foraging paths by predators (Fauchald & Tveraa 2003; Fritz *et al.* 2003; Pinaud & Weimerskirch 2005; Bailey & Thompson 2006). Our results suggest that alternatively, sea-ice concentration around Antarctica could represent a major constraint on seal movement. During

winter, in regions of high sea-ice concentration, elephant seals exhibited restricted FPT. However, there was no increase in rFBT nor was there an improvement in body condition using drift dives, in fact it actually tended to deteriorate. Restricted movement in surface does not always correspond to foraging activity. This confirms the hypothesis of Bailleul *et al.* (2007a), suggesting that increasing winter sea ice could be a constraint for southern elephant seals on the Antarctic shelf, by trapping animals within very high sea-ice concentrations and limiting their movements. When sea-ice concentration is very high, open water, needed for breathing and resting, is probably scarce and ephemeral and elephant seal become 'central place breathers' dependent on their ice hole or cracks regardless of the foraging quality of the area. As elephant seals are continuous divers, they keep diving but exhibit shorter bottom times. During these periods, seals are confined in a small area and therefore their track appears to be highly sinuous. We have shown that to always consider an increase in FPT as a response to a priori food distribution could be unrealistic.

Finally, the improving estimates of foraging spatial scale of predators contributes to a better understanding of the marine ecosystem. The rFBT method could find application in other ecological studies. Indeed, numerous works in marine ecology have revealed complex biophysical interactions from tracks of top predators. Because they have to search efficiently for their patchy distributed prey, marine predators use a variety of environmental cues (Nevitt, Veit & Kareiva 1995; Bost *et al.* 1997; Charrassin & Bost 2001; Luschi *et al.* 2003). Frontal areas in the Southern Ocean revealed, for instance, intense meso-scale activity with many eddies (Park *et al.* 2002; Strass *et al.* 2002). These environmental factors could affect the behaviour of diving predators but remain largely undetected because of inappropriate determination of spatial scales where the interactions occur. Therefore, it is crucial, in order to more precisely identifying these kinds of interactions, to work at the scale at which animals discern environmental heterogeneity. In this case, diving predators seem to better respond to food resource heterogeneity at depth (where they encounter prey) than at surface.

Although attention is often focused on horizontal pathways in the description and analysis of spatial scales used by animals, this approach can be incomplete for diving species. Fixed coordinates of position on the surface do not fully reveal the foraging properties of diving feeders, and incorporation of those underwater activities increases the accuracy of the spatial scales appropriate to describe these habitats. Our method enables a more realistic assessment of the size and location of foraging areas and of the key environmental features that influence foraging success of top marine predators. Although this method has only been applied to elephant seals so far, integrating the foraging behaviour in three dimensions to determine the foraging behaviour at a fine scale, could be of major interest for all diving top predators. This is particularly true for predators foraging in the sea ice, such as crabeater seals (Burns *et al.* 2004), Weddell seals (Plötz *et al.* 2001), Adélie penguins (Rodary, Wienecke & Bost 2000) and

Emperor penguins (Kirkwood & Robertson 1997), but also for sub-Antarctic species such as penguins (Hull, Hindell & Michael 1997; Charrassin & Bost 2001) and fur seals (Lea & Dubroca 2003) that regularly associate with oceanic features such as the Polar and Subantarctic fronts.

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