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BEHAVIORAL ECOLOGY - ORIGINAL RESEARCH

Stable isotope analyses reveal individual variability in the trophic ecology of a top marine predator, the southern elephant seal

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Abstract Identifying individuals' foraging strategies is critical to understanding the ecology of a species, and can provide the means to predict possible ecological responses to environmental change. Our study combines stable isotope analysis and satellite telemetry to study the variability in individual foraging strategies of adult female southern elephant seals (*Mirounga leonina*). Our hypothesis is that female elephant seals from the Western Antarctica Peninsula (WAP) display individual specialization in their diets. We captured adult female elephant seals ($n = 56$, 2005–2009) at Livingston Island (Antarctica), and instrumented them with SMRU-CTD satellite tags. We collected blood, fur, and vibrissae samples for $\delta^{13}C$ and $\delta^{15}N$ analyses. The mean values for all vibrissae were $-21.0 \pm 0.7‰$ for $\delta^{13}C$, and $10.4 \pm 0.8‰$, for $\delta^{15}N$. The individual variability of $\delta^{13}C$ (60%) was more important than the within-individual variability (40%) in explaining the total variance observed in our data. For $\delta^{15}N$, the results showed the opposite trend, with the within-individual variability (64%) contributing more to the total variance than the individual variability (36%), likely associated with the effect that the fasting periods have on $\delta^{15}N$ values. Most individuals were specialists, as inferred from the low intra-individual variability of $\delta^{13}C$ values with respect to the population variability, with half the individuals utilizing 31% or less of their available niche. We found eight different foraging strategies for these animals. Female elephant seals from the WAP are a diverse group of predators with individuals utilizing only a small portion of the total available niche, with the consequent potential to expand their foraging habits to exploit other resources or environments in the Southern Ocean.

Keywords *Mirounga leonina* · Foraging strategies · $\delta^{13}C$ · $\delta^{15}N$ · Telemetry

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Introduction

Knowledge about the food habits of marine top predators is critical for understanding their role in marine ecosystems

because it provides information on feeding locations, seasonal prey utilization, and prey availability. Marine predators must be able to acquire food resources in highly heterogeneous and unpredictable environments, and their foraging behavior is inextricably linked to prey distribution and abundance (Harcourt et al. 2002; McCafferty et al. 1998). We could expect that, in response to the low predictability of the marine environment, individuals from the same species should tend to reduce intra-specific competition by displaying resource partitioning in order to maximize their foraging success.

A specialist species is composed of individuals that consume the same type of prey, with very little or no variation among individuals. Conversely, there are at least two potential mechanisms that can explain a generalist strategy for a species: (1) generalist individuals, or individuals exploiting a wide variety of prey, displaying large within-individual variation, and (2) specialist individuals, each individual specializing on a restricted and particular subset of resources that is different from that being used by other individuals of the same species, displaying large individual variation (Araujo et al. 2007; Bearhop et al. 2004; Bolnick et al. 2007; Harcourt 1993; Newsome et al. 2009; Riedman and Estes 1988; Woo et al. 2008). Thus, the identification of foraging strategies of individuals is critical to our understanding of the ecology of a particular species, and can provide tools to understand and predict possible ecological responses to environmental change.

Naturally occurring stable isotopes of carbon ($^{13}C/^{12}C$, or $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, or $\delta^{15}N$) are commonly used to study trophic relationships and feeding habitats of marine mammals (Hirons et al. 2001a; Hobson et al. 1996; Vander Zanden and Rasmussen 2001). Additionally, large-scale variations in $\delta^{13}C$ and $\delta^{15}N$ values allow us to reconstruct migratory movements of animals, and provide a useful metric to determine foraging grounds in animals whose foraging habitats encompass hundreds of kilometers (Kelly 2000; Newsome et al. 2006, 2007). Given the variability in tissue-specific metabolic turnover rates, we can also gain information from different time scales by analyzing isotopic ratios in different tissues (Hobson et al. 1996; Kelly 2000). The study of metabolically slower and continuously growing tissue, such as vibrissae or nails, integrates information on the feeding ecology on scales of several months to years, and provides a temporal (longitudinal) record of dietary change because these tissues can be serially sampled (Cherel et al. 2009; Newsome et al. 2009).

A less explored application of stable isotopes in ecology is their use to study individuality in niche width and foraging strategies (Araujo et al. 2007; Bearhop et al. 2004; Jaeger et al. 2010; Newsome et al. 2009). Briefly, we can use the total variance in stable isotopes between individuals as an indicator of the dietary variation among individuals in a population, while the variance along a continuously growing inert tissue, i.e., vibrissae, can be considered an indicator of dietary variation of a particular individual (see Bearhop et al. 2004; Newsome et al. 2009 for assumptions).

Studies based on at-sea movement and diving patterns of pinnipeds have successfully identified the existence of different individual foraging strategies (Lea et al. 2002; Villegas-Amtmann et al. 2008; Weise et al. 2010). Whereas some studies have shown separation in space according to foraging strategies (Villegas-Amtmann et al. 2008), others have shown spatial overlap among strategies, indicating a degree of niche separation among individuals from the same sex or age class that effectively occupy the same areas (Weise et al. 2010). However, the study of individual strategies in pinnipeds, and other cryptic species, can greatly benefit from using a combination of telemetry data with stable isotopes analysis, since this will provide us with complimentary information on behavior, habitat use and dietary preferences from the level of individuals up to populations, and on a range of temporal and spatial scales (Bailleul et al. 2010; Newsome et al. 2010).

Southern elephant seals *Mirounga leonina* play an important ecological role in the Southern Ocean and adjacent ecosystems as major consumers of fish and squid (Bradshaw et al. 2004a; Daneri and Carlini 2002). Differences in foraging strategies and niche separation have been well documented in southern elephant seals from different age and sex groups (Bailleul et al. 2010; Lewis et al. 2006; Newland et al. 2009), although previous studies have focused mostly on individual strategies in adult males (Lewis et al. 2006) or juvenile seals (Eder et al. 2010). Regardless of their intrinsic importance of adult females for the population, and the extensive literature on their foraging ecology as a group, the existence of individual differences within this population class has been somehow less explored, despite the fact that significant individual variation can occur within sex, age, or other a priori morphological groups (Bolnick et al. 2003).

