In situ measures of foraging success and prey encounter reveal marine habitat-dependent search strategies

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Abstract. Predators are thought to reduce travel speed and increase turning rate in areas where resources are relatively more abundant, a behavior termed "area-restricted search." However, evidence for this is rare, and few empirical data exist for large predators. Animals exhibiting foraging site fidelity could also be spatially aware of suitable feeding areas based on prior experience; changes in movement patterns might therefore arise from the anticipation of higher prey density. We tested the hypothesis that regions of area-restricted search were associated with a higher number of daily speed spikes (a proxy for potential prey encounter rate) and foraging success in southern elephant seals (*Mirounga leonina*), a species exhibiting both area-restricted searches and high interannual foraging site fidelity. We used onshore morphological measurements and diving data from archival tags deployed during winter foraging trips. Foraging success was inferred from in situ changes in relative lipid content derived from measured changes in buoyancy, and first-passage time analysis was used to identify area-restricted search behavior. Seals exhibited relatively direct southerly movement on average, with intensive search behavior predominantly located at the distal end of tracks. The probability of being in search mode was positively related to changes in relative lipid content; thus, intensively searched areas were associated with the highest foraging success. However, there was high foraging success during the outward transit even though seals moved through quickly without slowing down and increasing turning rate to exploit these areas. In addition, the probability of being in search mode was negatively related to the number of daily speed spikes. These results suggest that movement patterns represent a response to prior expectation of the location of predictable and profitable resources. Shelf habitat was 4–9 times more profitable than the other habitats, emphasizing the importance of the East Antarctic shelf for this and other predators in the region. We have provided rare empirical data with which to investigate the relationship between predator foraging strategy and prey encounter/foraging success, underlining the importance of inferring the timing and spatial arrangement of successful food acquisition for interpreting foraging strategies correctly.

Key words: area-restricted search; first-passage time; foraging success; Macquarie Island, Australia; Mirounga leonina; movement patterns; predictability; profitability; southern elephant seal.

Introduction

Successful foraging by animals depends largely on the spatial and temporal distribution of food resources and the search method employed to find them (Bell 1991), such that natural selection gives rise to searching strategies that maximize net energy gain (MacArthur and Pianka 1966, Sims et al. 2008) while minimizing predation risk (Verdolin 2006). The spatial and temporal patchiness of food resources have a hierarchical spatial structure where high-density patches at fine

scales can be nested within low-density patches at broader scales (Kotliar and Weins 1990). In areas of low prey quality or abundance, the simplest foraging strategy is directed straight line travel, which reduces the time spent between patches (Zollner and Lima 1999). When in areas of high prey density, predators should slow down and increase their turning rate, thereby increasing their encounter rate with prey (Kareiva and Odell 1987). This behavior has been termed "area-restricted search" and results in increased search effort in the most profitable areas (Kareiva and Odell 1987).

Our ability to describe foraging strategies is made difficult, however, by the many impediments to collecting observations of wild animal behavior (e.g., dense vegetation, deep water, clouds; Ropert-Coudert and Wilson 2005). Further, measuring and interpreting the costs and benefits of particular strategies can be even

more challenging, with the corollary that we still have a poor understanding of how many species locate productive areas and how they adjust their search behavior to find prey. Because of the predicted movement patterns arising from search theory, various proxy methods have been developed to overcome these problems. Typically, spatially explicit transit rate, turning rate, or residency time have been measured to identify area-restricted search behavior in tracking data. Although such methods are useful for identifying search effort, empirical evidence of the relationship between movement patterns and food distribution is difficult to test due to the difficulty of quantifying the prey field and ingestion events. For some species, this has been estimated by the use of stomach or esophageal temperature sensors, intra-mandibular angle sensors, or video and image recorders (see Naito 2007). However, none of these methods is able to infer long-term foraging success due to our inability to ensure the equipment remains on or in the animal for sufficient duration and because of current on-board memory limitations. Consequently, proxies of the prey field and foraging success inferred indirectly from animal behavior are used instead.

One such approach is to infer foraging success based on surrogate measures of in situ body composition (Biuw et al. 2003). For some marine mammal species, changes in body composition at sea can be measured as fluctuations in buoyancy (Crocker et al. 1997, Webb et al. 1998). In pinnipeds, buoyancy (measured via the rate of vertical passive drift when diving) is determined principally by the relative proportions of lipid and lean body tissue (Webb et al. 1998, Beck et al. 2000). Drift rates have been used successfully as proxies for relative lipid content and thus foraging success in free-ranging elephant seals (*Mirounga* spp.; Biuw et al. 2003, 2007, Bailleul et al. 2007*b*, Thums et al. 2008). Thums et al. (2008) developed models to predict the relative lipid content of seals at sea, a more informative index of foraging success than drift rate measurements alone because it allows for the quantification of relative lipid gain.

Not only do predators play key roles in ecosystems by structuring community composition (Terborgh 1988, Menge and Olson 1990, Estes 1996, Terborgh and Estes 2010), these wide-ranging marine predators are particularly valuable subjects for studies of search behavior because they are confronted constantly with rapidly changing environmental conditions as their long migrations cross aquatic biomes and/or climatic regions (Fritz et al. 2003). Within these broadscale biomes, physical processes such as fronts, shelf and ice edges, or upwelling enhance productivity or concentrate prey (Sullivan et al. 1993, Rintoul et al. 2001, Brierley et al. 2002), and many have found associations between predator movement patterns and oceanographic features (e.g., Lea and Dubroca 2003, Sims et al. 2003, Bost et al. 2004, Weimerskirch 2007, Kobayashi et al. 2008, Cotté

et al. 2009). That many species' distributions are associated with these mesoscale features suggests that locations of concentrated prey are somewhat predictable, at least relative to surrounding areas (Field et al. 2001, Bradshaw et al. 2004, Weimerskirch 2007). Moreover, some individual predators show fidelity to foraging sites (both within and between years), suggesting a predictable resource in space and time (Bonadonna et al. 2001, Bradshaw et al. 2004, Weimerskirch 2007).

