

Temporal consistency of individual trophic specialization in southern elephant seals *Mirounga leonina*

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ABSTRACT: Individual specialization can be an advantageous strategy that increases predation success and diminishes intra-population competition. However, trophic specialization can be a handicap in changing environments if the individuals are unable to use different prey or feeding grounds in response to change. Southern elephant seals *Mirounga leonina* allow us to explore this trade-off as they migrate, returning to haul out on land, for 2 extended periods, to breed and to moult. They fast during both periods, but the energetic cost is higher during the breeding season, leading to a poorer body condition after the breeding fast than after the moulting fast. We analysed the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic composition of skin and fur samples from Falkland Islands elephant seals. The isotopic values provided information about the foraging strategy of the seals during the pre-breeding season and pre-moulting season, respectively. We assessed individual specialization as the variation between periods of an individual with respect to the variability of the whole population. The high specialization and the correlation between periods suggest that each animal feeds in a similar region and on similar prey during both feeding migrations. The comparison with data from other populations and particulate organic matter suggests that the Falkland Islands elephant seals fed both on the Patagonian Continental Shelf and in the Southern Ocean. The high specialization among individuals within this species could potentially limit the individual capacity of adaptation in the face of changing conditions or leave those abilities to the few generalist individuals.

KEY WORDS: Southern elephant seal · *Mirounga leonina* · Stable isotopes · Skin · Fur · Falkland Islands · Feeding zone · Individual specialization

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INTRODUCTION

Individual foraging specialization is a widespread phenomenon in vertebrates, and many populations of generalist consumers are indeed a mixture of specialized individuals (Bolnick et al. 2003, Vander Zanden et al. 2010, Terraube et al. 2014, Pagani-Núñez et al. 2015). Morphological differences (Grant & Grant 1996, Svanbäck & Eklöv 2002), imprinting during juve-

nile stages (Scott et al. 2014) and cultural transmission (Valenzuela et al. 2009) are some of the causes for individual foraging specialization. Foraging specialization in species with limited movement results in the use of different microhabitats and the consumption of different prey (e.g. Grant & Grant 1996, Svanbäck & Eklöv 2002), whereas individual specialization in migratory species may involve the use of foraging grounds 100s of km apart (Valenzuela et al. 2009, Eder et al. 2012).

Reversibility of foraging specialization is critical in determining the individual capacity to adapt to changing environments (Mery & Burns 2010, Araújo et al. 2011), as the individuals of some long-lived species exhibit very limited behavioural flexibility once they reach adulthood (Vander Zanden et al. 2016, Cardona et al. 2017a). Stable isotope analysis is a useful tool for identifying temporal changes in the diet, as stable isotope ratios in consumer tissues reflect prey assimilated in the diet and habitat use (Hobson et al. 1994, 2010, Vales et al. 2015, Zenteno et al. 2015, Yurkowski et al. 2016). Temporal changes in diet and habitat use patterns can be studied without re-sampling the same individual, since stable isotope ratios are recorded in inert tissues (Ayliffe et al. 2004, Reich et al. 2007) or in tissues integrating different time windows (Hobson 1999, Newsome et al. 2010). After a behavioural or environmental change, stable isotope ratios change after a few days or weeks in tissues with a high turnover rate (Hilderbrand et al. 1996, Narita et al. 2006, Caut et al. 2011), whereas they may change over months or even years in tissues with a low turnover rate (Sponheimer et al. 2006, Alves-Stanley & Worthy 2009, Bahar et al. 2009). In true generalist species, the variability among the tissues of an individual (within-individual component: WIC) is similar to the total population variability (total niche width: TNW), because all individuals of the population use similar feeding strategies (Bolnick et al. 2003). On the other hand, in generalist species composed of a collection of specialized individuals, the individual variability among tissues (WIC) is much lower than the total population variability (TNW), because, from the repertoire of feeding strategies displayed by the population, each individual will use always the same strategy (Bolnick et al. 2002).

Elephant seals (*Mirounga* spp.) are highly dimorphic marine predators with high levels of individual specialization both between and within sexes (Lewis

et al. 2006, Hückstädt et al. 2012). Their unique life cycle makes them a good model to study the capacity of individual specialists to adapt to contrasting situations. Elephant seals differ from other long-distance migratory air-breathing marine vertebrates in that they migrate twice annually: once during the breeding season in late winter and again during the moulting season in summer (Hindell & McMahon 2000, Bailleul et al. 2007). Similar to other capital breeders, elephant seals fast during the breeding and the moulting seasons (Le Boeuf et al. 1973, Riedman 1990), but the cost is higher during breeding than during moulting due to mating activity in males and lactation in females (Boyd et al. 1993). This possibly leads to differences in their dietary requirements during the pre-breeding and pre-moulting feeding periods. Furthermore, elephant seals forage for only 2 to 3 mo between breeding and moulting but for 6 to 7 mo between moulting and breeding (Fig. 1). Given the differences in nutritional requirements and length of foraging periods, elephant seals are expected to use different trophic resources (prey and/or foraging grounds) while at sea in each feeding period.