Along the Western Antarctic Peninsula (WAP), southern elephant seals often venture into the continental shelf waters (Costa et al. 2010; Field et al. 2001; McConnell and Fedak 1996). Adult female elephant seals utilize some islands of the WAP as haul-out sites, mainly during the molting season (January–February), but also during the reproductive season (October–November), when adults give birth to a fluctuating number of pups every year. Recent tracking data suggest the existence of at least two main foraging strategies of adult females elephant seals tagged in the WAP: about 85% of instrumented adult females display benthic foraging associated with the shelf break along the WAP and the Bellingshausen Sea, while the remaining 15% have an open water mesopelagic foraging strategy (Costa et al. 2010).

Since the majority of the individual adult female elephant seals from the WAP utilize common foraging areas, we expect them to exhibit mechanisms to minimize competition among individuals. Hence, we hypothesize that shelf-foraging elephant seals, which represent the majority of the WAP animals, will display high individual specialization in their diets, as observed from the stable isotopes record along their vibrissae. Consequently, we predict that pelagic foragers, a much smaller fraction of the individuals from the WAP, will have a more generalist strategy. Further, we hypothesize the existence of different foraging strategies for shelf foraging elephant seals, as defined from the stable isotope values, movement patterns, and diving behavior. Specifically, our aims are (1) to describe the individual variations in the use of resources (i.e. individual specialization or individual generalization), and (2) to identify foraging strategies used by female southern elephant seals from the WAP.

Materials and methods

Animal handling and sample collection

Animal captures were conducted under National Marine Fisheries Service permit No. 87-1851-00. All animal procedures were approved by the Institutional Animal Care and Use Committee (IACUC) at University of California Santa Cruz. Adult female southern elephant seals ($n = 56$) were captured and instrumented during the late molting season (January–February) at Cape Shirreff, Livingston Island (62°39′S, 60°46′W), South Shetland Islands (Electronic Supplementary Material 1), between 2005 and 2009 (Table 1). Animals were immobilized with tiletamine HCl/zolazepam HCl (Telazol®, Fort Dodge Animal Health) administered intramuscularly (1.0 mg/100 kg), and immobilization was maintained with intravenous injections of Ketamine (100 mg/ml, Ketaset; Fort Dodge Animal Health). Females were weighed (Measurement Systems International, capacity 1,000 ± 1 kg) and body length was measured.

During the capture, we selected the longest vibrissae for each animal, and collected it for analysis by pulling it from the root using a pair of tweezers. Samples were washed with distilled water and detergent and allowed to air dry, and then rinsed in an ultrasonic bath with petroleum ether for 15 min in order to eliminate any lipids and debris from the samples. Vibrissae were measured to the nearest cm, and cut into 1-cm segments, with the distal and proximal ends identified. A 0.5 ± 0.05-mg sub-sample was obtained from the proximal end of each segment.

In addition to vibrissae and serum, in 2009 ($n_{2009} = 15$) we also collected fur, serum and red blood cells (RBC) to determine variability in $\delta^{13}C$ and $\delta^{15}N$ in tissues of differing metabolic activity. Fur samples were cleaned following the same protocol as with vibrissae samples. Blood samples were collected from the extradural vein using serum vacutainers and heparinized vacutainers, for serum and RBC, respectively. After centrifugation, serum and RBC samples were frozen until analysis at −20°C. In the laboratory, serum and RBC samples were freeze-dried and lipids were extracted in petroleum ether using an accelerated solvent extractor (Dionex; Light Stable Isotope Lab, UCSC). Lipid-free serum and RBC samples were then weighed (0.5 ± 0.05 mg) for stable isotope analysis.

Six of the females in our study were recaptured 1 year after the first handling, and a second vibrissa sample was collected to examine between-year variability in foraging strategy of adult female southern elephant seals (Table 2).

As part of a concurrent study, the females were instrumented with conductivity-temperature-depth (CTD) satellite relay data loggers (SRDL) (Sea Mammal Research Unit, University of St Andrews). These instruments allowed us to track individual seals and monitor their diving behavior during their 8 months post-molt foraging migration following their capture (see Costa et al. 2010).

Sample analysis

Samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ using a Carbo-Elba elemental analyzer interfaced with a Finnigan Delta

Table 1 Vibrissae stable isotope values ($\delta^{13}C$, $\delta^{15}N$), C:N ratio, body mass and length of adult female *Mirounga leonina* from the Western Antarctica Peninsula, 2005–2009

Year	*n*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	**C:N**	**Mass** (kg)	**Length** (m)
2005	6	−21.23 ± 0.69	10.38 ± 0.26	2.98 ± 0.06	419 ± 98.67	2.86 ± 0.14
2006	12	−21.11 ± 0.8	10.43 ± 0.5	2.94 ± 0.03	362.17 ± 65.21	2.73 ± 0.18
2007	12	−21.24 ± 0.55	10.35 ± 0.37	2.99 ± 0.02	343.09 ± 35.6	2.71 ± 0.08
2008	11	−20.9 ± 0.5	10.28 ± 0.43	2.97 ± 0.02	344.6 ± 51.55	2.67 ± 0.1
2009	15	−21.28 ± 0.31	10.64 ± 0.66	2.96 ± 0.02	422.92 ± 67.85	2.79 ± 0.11

Results are presented as mean ± standard deviation (SD). Variables shown in bold indicate significant differences between year, found only for C:N Ratio (ANOVA, $F_{4,50} = 3.93$, $p = 0.008$), body mass (ANOVA, $F_{4,47} = 4.001$, $p = 0.007$) and length (ANOVA, $F_{4,50} = 3.022$, $p = 0.026$)

Table 2 Variability in isotopic values of vibrissae samples of adult female *Mirounga leonina* collected in consecutive years from the same individuals

Individual	δ^{13}C		δ^{15}N	
	F-ratio	*p*	*F*-ratio	*P*
SE06-01	2.42	0.15	0.013	0.91
SE06-08	1.62	0.22	0.2	0.66
SE06-12	0.285	0.6	0.116	0.74
SE07-01	0.031	0.86	1.235	0.283
SE07-03	1.65	0.22	0	0.98
SE07-07	**15.469**	**0.001**	1.341	0.262

Values in bold indicate significant differences between years

Plus XP mass-spectrometer (Light Stable Isotope Lab, UCSC). Experimental precision, estimated as the standard deviation of replicates of our within-run standards (Pugel) was 0.06‰ for δ^{13}C and 0.1‰ for δ^{15}N ($n = 209$).