Here we link, for the first time, movement behavior, habitat choice, relative prey abundance, and predator foraging success for a wide-ranging marine predator, the southern elephant seal (*Mirounga leonina*). The capacity of southern elephant seals to ingest considerable quantities of prey (well in excess of 4.5 million metric tons of fish and squid annually; Santos et al. 2001) and their large circumpolar population (at least 700 000 individuals; McMahon et al. 2005) make them important Southern Ocean consumers (Boyd et al. 1994, Santos et al. 2001). They exploit specific oceanic regions while foraging during their long-distance migrations, thus providing an opportunity to quantify foraging success in a range of Southern Ocean habitats.

Specifically, we measured area-restricted search patterns, swim speed bursts on the bottom of dives (proxy for prey encounter), and foraging success inferred from changes in relative lipid content to test the hypothesis that regions of area-restricted search are associated with a higher number of daily speed spikes (assumed to represent higher prey encounter rate) and foraging success. We also tested whether rates of prey encounter and foraging success are habitat dependent and if patterns of movement are a response to prior expectation of the location of profitable resources as suggested by the foraging-site fidelity observed. We are thus able to quantify habitat-dependent foraging success and test a key assumption of maximizing net energy intake rate as a currency useful for measuring the predictions of search theory.

Materials and Methods

We instrumented known-age (born in 1993 and 1994) adult female southern elephant seals at Macquarie Island, Australia (54°35′ S, 158°58′ E) with velocity–time–depth recorders (VTDR; Wildlife Computers MK8, Redmond, Washington, USA) prior to the 2002 ($n = 14$), 2004 ($n = 16$), and 2005 ($n = 4$) post-molt foraging trips (see Plate 1). Seals were captured and sedated following the procedures outlined in Field et al. (2002). The VTDRs were attached to the pelage above the shoulders following the procedures outlined in Hindell and Slip (1997) and sampled time, depth, light level, revolutions of a flow-driven turbine, and temperature every 30 s for the total duration of the foraging trips. Raw data from the VTDRs were extracted using Wildlife Computers software. Twice daily at-sea positions were derived from the logged light levels with the R (R Development Core Team 2009) package tripEstima-

tion (Sumner and Wotherspoon 2007), which uses a Markov chain-Monte Carlo approach. This method uses a Bayesian framework for determining location that uses all the data available, and provides location estimates with measures of uncertainty (Sumner et al. 2009). A single-twilight solar model incorporating a topographic mask and likely lognormal speed (1.5 ± 1.6 km/h, mean ± SD) between fixes was used to derive a probability distribution for each twilight position (Sumner et al. 2009). The speed data were log-normally distributed. The spatial mean of each distribution was used for point estimates.

Movement patterns

We used first-passage time to identify transitions in movement behavior along each seal's path (Fauchald and Tveraa 2003). First-passage time is the time required for an animal to cross a circle with a given radius (Johnson et al. 1992). The rationale of this method is that all the points of a pathway are associated with a circle of a given radius and measuring the time between the first passage of the circle backward and forward along the path equates to search effort at each point (Fauchald and Tveraa 2003). First-passage time increases with increasing radius of the circle and, by plotting variance in first-passage time vs. a range of radius values, it is possible to identify the spatial scale at which search effort is concentrated (Fauchald and Tveraa 2003). We used R source code developed by D. Pinaud, CNRS, France (R Development Core Team 2009). We interpolated each track at 10-km intervals (to remove any bias resulting from the irregular spacing of locations) while retaining the original locations, calculating first-passage time at each location along the track for radii ranging from 25 to 1000 km, incrementing at 25 km. While this threshold value is smaller than the resolution typically achieved with geolocation data (see Bradshaw et al. 2002), the Bayesian method used here to estimate locations ensures that many of the problems involved with uncertainty are reduced (Sumner et al. 2009). The spatial scale at which search effort is concentrated was defined for each seal as the mean (for all seals) peak in the log-transformed (to make the variance independent of the magnitude of the mean first-passage time) variance in first-passage time relative to radius size ($S \times \log[\text{first-passage time}]$) (Fauchald and Tveraa 2003). We then plotted the first-passage time in days against day of trip for each seal at this spatial scale. Fauchald and Tveraa (2003) identified the search area as the area giving the longest first-passage time. This required the development of a threshold time; we established this based on the multimodal distribution of first-passage time where search areas are the mode of higher values (Pinaud and Weimerskirch 2007). We used the density function in R to obtain density estimates of each seal's data using a Gaussian kernel and normal reference bandwidth. We commonly found multimodal distributions with two to three clear modes (Appendix:

Fig. A1). We thus identified "transit" as the mode of lower first-passage time values and all other higher modes we identified as "search." Within transit we identified the outward transit as all positions between Macquarie Island and the first location where the seal was in search state. Similarly, we identified inward transit as all locations between the last location in search and Macquarie Island. Remaining transit locations were considered to be transit between patches.

To assess whether sampling rate or location precision affected the spatial scale found by first-passage-time analysis, we also repeated the analysis for locations estimated from ARGOS locations obtained via a Sea Mammal Research Unit (St. Andrews, Scotland) satellite-relayed data logger (SRDL) deployed on one of the seals carrying a VTDR. At-sea positions were derived from the Argos data with the R package tripEstimation (Sumner and Wotherspoon 2007). The model is identical in derivation to that used for the VTDRs, but using the considerably more precise Argos estimates in place of light level-derived geolocation estimates. The contribution of each Argos estimate was weighted by the standard deviation (1000, 800, 200, 30, 7, 1.5, 1.0 km) for each position class (Z, B, A, 0, 1, 2, 3), respectively (Vincent et al. 2002). This method handles erroneous existing location estimates and other problems by incorporating all available sources of information. It provides location estimates with built-in measures of uncertainty; this is important for species for which rates of satellite uplink are low (Sumner et al. 2009).

Prey encounter and relative prey abundance

Speed spikes (acceleration events) at the bottom of dives have been associated with feeding events detected by stomach temperature recorders, and therefore should indicate prey encounter and provide a relative measure of prey abundance (Horsburgh et al. 2008). Speed was derived from the logged revolutions of the VTDR turbine using the post hoc calibration method outlined in Fletcher et al. (1996). Speed spikes were identified using the procedures in Horsburgh et al. (2008) and were the number of accelerations in the bottom phase of a dive that were >0.5 m/s. The bottom period of each dive was established using "DIVE," a custom dive-analysis program (S. Greenhill, *unpublished software*). Here, the bottom period was defined as the time of the dive between the end of the descent phase and the beginning of the ascent phase. The end of descent and start of ascent were detected as spikes in the first differential of depth and time. We summed speed spikes for each day of the foraging trip to obtain a daily rate of prey encounter.

Relative lipid content estimated from drift rate

Periods of passive drifting during individual dives were extracted and used to predict relative lipid content following the method described in Thums et al. (2008). Briefly, drift components were defined as periods when

the turbine was stalled, thus giving a swim speed reading of 0 m/s. We then used generalized linear models to examine the relationship between relative lipid content measured on land and drift rate and several other diving variables collected quasi-simultaneously (i.e., within a week). The highest information-theoretic-ranked model explained 90% of the deviance in relative lipid content. Using this model we predicted relative lipid content for each day of the foraging trips for each individual.

We used a constrained quadratic regression B-spline from the COBS library in R to fit a function to the pattern of change in relative lipid content over the course of each seal's foraging trip (Thums et al. 2008). This summarizes the trend in relative lipid content as a function of day since leaving the island and interpolates values for days when no drift dives were detected. The function's roughness is controlled by the number of internal knots. The number of knots was chosen via the automated knot-selection procedure in which COBS uses a stepwise knot deletion and addition process, and then makes adaptive choices using an information criterion (X. He and P. Ng, *unpublished software documentation*). The fitted values provided daily estimates of relative lipid content and based on the direction of change in relative lipid content from day i to $i+1$, we could determine when seals were increasing relative lipid and when there was a reduction in relative lipid (Thums et al. 2008). It was not possible to determine unequivocally a loss in relative lipid per se because drifting rates do not necessarily reflect absolute changes in lipid composition, even though they can provide good estimates of relative lipid content (Biuw et al. 2003). Other determinants of reduced relative lipid composition include (1) recovery of lean tissue losses from breeding early in the trip, and (2) exponential growth of the lean tissue fetus late in the trip (Thums et al. 2008). Even with these limitations, the method is still informative because buoyancy increase laid over potential lean tissue deposition equates to even greater gains; thus, the regions where these inferred relative lipid gains occur are unquestionably the regions where maximal foraging success is occurring.

Characterization of habitats

To identify foraging habitats we applied a hierarchical cluster analysis to all seal locations using the hclust function in R based on a dissimilarity matrix produced from Euclidean distances and average linkage as the agglomeration method. The variables included to define habitats were distance to ice edge and water depth (Bailleul et al. 2007*a*). We chose these variables because they are easily calculated and should adequately distinguish the three habitats used by Macquarie Island elephant seals: marginal ice zone, Antarctic shelf, and within the major frontal zones of the Antarctic Circumpolar Current (Hindell et al. 2003, Bradshaw et al. 2004, Biuw et al. 2007). Data were standardized such that each observation was expressed as a proportion of the difference of the range of that variable.

The northern-most limit of the sea ice was calculated from daily SMMR-SSM/I passive microwave estimates of sea ice concentration (Cavalieri et al. 2006). The limit was estimated for each day of the study period in each one-degree sector of longitude from 100° to 240° E. For each one-degree sector, the daily extent of the sea ice was taken as the northern-most latitude at which the sea ice concentration changed from ≥15% to <15%. False ice is a minor issue in the SMMR-SMM/I data, but one which can have a large effect on estimates of ice boundaries. The daily estimates of ice edge location were therefore filtered to remove any points associated with a change in ice edge location of more than one degree of latitude per day. Monthly median ice edge locations were then estimated from the filtered daily data. We developed a custom function in R to measure the distance from each seal's daily location to the closest point on the median monthly ice edge. We determined the ocean depth corresponding to each seal's daily locations using the ETOPO2v2 data set (U.S. Department of Commerce 2006).

Area-restricted search validation

We summarized the data daily so that each day of the foraging trips were scored as search or transit (all transit states were combined) within each habitat. Within these daily behavioral states, prey encounters were evaluated as the number of speed spikes per day and foraging success evaluated from the daily change in relative lipid content. The probability of being in search mode was modeled as a function of daily change in relative lipid content, number of daily speed spikes, and habitat. Because the effect of a predator's foraging success or prey encounter rate on search mode might differ between habitats, we tested for an interaction between each of these variables with habitat type on the response of search mode. We constructed a suite of generalized linear mixed-effect models (GLMM) where the random effect was the individual seal nested in year with a binomial distribution and a logit link function. The GLMMs were fitted in the R package lme4. Models were compared and ranked according to Akaike's information criterion, corrected for small sample size (AIC$_c$), and by their relative goodness of fit, the AIC$_c$ weight. The AIC$_c$ weight varies from 0 (no support) to 1 (complete support) (Burnham and Anderson 2002). The amount of variance (percentage deviance) in the response variable (probability of being in search mode) explained by each of the candidate models was used as a measure of a model's goodness of fit to the data (Burnham and Anderson 2002).

If these predators modify their movement pattern in response to intake rate or prey encounter rate (Kareiva and Odell 1987), number of daily speed spikes and daily relative lipid change should differ between outward transit and search. Linear mixed-effects models were
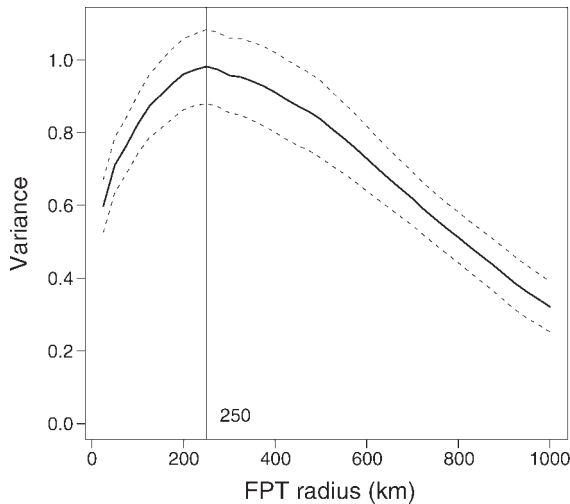
FIG. 1. The variance (mean ± SE) in the log-transformed first-passage time (FPT) as a function of spatial scale (radius size) for all southern elephant seals (*Mirounga leonina*) sampled at Macquarie Island, Australia. The vertical line shows the mean peak in variance.

used to examine these relationships. Models were fit using the nlme library in R where the random effect was the individual seal nested in year with a Gaussian distribution and an identity link function. We used an information-theoretic approach to test for an effect of behavioral mode by comparing model weights and the evidence ratio (ER; Burnham and Anderson 2002) of the slope model (daily change in relative lipid gain ~ behavioral mode + random effect) to the intercept-only model (daily change in relative lipid gain ~ 1 + random effect). Data were autocorrelated so we used the corAR1 function to account for the within-group correlation structure.