Data analysis

All data were tested for normality and homogeneity of variance before analysis. Non-parametric statistics were used when assumptions of normality and homogeneity of variance were not satisfied and transformations did not improve our data. Significance level was set at 95% for all statistical tests. Results are reported as mean ± standard deviation (SD), unless otherwise stated.

Individual variation (specialization)

We used a Mixed-Effect Model Variance Component Analysis to determine the source of the observed variability in isotopic values (Table 1), selecting year as the fixed variable, and individuals nested within year and Body Condition Index (mass/length^2, BCI) as the random components in our model. The error (residual) term in our model corresponds to the intra-individual variability in δ^{13}C and δ^{15}N.

To evaluate the individual variability in trophic niche of elephant seals, we followed the approach proposed by Bearhop et al. (2004), and used by Newsome et al. (2009) on sea otters (*Enhydra lutris*) and Jaeger et al. (2010) on procellariiforms. The between-individual component (BIC) was estimated as the total standard deviation in the isotopic values of our sampled population. The within-individual component (WIC) was the along-vibrissae standard deviation in isotopes for a particular individual. Given the confounding factors that might affect δ^{15}N (i.e., periods of fasting, which affect the δ^{15}N values), we only used the standard deviation of δ^{13}C for this portion of our analysis. The degree of individual specialization (*S*) was calculated accordingly as $S = \text{WIC/TNW}$, where, *S* is the Specialization Index, and TNW is the total niche width (WIC + BIC). Lower values of *S* indicate higher specialization, while higher *S* values indicate generalist individuals. For this dataset, we defined an extreme specialist as an individual occupying less than 20% of the available niche ($S \leq 0.2$), whereas those occupying 50% or more of the niche ($S \geq 0.5$) were defined as generalists.

Foraging strategies

Tracking data from our seals were filtered using a particle filter (Tremblay et al. 2009), and diving locations were then estimated by interpolation along the resultant filtered track. Water column depth for each dive was obtained for each dive location using cubic interpolation from the ETOPO 1 dataset. Six different parameters were obtained from the SRDLs: (1) dive depth (m), (2) bottom time (%), or percentage time that the seal spent within 80% of its maximum dive depth, (3) dive ratio, ratio between the dive depth and bathymetry at that location, (4) transit rate (km h^{-1}), (5) angle between successive locations, and (6) distance to rookery (km). We calculated utilization distribution probabilities (kernel analysis) based on the tracking data (see Costa et al. 2010), weighted by tracking effort. Smoothing parameters (*h*) for the kernel analyses were calculated using the ad hoc method (Worton 1989), within the package *adehabitat* in *R*.

We used a complimentary approach based on the use of both tracking and diving, and isotopic data to investigate the individual variability in foraging strategies of adult female southern elephant seals from the WAP. After checking for cross-correlation among variables (Pearson correlation), variables were analyzed using principal component analysis (PCA) with a varimax rotation. Seven principal components (PCs) accounted for 84.7% of the variance and were loaded into a hierarchical cluster analysis (HCA), using Ward Linkage and Euclidean distance. The optimal number of clusters obtained was determined using a combination of the root mean square standard deviation (RMSSTD) and pseudo-*F* indices.

Vibrissae and foraging ecology

The variation of stable isotopes along the vibrissae of mammals has been used by several authors in studies of trophic ecology of different species (e.g., Cherel et al. 2009; Eder et al. 2010; Lewis et al. 2006; Newland et al. 2011; Newsome et al. 2009), yet there are several unknowns regarding growth rate and retention of vibrissae, which complicates the interpretation of the results of such studies. Some attempts have been conducted to estimate a rate of growth of vibrissae in both otariids and phocids,

with values that range between 0.1 and 0.8 mm day^{-1} (Greaves et al. 2004; Hall-Aspland et al. 2005; Hirons et al. 2001b). If we apply these rates to elephant seals, then the time period reflected in our vibrissae samples (mean length 11.1 cm) ranges between 139 and 1,110 days (mean of 246 days). Additionally, the shedding pattern of vibrissae is asynchronic (Greaves et al. 2004; Hirons et al. 2001b; Newland et al. 2011), and it is unlikely that phocids grow their vibrissae continuously or retain them between years, which makes attempts to trace back the changes in diet using vibrissae isotopic data problematic. However, for the purposes of our study, we assume that the along-vibrissae isotopic data represent tissue metabolized during the previous period (year) at sea, as suggested by Newland et al. (2011).

Results

A total of 745 vibrissae segments were analyzed for δ^{13}C and δ^{15}N. Mean vibrissae length was 11.1 ± 2.5 cm. The mean values for all vibrissae including the basal segment were −21.1 ± 0.8‰ for δ^{13}C and 10.5 ± 0.9‰ for δ^{15}N. The C:N ratio (% weight) was 3.0 ± 0.1. We found significant variation in the C:N ratio (% weight) along the vibrissae (Kruskal–Wallis, $H = 232.659$, $p < 0.001$), due to a significantly higher C:N ratio of the proximal segment compared with the rest of the vibrissae (post hoc Dunn's method), and consequently, we eliminated this segment from further analysis. It is likely that the proximal segment is not pure keratin, but a combination of different tissues that form the follicle. After eliminating the basal segments from our sample ($n = 683$), mean values were −21.0 ± 0.7‰, 10.4 ± 0.8‰, and 2.9 ± 0.1, for δ^{13}C, δ^{15}N and C:N ratio, respectively.

A multi-tissue comparison of individuals captured in 2009 ($n_{2009} = 15$) provided further evidence of the different isotopic values at the base of the vibrissae (Fig. 1). Based on tissue-specific turnover rates, serum represents a period of days prior to its collection (i.e., fasting period), while RBCs are representative of a longer period of time, in the order of weeks to a month (i.e., foraging at-sea) (Dalerum and Angerbjorn 2005; Hobson and Clark 1992; Kelly 2000). Fur is grown during the fasting period on land just prior to sampling. Both serum and fur are enriched in δ^{15}N compared with RBC. The base of the vibrissae lines up with serum and fur in δ^{15}N (Fig. 1), suggesting that this section corresponds to the fasting period, not the foraging period that we are interested in for the purposes of this paper.

Individual variation (specialization)

We analyzed the between-year variability in the foraging strategies of individual adult female elephant seals in a subsample of animals that were opportunistically recaptured the year after the initial sampling ($n = 6$). Our results showed that only one individual significantly differed between years for both isotopic systems, while the rest presented no difference in the along-vibrissae values for either δ^{13}C or δ^{15}N (Table 2). The δ^{13}C and δ^{15}N values did not vary significantly between years (Table 1; ANOVA δ^{13}C $F_{4,50} = 0.89$, $p = 0.47$; δ^{15}N $F_{4,50} = 1.13$, $p = 0.35$), and consequently data were pooled for further analysis. There was a negative relationship between δ^{13}C and mass ($R^2 = 0.096$, $p = 0.025$), and length ($R^2 = 0.01$, $p = 0.019$); whereas δ^{15}N was positively related to mass ($R^2 = 0.123$, $p = 0.011$), and length ($R^2 = 0.023$, $p = 0.001$) (Fig. 3), although in all cases mass and length only accounted for a small amount of the variation.

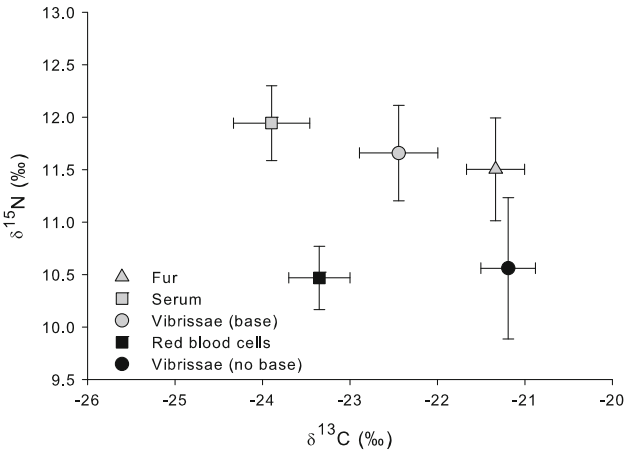

Fig. 1 Multi-tissue comparison of δ^{13}C and δ^{15}N values of adult female southern elephant seals (*Mirounga leonina*), from the Western Antarctica Peninsula ($n = 15$) in 2009. *Symbols* represent mean values and *bars* standard deviations (SD). *Gray symbols* correspond to tissue grown during the molting fast. *Black symbols* correspond to tissue metabolized previous to fasting (i.e., at-sea foraging)

The results from our Mixed-Effect Model Variance Component Analysis indicate that neither Year nor Body Condition Index were significant in explaining the variance of either isotopic system (Table 3). The individual variability of δ^{13}C (60%) is relatively more important than the within-individual variability (40%) in explaining the total variance observed in our data, indicating that female elephant seals are a group of generalist predators composed of individuals that specialize on subsets of resources. For δ^{15}N, the results showed the opposite trend, with the within-individual variability explaining 64% of the variance of this isotope, while the individual variability accounted for 36% of the variance (Table 3), likely associated with the effect that the fasting periods have on δ^{15}N values.

The calculation of the degree of individual specialization S, revealed that adult female elephant seals from the WAP are mostly specialists (Fig. 2). Half the individuals included in this study had specialization indices of 0.31 or

Table 3 Variance component analysis for vibrissae $\delta^{13}C$ and $\delta^{15}N$ data of adult female *Mirounga leonina* from the Western Antarctica Peninsula (ANOVA estimation method, Type III sums of squares)

Effect	Variance explained (%)	
	$\delta^{13}C$	$\delta^{15}N$
Year	NS	NS
Individual (year)	60	36.02
BCI	NS	NS
Intra-individual	40	63.98

Year was selected as a fixed variable, while individuals nested within year and Body Condition Index (BCI) were included as random effects. The error (residual) term corresponds to the intra-individual variability

NS non-significant effect

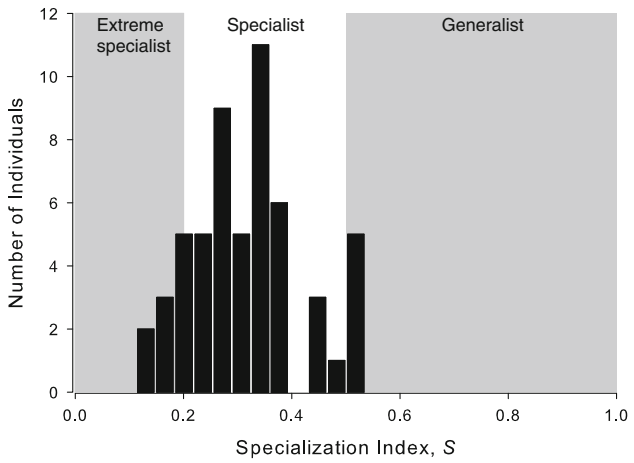

Fig. 2 Frequency distribution of the Specialization index (*S*) of adult female elephant seals (*Mirounga leonina*) from the Western Antarctica Peninsula ($n = 56$). Most of the individuals studied were identified as specialists (*bars with white background*). Extreme specialists are identified as those individuals with an $S \leq 0.2$, whereas generalist individuals have an $S \geq 0.5$

less (Fig. 2). Our analysis indicated the presence of seven extreme specialists ($S \leq 0.2$), while five individuals (9.3% of individuals in our sample) were identified as generalists ($S \geq 0.5$).