Habitat-dependent foraging success

Linear mixed-effects models were used to examine whether prey encounter and foraging success differed between habitats using the exact same methods as outlined previously. We thus compared the slope models to the intercept-only models.

RESULTS

We obtained data on all datalogging channels for the entire post-molt foraging trips for 13 of the 34 deployments. The foraging trip duration for these seals was 235.24 ± 7.55 d (mean ± SD). Five seals were not relocated after datalogger deployment and for 16 others, either speed or light sensors malfunctioned for all or part of the trip.

Movement patterns

All seals adopted an area-restricted search pattern as indicated by a peak in first-passage time variance. The

mean log-transformed variance in first-passage time peaked at radius size 250 km (Fig. 1). Seals spent 61% ± 7% (mean ± SD) of their trips in search and 39% ± 7% in transit. Within transit, seals spent 18% ± 10% of the trip in outward transit, 11% ± 5% in inward transit, and 10% ± 14% transiting between patches. The first-passage time (of the mean radius size of 250 km) was 11.18 ± 3.46 d (mean ± SD) when in transit and 52.51 ± 24.86 d when in search. Within transit, the first-passage time was similar for all three types of transit (outward, inward, and between patches), ranging from 9 to 11 (± 3 to 4) days. The maximum distance from Macquarie Island was 5695 ± 1952 km (mean ± SD) and the total distance covered during the trips was 12 317 ± 2548 km. Most seals exhibited directed, commuting-type movement where search activity was mostly located at the distal end of the tracks, although some of these exhibited search activity at more than one area along the track (Fig. 2, b34704, c31002, c69902). Some seals also exhibited a type of movement that was less directed, with search activity at more than one area and typically not at the distal end of the track (Fig. 2, c16302, c31202, b90004). Most seals traveled either to the sea ice zone in the north of the Ross Sea and off the coast of East Antarctica, or to the shelf break of East Antarctica, with only two remaining in the frontal zones of the Antarctic Circumpolar Current; however, the majority used more than one habitat during a trip (Fig. 2). First-passage time during search was 59.36 ± 32.82 days in ice habitat, 38.33 ± 21.99 days in oceanic, and 35.56 ± 13.39 days in shelf habitat. There was no evidence for a difference in first-passage time during search between habitats with the intercept model (wAIC$_c$ = 0.78; ER = 3.54) having much higher support than the slope model (wAIC$_c$ = 0.22). In transit, first-passage time was 14.58 ± 8.22 days in ice habitat, 10.26 ± 5.50 days in oceanic habitat, and 14.12 ± 5.76 days in shelf habitat. As for search first-passage time there was no difference, with the intercept model (wAIC$_c$ = 0.83; ER = 4.88) having much higher support than the slope model (wAIC$_c$ = 0.17).

Comparison of the spatial scale of use calculated from first-passage time analysis using both location precision-types (geolocation vs. Argos) indicated the same spatial scale of use (i.e., 250 km; Appendix: Fig. A2). We obtained 5.02 ± 2.87 positions per day from the satellite-relayed datalogger deployed.

Characterization of habitats

Five clusters were identified using cluster analysis (Appendix: Fig. A3). These were locations occurring predominantly (1) in the sea ice zone off East Antarctica and in the north of the Ross Sea, (2) between the Sub-Antarctic Front and the southern boundary of the Antarctic Circumpolar Current Front, (3) over the 1000-m contour of the coast of East Antarctica, (4) over the 1000-m contour of the Campbell Island Plateau, New Zealand, and (5) above the Sub-Antarctic Front. We combined the locations from habitat five with those of
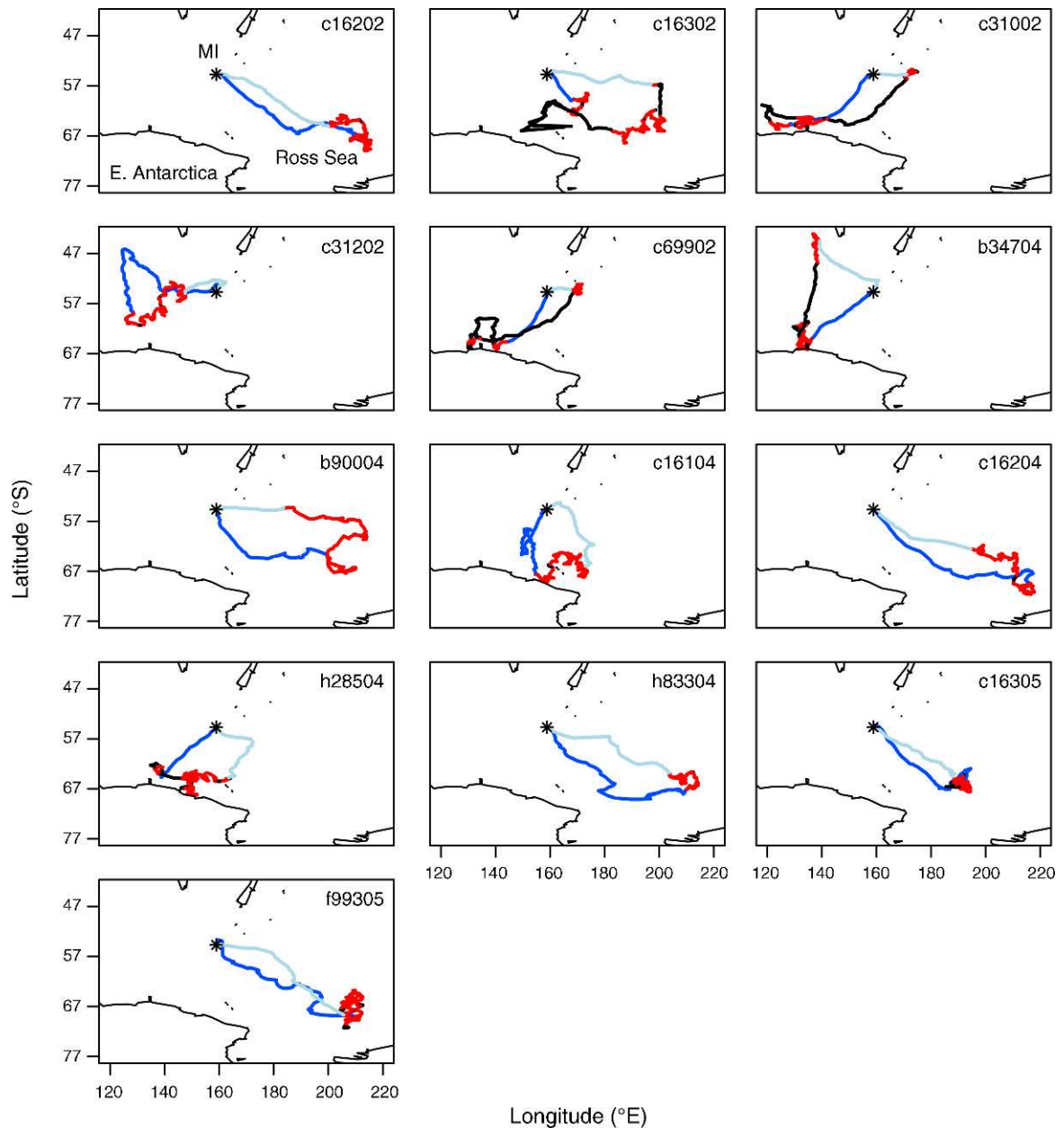
FIG. 2. Maps representing the movement path of each seal for its entire foraging trip. Seal ID is indicated in the top right of each map. Each seal's path is color coded by behavioral state: blue, outward transit; red, search; black, transit between patches; and light blue, inward transit. Maps show the bottom of Tasmania and New Zealand (top) and the coast of East Antarctica (bottom). The black asterisks show Macquarie Island.