Foraging strategies

We identified eight groups within our data, or foraging strategies, which varied in size between 1 and 18 individuals (Fig. 3a) using PCA and HCA. Seven principal components (PCs) explained 84.7% of the variation observed in our data. PC1, PC2, and PC3 were associated with three different sets of variables (movement pattern, diving behavior, and stable isotope values, respectively), while PCs 4–7 corresponded to different combinations of these sets (Electronic Supplementary Material 3). Movement patterns (PC1) explained 24.8% of the variance, while diving (PC2) explained 18.1% and stable isotopes (PC3) 12.6% of the variance. The groups identified in our analysis showed differences in both their isotopic values and foraging behavior, as inferred from the telemetry data. There was a clear distinction between Cluster 1 ($n_{\text{Cluster 1}} = 8$) and the rest of the groups found in our analysis. Cluster 1 was characterized by animals that fed pelagically, as evident from their home range (Fig. 3b), transit rate, diving behavior, and particularly their very low dive ratio (Fig. 4c–d), with a median $\delta^{13}C$ of −20.6‰, and the lowest median $\delta^{15}N$ (9.8‰). All remaining clusters, except Clusters 2 and 6, corresponded to animals that foraged along the shelf break (500 m isobath), or on the shelf of the WAP and Bellingshausen Sea (Fig. 3c–i), and consequently had relatively high dive ratios (Fig. 4d).

A clear structure was observed in the dendrogram for these 'shelf-break' groups (Fig. 3a), and spatial differences in their home ranges and hot spots were evident (Fig. 3c–i). For instance, Cluster 3 had two primary core areas in the northern half of the WAP (Fig. 3d), in addition to having the shallowest dive depths of all clusters (median 304 m) and the second lowest $\delta^{15}N$ (median 10.1‰). Cluster 4 had a well-defined and restricted hot spot on the continental shelf west of Alexander Island (Fig. 3e), while having the deepest dives (median 423 m) and the highest $\delta^{15}N$ (median 10.7‰, Fig. 4b). Individuals from Clusters 5 were highly variable in their $\delta^{13}C$ values, and were among the more generalist groups after Clusters 1 and 8 (median $S = 0.4$), with a core area that extends along the shelf break from Marguerite Bay south, and into the Bellingshausen Sea (Fig. 3f). Cluster 7 included specialist individuals (median $S = 0.3$) with the highest median $\delta^{15}N$ values among all clusters (10.8‰), and were clearly restricted to the mouth of Marguerite Bay on the WAP (Fig. 3h). Cluster 8 included animals that focused their foraging on a restricted section beyond the shelf break west of Alexander Island (and west of the core area of Cluster 4) in the Bellingshausen sea (Fig. 3i), had the lowest $\delta^{13}C$ values of all clusters (median $\delta^{13}C = -21.7$‰, Fig. 4a), and included the most generalist individuals among the shelf foragers (median $S = 0.4$; Fig. 4e).

The only two exceptions within our model of pelagic versus shelf foragers corresponded to Clusters 2 and 6. Cluster 2 included the most extreme generalist individuals of our study animals (median $S = 0.6$; Fig. 4e), with the second highest $\delta^{13}C$ (median $\delta^{13}C = -20.1$‰; Fig. 4a), with the largest core area along the WAP expanding well beyond the shelf break, and some secondary core areas as far as Bellingshausen/Amundsen transition and the Falkland Islands (Fig. 3c). Cluster 6 constitutes a clear outlier within our model. This cluster corresponded to one individual (SE06-12) that fed in the Drake Passage (Fig. 3g),

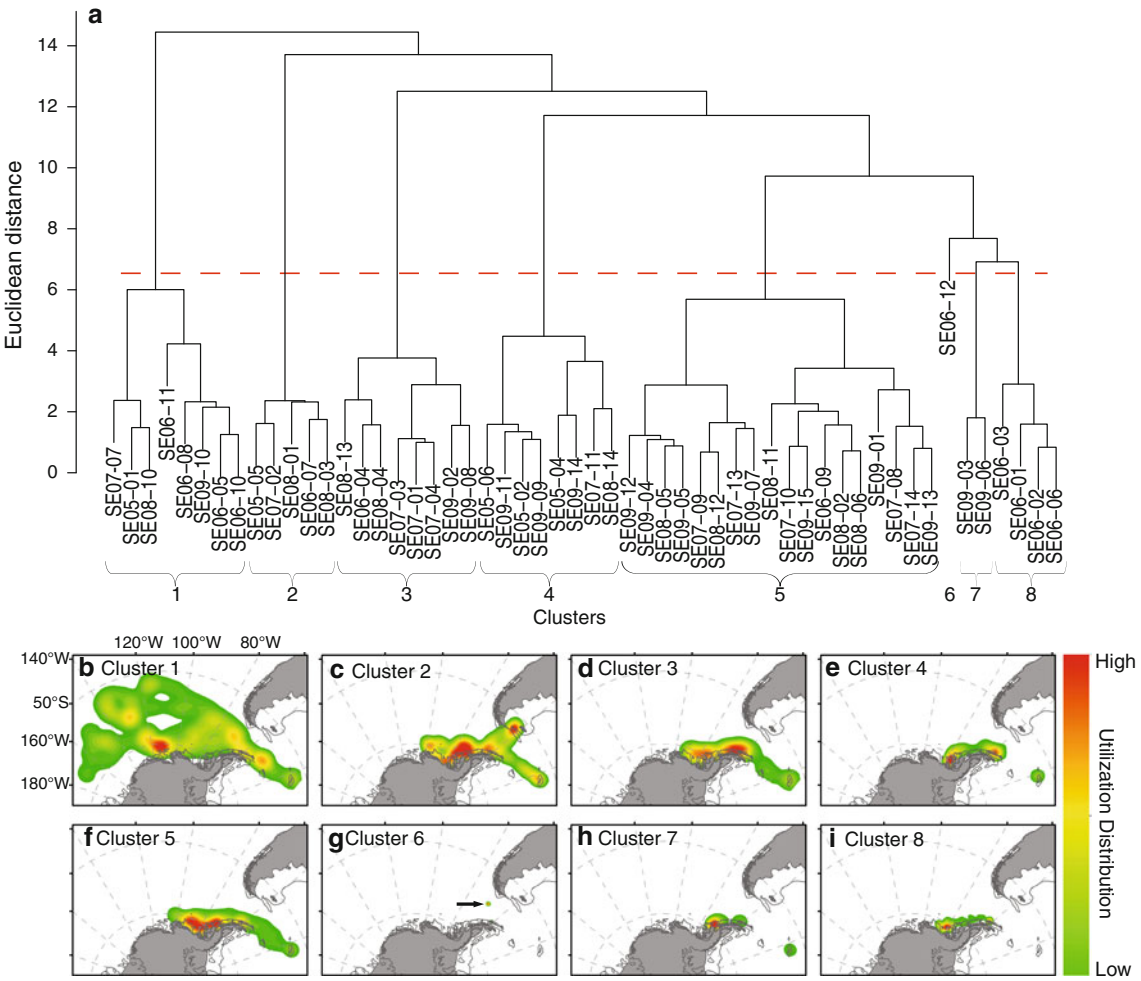

Fig. 3 **a** Cluster analysis of foraging strategies of adult female elephant seals (*Mirounga leonina*) from the Western Antarctica Peninsula determined by Ward Linkage and Euclidean distance. The analysis incorporated a suite of variables (including δ^{13}C and δ^{15}N values and movement and diving data obtained from satellite tags) into seven Principal Components (Varimax rotation). The optimal number of clusters for the model (*dashed red line*) was obtained using the RMSSTD and Pseudo-*F* indexes. Lower panels (**b**–**i**) show the utilization distribution probabilities of the different clusters of individuals identified by kernel analysis. The *arrow* in (**g**) highlights the limited habitat utilized by that individual

characterized by the highest δ^{13}C value among all individuals included in our study ($\delta^{13}C = -19.4‰$), one of the lowest transit rates (0.7 km h^{-1}) and, despite diving to a mean depth of 457 m, it presented a low dive ratio (33.4%), indicating pelagic behavior.

Discussion

We have clearly identified marked individual variability in the trophic ecology of adult female elephant seals from the WAP, using stable isotope analyses (δ^{13}C and δ^{15}N) in conjunction with tracking and diving data. Rather than being uniformly generalist predators, we have identified that a variety of foraging strategies are extant in the WAP population within any single year, ranging from extreme specialists to true generalists.

Vibrissae and foraging ecology

We did not observe a cyclical pattern for vibrissae δ^{13}C or δ^{15}N (Electronic Supplementary Material 2) like the one described for Antarctic fur seals (Cherel et al. 2009), which would indicate that the vibrissae were limited in their growth to the time elapsed between two fasting periods. A cyclical pattern is also absent in the data presented by Newland et al. (2011) for several vibrissae collected from the same animal, reinforcing the idea that the information derived from an elephant seal vibrissae does not extend for longer than a year. On the other hand, the lack of a secondary peak in δ^{15}N before the proximal end (i.e. most recent) would also suggest that the two fasting periods (breeding and molting) could be confounded into one high δ^{15}N value at the base of the vibrissae, indicating limited growth for whiskers between