habitat two as they did not comprise a large enough sample to include as a separate cluster and were functionally similar in that they were within the major Antarctic Circumpolar Current fronts. We omitted from the analyses the locations associated with habitat four because they did not comprise a large enough sample to include as a separate cluster and were functionally too different from the East Antarctic shelf to combine. We therefore ended up with three habitat groups that we

termed "shelf," "oceanic," and "sea ice" habitats (Fig. 3a). The ice habitat was the most commonly used when in search, with 50% of search locations occurring there, followed by the oceanic habitat (42%) and last, the shelf habitat (8%). When in search, the majority of the locations were south of the major Antarctic Circumpolar Current fronts (Fig. 3b). The distances to ice edge and water depth for each of the habitats were 975.52 ± 515.93 km and 3948.83 ± 717.22 m (oceanic), 184.03 ±
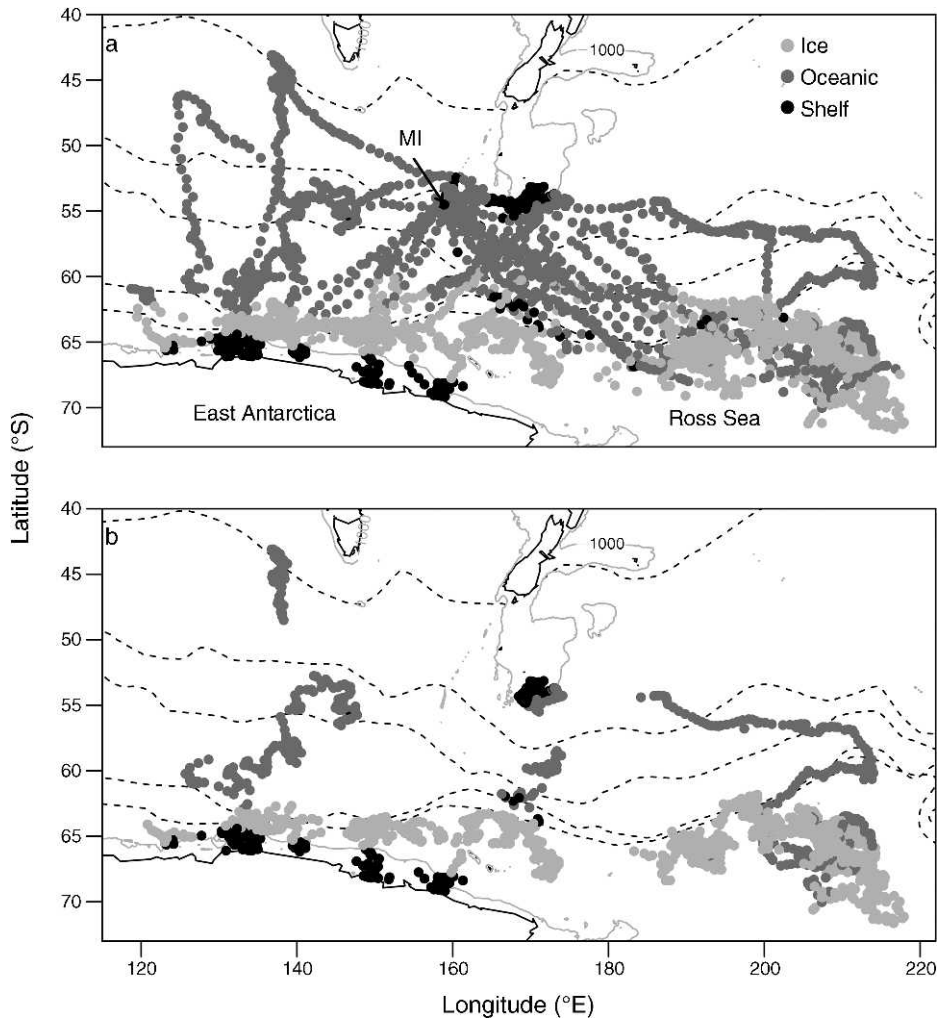
FIG. 3. (a) All locations for all seals for their total post-molt foraging trip coded in grayscale by the habitat classifications found by the cluster analysis. (b) Only search locations coded by habitat. Maps show the bottom of Tasmania and New Zealand in the top of the map and the coast of East Antarctica on the bottom of the map. The 1000-m contour is shown in gray. The major Antarctic circumpolar current fronts (dashed lines) are shown from north to south: Subtropical Front, Sub-Antarctic Front, Antarctic Polar Front, and Southern Boundary of Antarctic Circumpolar Current Front.