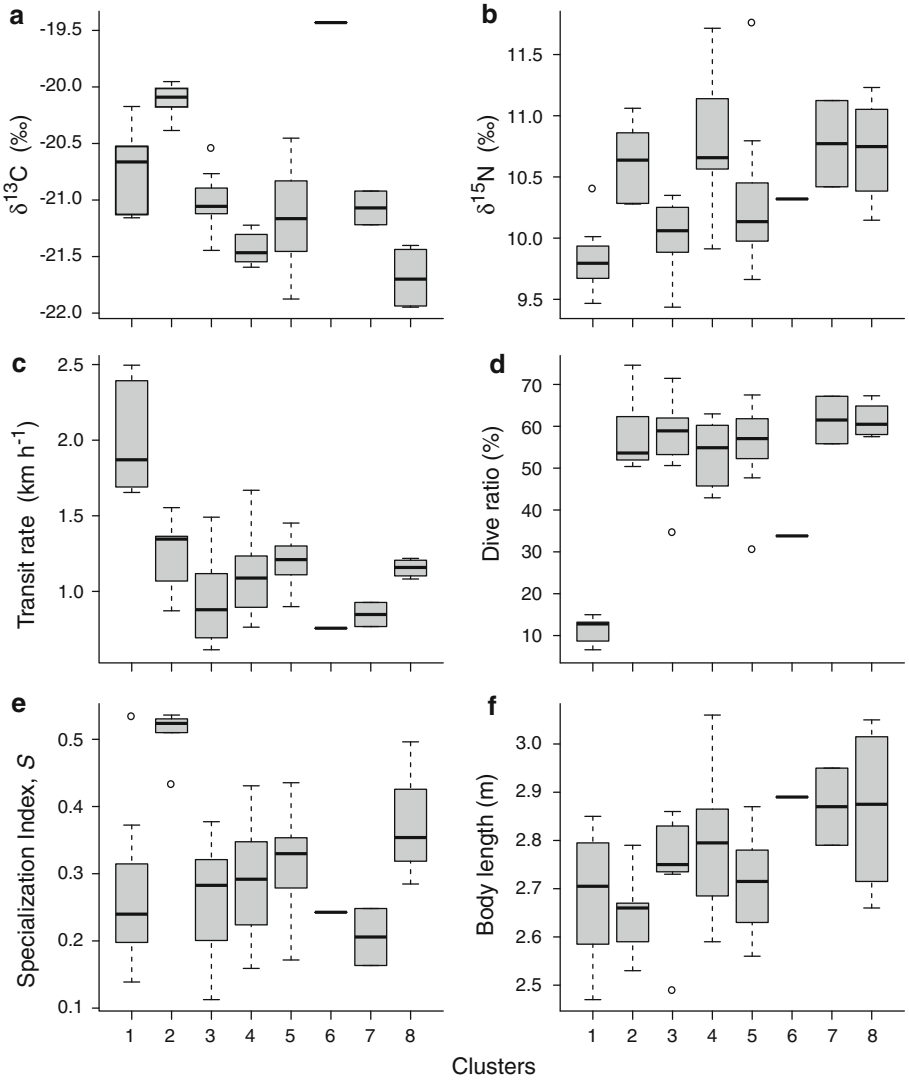

Fig. 4 Differences in the foraging strategies of eight clusters of adult female elephant seal (*Mirounga leonina*) from the Western Antarctica Peninsula. The *thick black lines* correspond to the median, the *limits of the boxes* denote the data encompassed within the 1st and 3rd quartiles, and outliers are shown as *open circles*. **a** δ^{13}C, **b** δ^{15}N, **c** mean transit rate, **d** mean dive ratio, **e** specialization index (*S*), and **f** body length. Cluster 6, composed of only one individual, constitutes an outlier within the model

these two periods. However, further investigation is necessary to clarify this aspect.

We were able to recapture a subset of six individuals 1 year after the original vibrissae sampling (Table 2). The comparison of the isotopic data from vibrissae collected in successive years can provide insight into the inter-annual variability of foraging habits of the same individuals and validate our approach to compare past isotopic data with satellite telemetry data. Only one animal presented significant differences in both δ^{13}C and δ^{15}N between sampling years (SE07-07; Table 2), although these differences were associated with a smaller SD in both isotopes for the sample collected in early 2007 (i.e., representing the foraging activity of that individual in 2006) compared with the sample collected in 2008. This particular individual was among the smallest seals included in our sample (mass = 317 kg, length = 272 cm), and presumably one of the youngest animals included in this study.

The consistency in isotopic values for animals recaptured in consecutive years confirmed previous results obtained from tracking data about elephant seals displaying fidelity to foraging grounds between years (Bradshaw et al. 2004b). Satellite telemetry tracking data obtained from individual northern elephant seals followed during two or more foraging migrations in the North Pacific indicate a high degree of fidelity, not only with respect to foraging areas but also to migratory routes (Simmons 2008), and similar consistency has been observed for individual female southern elephant seals from the WAP captured in different years (Hückstädt et al., unpublished). Furthermore, it has been observed that adult female southern elephant seals demonstrate a high degree of fidelity to foraging grounds between years, with an overlap of foraging areas of about 65% between successive foraging grounds (Bradshaw et al. 2004b).

Fasting and $\delta^{15}N$

The interpretation of $\delta^{15}N$ values from fasting animals is complicated by the fact that animals "feed on themselves", which results in an artificially high $\delta^{15}N$ value as a consequence of the preferential excretion of ^{14}N from the already ^{15}N-enriched consumer's body (Cherel et al. 2005; Hobson et al. 1993; Kelly 2000). The magnitude of this enrichment, however, is tissue-dependent (Cherel et al. 2005), which adds uncertainty to the analysis of feeding habits of consumers based on $\delta^{15}N$ values of tissues that are affected by a fasting signal.

Blood serum, with a turnover rate of days, and fur, which grows rapidly during the haul-out molting period, can be assumed to represent isotopic values corresponding to the fasting period. We observed that both tissues have high $\delta^{15}N$ values (12.0 and 11.6‰, respectively; Fig. 1). RBCs, on the other hand, represent a period of weeks to months of active foraging at sea, and their lower $\delta^{15}N$ value (10.5‰) is indicative of foraging, not fasting. The root of the vibrissae (i.e., most recent deposition) presented $\delta^{15}N$ values higher than the rest of the vibrissae (11.7 vs. 10.6‰), indicating that this segment grew while the animals were fasting, and therefore the root was discarded from further analyses. Additionally, the C:N ratios were higher at the base of the vibrissae, even after lipid extraction, indicating a different tissue composition. It is likely that the base of the sample includes some skin and parts of the follicle that are not pure keratin. Thus, future studies should consider this variability in isotopic values along samples like vibrissae or feathers, whether associated with metabolic processes like fasting or differences in tissue composition, when using them to describe the foraging behavior or ecology of a particular species.

Individual specialization and foraging strategies

Individual seals included in our study are part of the South Georgia stock, the largest stock of the species representing ca. 54% of the world's population, which has been suggested as stable after experiencing a rapid recovery following the cessation of sealing activities in the mid-1900s (Boyd et al. 1996; Laws 1994). This stock includes colonies and haul-out sites in the South Georgia and Falkland archipelagos and other sub-Antarctic Islands in the Atlantic sector of the southern ocean, as well as the South American and Antarctic continents. Given the large population size of this stock, we expect individual seals to exhibit mechanisms to minimize competition with conspecifics.

$\delta^{13}C$ presents a latitudinal variation (lower values in high latitudes) as a consequence of biochemical processes at the level of primary producers, which is ultimately reflected throughout the trophic web (Goericke and Fry 1994; Popp et al. 1999), thus becoming a powerful indicator of habitats used by consumers, particularly in the southern ocean where this latitudinal variation is more accentuated. Hence, the low $\delta^{13}C$ values observed in the animals included in our sample confirm that female elephant seals from the WAP utilize Antarctic waters, as observed from satellite telemetry (Costa et al. 2010; this study). Taking into consideration the differential trophic enrichment between whole blood and vibrissae (Hobson et al. 1996), we can compare our results with isotopic data on adult female elephant seals from other colonies.