116.11 km and 3496.64 ± 555.09 m (ice), and 123.35 ± 91.13 km and 713.96 ± 614.15 m (shelf), respectively.

Area-restricted search validation

The highest-ranked model describing whether a seal was in or out of search state included change in relative lipid content, number of daily speed spikes, habitat type, and interactions and explained 25% of the deviance (Table 1). There was a positive relationship between the daily probability of being in search mode and daily relative lipid change (Fig. 4). At highly negative values of relative lipid change, the probability of being in search mode was low, with the probability increasing rapidly from about −0.5% of body mass for seals in ice habitat and −0.25% for seals in shelf habitat (Fig. 4). Seals in oceanic habitat had a 0–30% chance of being in search mode across the full range of relative lipid change

(Fig. 4), suggesting that seals did not engage in search mode in oceanic habitat as often as in the other two habitats, although they still gained relative lipid.

Contrary to expectations, the number of daily speed spikes (a proxy for prey encounters) followed the opposite trend to relative lipid gain, and there was an interaction with habitat (Fig. 5). There was a negative relationship between the daily probability of being in search mode and the number of daily speed spikes, but only in ice and oceanic habitats (Fig. 5). In shelf habitat, there was a high probability of being in search mode across the full range of prey encounters (Fig. 5), suggesting that seals did not engage in transit in shelf habitat as often as in the other two habitats. There was, however, higher variability in the predictions for shelf habitat (Fig. 5). At lower rates of prey encounter, the probability of being in search mode was high, with the

TABLE 1. Ranked generalized linear mixed-effects models of behavioral state (search or transit) explained by change in relative lipid (FAT), number of speed spikes (SS), habitat (HAB), and random effects (individual seal [ID] nested in year [YR]) for southern elephant seals (*Mirounga leonina*).

Model	%DE	AIC$_c$	ΔAIC$_c$	wAIC
~FAT + SS + HAB + FAT × HAB + SS × HAB + (1 | YR/ID)	24.83	2984.58	0.00	0.99
~FAT + SS + HAB + SS × HAB + (1 | YR/ID)	24.47	2994.54	9.96	<0.01
~FAT + SS + HAB + FAT × HAB + (1 | YR/ID)	24.06	3010.69	26.11	<0.01
~FAT + SS + HAB + (1 | YR/ID)	23.55	3026.69	42.11	<0.01
~FAT + SS + HAB + SS × FAT + (1 | YR/ID)	23.09	3046.81	62.24	<0.01
~SS + HAB + (1 | YR/ID)	22.24	3075.95	91.38	<0.01
~HAB + (1 | YR/ID)	16.23	3310.97	326.40	<0.01
~SS + (1 | YR/ID)	10.74	3524.82	540.24	<0.01
~FAT + (1 | YR/ID)	2.64	3843.89	859.31	<0.01
~1 + (1 | YR/ID)	0.00	3945.83	961.26	<0.01

Note: Shown are the percentage deviance explained (%DE), Akaike's information criterion corrected for small samples (AIC$_c$), change in AIC$_c$ relative to the top-ranked model (ΔAIC$_c$), and AIC$_c$ weights (wAIC).

probability decreasing rapidly ~300 spikes per day for seals in ice habitat (Fig. 5). Seals in oceanic habitat had a 0–60% chance of being in search mode across the full range of daily speed spikes (Fig. 5), again suggesting that seals did not engage in search mode in oceanic habitat as often as often as in the other two habitats.

There was little evidence for a difference in daily relative lipid change between outward transit (0.044% ± 0.121% of body mass) and search mode (0.035% ± 0.140% of body mass) (wAIC$_c$ = 0.28), with the intercept model (wAIC$_c$ = 0.72; ER = 2.57) having higher support. However, the daily rate of speed spikes did vary between search (227.67 ± 109.60) and outward transit (318.95 ± 87.16), with the slope model (wAIC$_c$ = 0.99) having much higher support than the intercept model (wAIC$_c$ = 0.01). Thus, the change from outward transit to search behavior was not associated with a change in intake rate, but it was associated with a change in the number of

daily speed spikes; however, this relationship was negative.

Habitat-dependent foraging success

The daily rate of relative lipid change in search mode varied with habitat; the slope model (wAIC$_c$ = 0.97) had much higher support than the intercept model (wAIC$_c$ = 0.03; ER = 32.3). When searching, seals in oceanic habitat gained the least relative lipid (0.016% ± 0.014% body mass/d, mean ± SD; Fig. 6). Seals in the ice habitat were intermediate (0.035% ± 0.008%), and those foraging in shelf habitat had the highest rates (0.137% ± 0.016%; Fig. 6). The latter equates to around a fourfold increase in relative lipid content over the ice habitat and a ninefold increase over the oceanic habitat.