Previous studies on the trophic ecology of adult female elephant seals from the Eastern Pacific showed a squid-dominated diet of pelagic animals versus a fish-dominated diet of shelf foragers (Bradshaw et al. 2003). Studies on the feeding habits of elephant seals from the Kerguelen Islands in the Indian Ocean, using stable isotopes, found that the diet of the species was dominated by myctophid fishes rather than squid (Cherel et al. 2008). Our individuals had $\delta^{13}C$ values similar to animals from Sub-Antarctic colonies known to forage in Eastern Antarctic waters (Bailleul et al. 2010; Cherel et al. 2008; Ducatez et al. 2008), while the $\delta^{15}N$ values of seals in our sample were about 1‰ lower. We propose that these small differences, likely due to challenges associated with interpretation of isotopic data from different tissues, are indicative of female elephant seals occupying similar environments and feeding on similar prey throughout their Antarctic distribution.

Despite the similarity of isotopic values among individuals seals exploiting resources in different sectors of the Antarctic continent, female elephant seals from the WAP present a characteristic foraging behavior, with about 85% of the foraging in continental shelf waters of Antarctica (Costa et al. 2010; Field et al. 2001; McConnell et al. 1992; McConnell and Fedak 1996; Electronic Supplementary Material 1), as opposed to the most common pelagic foraging strategy of individuals from other sites. However, the lack of isotopic data of elephant seal prey for the entire spatial range utilized by individuals in this study prevents us from linking their relative low $\delta^{15}N$ with the potential importance of squid in the diet of elephant seals.

Individuals included in our study presented a wide variability in their $\delta^{13}C$ and $\delta^{15}N$ values (−22.65 to −18.47‰ and 8.79 to 12.75‰, respectively). The variance observed indicates that adult female elephant seals from the WAP are a diverse group of predators, exploiting prey in different regions of the Southern Ocean and at least at two different trophic levels. For $\delta^{13}C$, 60% of the variation observed in our data is associated with differences among individuals (Table 3), indicating that individual adult female elephant seals are exploiting different habitats, water column depths, and ultimately prey resources throughout their range.

The existence of niche partitioning among different age and sex classes has been described for both southern and northern elephant seals *M. angustirostris* (Bailleul et al. 2010; Bradshaw et al. 2004b; Eder et al. 2010; Le Boeuf et al. 2000; Lewis et al. 2006). Evidence of inter-individual niche differences of adult female elephant seals has also been studied in recent years using fatty acids and stable isotopes analyses (Bradshaw et al. 2003; Ducatez et al. 2008; Lewis et al. 2006), yet the topic of individuality, in terms of individual niche width relative to the population's niche width, is not well understood despite the fact that it can help discern variability among species, conspecifics populations, and even among individuals within a population (Bolnick et al. 2003).

Our data provided evidence that adult female elephant seals are specialized individuals, with a rather limited individual niche width relative to the total available niche. Half the individuals sampled for this study occupied less than 31% of the total niche width (Fig. 2), and, more interestingly, we identified extreme specialists in our sample. A similar study on sea otters (*Enhydra lutris*) found individuals to have low intra-individual variability (WIC) while having high inter-individual variability (BIC), confirming previous observational studies indicating that individual sea otters have highly specialized and constant diets through time (Newsome et al. 2009). Despite this similarity to our study, our data from recaptured animals showed that elephant seals are capable of feeding plasticity. One individual in our study (SE07-07) switched from an extreme specialized strategy in one year (2006, $S = 0.13$) to a relatively more generalist strategy two years later (2008, $S = 0.37$) (Table 2).

We found a clear distinction between animals that foraged on the shelf of the WAP (Fig. 3) and those which preferred open waters (i.e., pelagic animals) (Fig. 3). Furthermore, the diversity of strategies among the individuals that used the shelf as their habitat is particularly interesting. Cluster 2 (generalists) included animals with movement patterns and diving behavior indistinguishable from the other shelf foragers (Fig. 4c, d), yet it included individuals with the highest S (i.e., generalists), the second highest δ^{13}C values (indicating a 'northern' foraging range) and the smallest body sizes (Fig. 4f).

We found some evidence of ontogenetic changes in foraging strategy which is consistent with previous studies that observed juvenile males switching from a 'female-like' strategy to a more defined 'adult male strategy' with increasing age (Bailleul et al. 2010). A sigmoidal relationship between age and standard length of adult female elephant seals has been shown (Bell et al. 2005), suggesting that the smallest seals (Cluster 2) were likely the youngest in our sample. These individuals were also the more generalist seals in our sample (Fig. 4e). Conversely, we found that individuals from Cluster 7, which included the longest and presumably the oldest seals in our sample, presented the highest specialization (lowest S; Fig. 4e, f). However, we did not find a relationship between body length and Specialization Index when data for all individuals were pooled together. Thus, we propose that, instead of a constant trend towards specialization with age, female elephant seals go through an exploratory phase in terms of their foraging habits when they exhibit maximum generalization, until they reach an age after which they consistently display the same foraging strategy (more specialized), a pattern similar to the ontogenetic changes in foraging behavior observed in males (Bailleul et al. 2010). Evidence of this consistency on adult female foraging strategies has also been observed for northern elephant seal females (Simmons 2008).

The relative proportion of individual specialists and generalists varies widely among species and even among populations of the same species (Bolnick et al. 2003). Our sample consisted exclusively of individual elephant seals captured in the Antarctic continent, where most of them feed. Most colonies of the species, however, occur in sub-Antarctic islands, and consequently animals must travel considerable distances to forage in Antarctic waters, and are exposed to different environments during their post-molt migration. Given the variability in foraging behavior observed in this study, it would be instructive to examine the individual variability of the species throughout its range, which will provide a better understanding of the ability of southern elephant seals to cope with environmental change.

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