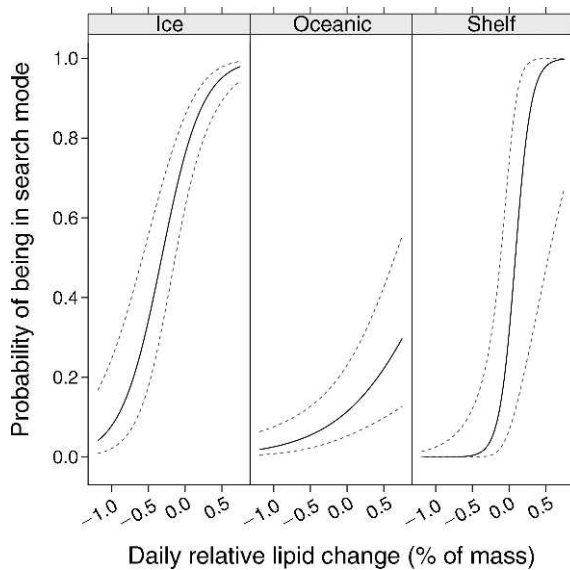When in search mode, the number of speed spikes per day was lowest in ice habitat (197.29 ± 5.76), with

FIG. 4. Population-averaged within-seal probability of being in search mode vs. daily relative lipid gain for each habitat. Dashed lines represent ±2 SE.
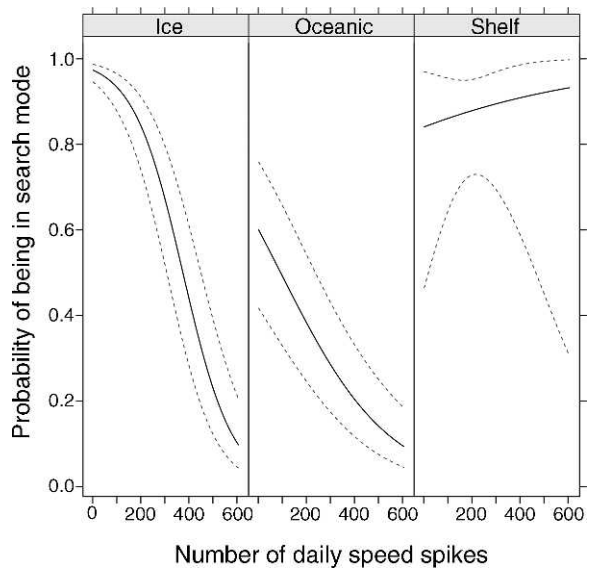

FIG. 5. Population-averaged within-seal probability of being in search mode vs. the number of daily speed spikes (assumed to be a proxy for prey encounter rate) for each habitat. Dashed lines represent ±2 SE.
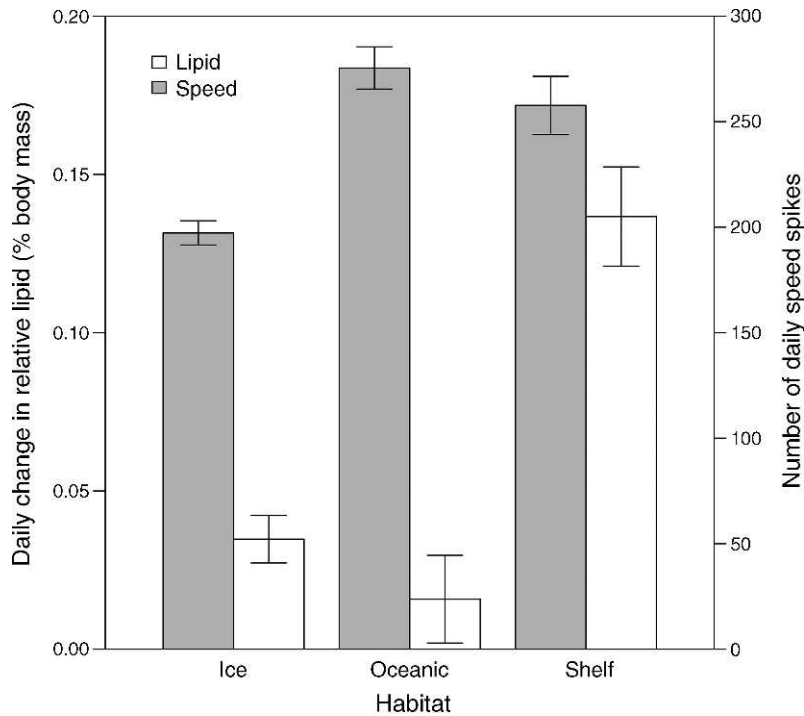
Fig. 6. Daily change in relative lipid content (mean ± 2 SE) (white bars, primary vertical axis) and total daily speed spikes (gray bars, secondary vertical axis). Data plotted are from search mode only.

oceanic (275.46 ± 10.02) and shelf habitat (257.71 ± 13.80) being similar (Fig. 6). There was majority support (wAIC$_c$ = 0.58) for the slope model on the relationship between the daily rate of speed spikes and habitat over the intercept model (wAIC$_c$ = 0.42; ER = 1.4).

DISCUSSION

We provide the first empirical evidence linking area-restricted search and foraging success for a wide-ranging predator. Predators are thought to increase their encounter rates with prey by regulating behavior in response to prey and searching more intensively in areas where resources are relatively high (Kareiva and Odell 1987, Hill et al. 2003). There was a positive relationship between probability of being in search mode and foraging success as identified by change in relative lipid content but the seals did not appear to regulate broadscale movement in response to foraging success. Foraging success in outward transit and in area-restricted search was the same. Animals exhibiting foraging site fidelity are thought to have some expectation of the locations where successful foraging occurred during previous trips (Schmidt 2001, Bradshaw et al. 2004, Weimerskirch 2007). The elephant seals had directed movement predominantly south of the major Antarctic Circumpolar Current fronts, even though they also foraged successfully during outward transit (without subsequently slowing down in these areas). This suggests that they had an expectation of higher energetic gains beyond the regions of transit. These findings

demonstrated the importance of integrating information on foraging success and considering life history strategies (e.g., foraging site fidelity) when interpreting track-based estimates of search effort.

Predictors of changes in movement behavior

Habitat was the strongest predictor of being in search mode. There was low probability of being in search mode in oceanic habitat, suggesting that oceanic habitat is less favored for area-restricted searches. These results are consistent with past studies, which found that seals traveled directly to their principal foraging areas mostly below the southern boundary of the Antarctic Circumpolar Current Front (Hindell et al. 1991, Bradshaw et al. 2003, 2004, Bailleul et al. 2007b, Biuw et al. 2007, Thums et al. 2008).

The proxy for prey encounter rate (number of daily speed spikes) was the next most important predictor of search mode, but counterintuitively, there was a negative relationship between the probability of being in search mode and the number of daily speed spikes (cf. Horsburgh et al. 2008). This pattern suggests that the total amount of energy gained might be more important than the encounter rate. Thus, the prey field could have changed from predominately small, abundant prey of low nutritive value (e.g., fish species of the family Myctophidae) when in transit, to one where larger, rarer prey of greater energetic value dominated (e.g., fish species of the families Nototheniidae and Moridae). Indeed, the abundance of key prey species is a better

PLATE 1. Package incorporating a VTDR and radio transmitter (to assist in recovery) being glued, using two-part epoxy to an adult female southern elephant seal at Macquarie Island, Australia. Photo credit: C. J. A. Bradshaw.

descriptor of foraging success in leatherback turtles than indices of higher productivity (Hays et al. 2006), and the switch from squid to energy-dense fish prey in low latitudes described by Bradshaw et al. (2003) supports our conclusions. Male harbor seals equipped with animal-borne video systems adopted different foraging tactics when pursuing sedentary bottom dwelling or active schooling prey (Bowen et al. 2002). Similarly variation in penguin swim speed and patterns of acceleration and deceleration events indicated different prey (Ropert-Coudert et al. 2000, Wilson et al. 2002). Alternatively, speed-spike frequency might not be an effective index of prey encounter because seals could also be feeding on items not requiring a burst of speed to catch.

While change in relative lipid content explained the lowest amount of deviance in the models considered, and the saturated model accounted for 25% of the deviance, this is a convincing finding given that numerous other attempts to relate area-restricted search patterns to foraging success have failed to detect any relationship (e.g., Robinson et al. 2007, Weimerskirch 2007, Simmons et al. 2010).

Low-precision geolocation data collected at low frequency (twice daily) might also be unable to detect fine-scale tortuosity (Pinaud 2008). The spatial scale of the search area (250 km) was larger than that found for southern elephant seals from Kerguelen Island (104.7 ± 67.3 km, mean ± SD; Bailleul et al. 2008) and for female northern elephant seals (*M. angustirostris*: 81.43 ± 32.37 km; Robinson et al. 2007). Finer spatial scales of foraging selection might be expected for northern elephant seal females because they tend to forage along their tracks rather than concentrating feeding in one

larger area (Le Boeuf et al. 2000). It is possible that low-frequency geolocations might bias estimated use scales upward, thus missing some fine-scale search areas. However, the similar results derived from medium-precision (Argos) and low-precision (geolocation) data from instruments deployed on the same animal suggest that at least for our data this problem is minimized.

Adjustment in movement in relation to foraging success

We tested for a difference in relative lipid gain between outward transit and search and found no clear distinction. Thus and in contrast to predictions from search theory, it appears that seals did not change their movement behavior (from a straight to sinuous path) in response to foraging success. This result supports the hypothesis that elephant seals possess a prior expectation of higher gains in areas known to be productive in previous years. Indeed, information use by animals can become an overriding mechanism driving movement (Dall et al. 2005). While some animal movement behavior is driven by factors other than resource distribution (e.g., rest, predator avoidance), elephant seals engage primarily in the long winter foraging trip to accumulate energy to fuel gestation and on-shore lactation (Fedak et al. 1994); thus, their movements are likely to be tightly coupled to food resources. The quantification of the relative lipid gained during outward transit shows that this is not trivial, opportunistic foraging and is likely an important strategy for animals that deplete the majority of their energy reserves such as elephant seals during on-shore fasts. Individuals will be highly motivated to restore energy reserves that might also be required to fuel their travel to their more

southerly feeding areas. This pattern of successful foraging associated with directed movement has also been observed or inferred in many other species (Sims et al. 2003, Austin et al. 2006, Weimerskirch et al. 2007, Kuhn et al. 2009), suggesting that the pattern is more common than previously thought. For example, for wandering albatross most prey were caught during directed movement rather than in area-restricted search (Weimerskirch et al. 2007).

Habitat-dependent foraging success

Our study inferred a large marine predator's relative foraging success in different marine habitats. Notably, the shelf off East Antarctica was highly productive, with daily rates of gain more than four times that of other habitats. Continental shelves in the Southern Ocean have the greatest area-normalized rates of primary production in that region (Arrigo et al. 2008). Examination of the tracks shows that seals foraging on the shelf went there early in the season, but left to forage in other areas. It remains unclear why female southern elephant seals do not remain in this productive zone for longer. The hypothesis of encroaching sea ice acting as a barrier appears to be the most likely explanation; however, the observation that similar-sized subadult males remain (Bailleul et al. 2007a) indicates the influence of some other variable such as different energetic requirements (Bailleul et al. 2007a) or predation risk (Verdolin 2006) could also be influential. Despite the large size of elephant seals and the low probability that predation limits their population growth (McMahon et al. 2005), elephant seals might still be at risk of attack from several shark and toothed whale species (Guinet 1992, Campagna et al. 1995). The high profitability in shelf habitat suggests that it might also be more predictable and that lower temporal variation in local conditions on the shelf provides more consistent prey resources than surrounding areas. Indeed, predictable pulses of food availability are thought to drive seasonal movements because breeding success depends on the amount of food available to parents for building body reserves prior to provisioning offspring (Sinclair 1983).

Conclusion

Southern elephant seals use a combination of movement strategies including (1) continuous directed travel while foraging on randomly distributed, abundant small prey items and (2) slow and sinuous movements with high residency within mesoscale productive and predictable resource patches. Although marine predators might have prior knowledge of the geographical locations of productive foraging areas, they are unlikely to have precise knowledge of the prey gradients within these areas because prey location differs in response to local conditions within and between years (Sims et al. 2006). Thus, prior knowledge of profitable and predictable areas appears to drive broadscale movements in this

species, and area-restricted search is used to focus search behavior once in these areas. In conclusion, the highest foraging success was associated with area-restricted search but movement patterns did not arise solely in response to changes in prey encounter and foraging success. Rather, expectations of prey availability and potentially changing prey quality also play a role, and we contend that animals displaying foraging site fidelity might not always move in ways predicted from search theory.

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APPENDIX

Figures showing examples of three seals' first-passage time plotted against day of trip and their corresponding density plots, variance in log-transformed first-passage time as a function of spatial scale for locations derived from light data and locations derived by Argos Satellites, and a dendrogram representing the results from the hierarchical cluster analysis on all seal locations (*Ecological Archives* E092-105-A1).