The southern elephant seal *M. leonina* inhabits the Southern Ocean and typically breeds in sub-Antarctic islands, with a few small rookeries along the Antarctic Peninsula and a major colony at Peninsula Valdés (northern Patagonia, Argentina) on the mainland of South America (Campagna et al. 1993, Boyd et al. 1996, McMahon et al. 2005). The foraging ecology of the largest colonies has been studied using satellite telemetry, often combined with stable isotope analysis (Campagna et al. 1995, Bost et al. 2009, Eder et al. 2010, Hückstädt et al. 2012, Muelbert et al. 2013, Hindell et al. 2016). Southern elephant seals have a preference for highly productive zones and take advantage of oceanic features such as eddies, fronts or shelf breaks (Campagna et al. 1998, 2007, Bost et al. 2009, Dragon et al. 2010, Hindell et

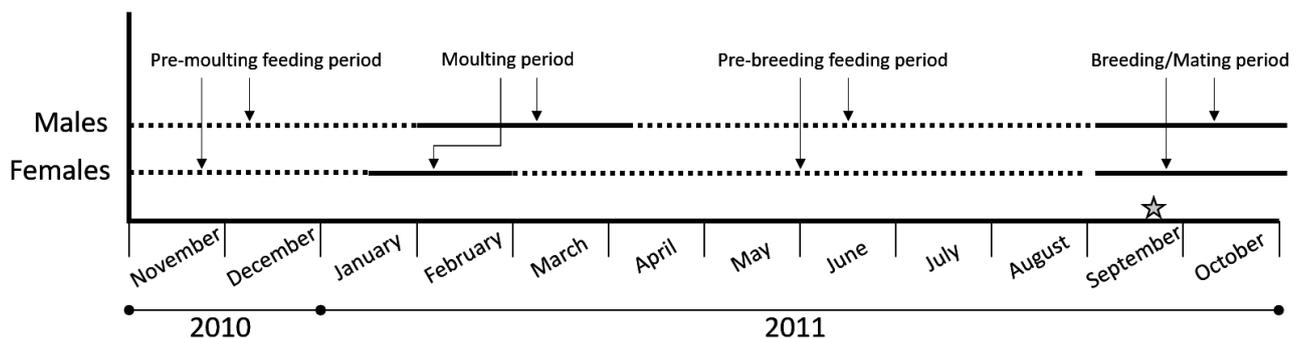


Fig. 1. Annual cycle of southern elephant seals. Dotted lines are feeding periods offshore and solid lines are fasting periods on land. The star represents the sampling period

al. 2016, Massie et al. 2016), but they may adopt 3 main foraging strategies: benthic feeding on the continental shelf, pelagic feeding near oceanic fronts and ice-related feeding (Bost et al. 2009, Hindell et al. 2016). In any case, diet is usually dominated by squid and mesopelagic fishes (Clarke & MacLeod 1982, Daneri et al. 2000, Daneri & Carlini 2002, Cherel et al. 2008), although high levels of individual foraging specialization and high fidelity to feeding grounds have been reported (Lewis et al. 2006, Hückstädt et al. 2012). Sex and age only partially explain such variability in foraging strategies (Field et al. 2005, Lewis et al. 2006, Walters et al. 2014, Labrousse et al. 2015), and nothing is known about its seasonal consistency.

Vibrissae are inert keratinous organs widely used in stable isotope ecology to track temporal diet shifts in eared seals due to their constant growth rate (Cherel et al. 2009, Kernaléguen et al. 2012, Vales et al. 2015, Cardona et al. 2017b). Unfortunately, this is not true in earless seals, which makes the use of vibrissae to reconstruct diet extremely complex in this group (Beltran et al. 2015). However, elephant seals experience the so called 'catastrophic moult', i.e. fur is shed simultaneously in less than 1 mo and grows back for about 12 wk starting slightly ahead of and finishing shortly after the moulting period (Riedman 1990, Ling 2012). Since elephant seals fast during the moulting period, and fasting has little effect on stable isotope ratios in the tissues of capital breeders (Habran et al. 2010, Aguilar et al. 2014), the stable isotope ratios in fur are expected to integrate the dietary information from the pre-moulting period (Ayliffe et al. 2004, Cardona et al. 2017b). On the other hand, the metabolically active skin integrates dietary information continuously (Alves-Stanley & Worthy 2009, Giménez et al. 2016). Given these differences (Fig. 1), a sample of fur and skin collected during the breeding season would provide information about the diet and habitat use of elephant seals during the last pre-breeding season (skin) and also during the last pre-moulting season (fur).

In this paper, we used the stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) to assess the degree of individual specialization of southern elephant seals and their consistency between the pre-breeding and pre-moulting periods. We compared our findings to previously published data on the latitudinal variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in particulate organic matter (POM) and other pinniped populations inhabiting the Southern Ocean to identify the potential foraging grounds used by the elephant seals breeding at the Falkland Islands.

MATERIALS AND METHODS

Sample collection

Fieldwork was conducted at Sea Lion Island, which hosts the main breeding colonies of southern elephant seals *Mirounga leonina* in the Falkland (Malvinas) Islands (Galimberti & Boitani 1999, Galimberti et al. 2001) (Fig. 2). We sampled 49 males and 47 females of known age during the 2011 breeding season (September–November). The age was known since animals were tagged at birth, and ranged from 2 to 13 yr for males and from 2 to 20 yr for females. We collected a sample of skin and fur from the interdigital membrane of the rear flipper of unrestrained individuals using ear-notching pliers. Each sample was approximately 3 mm deep and with a surface of 5 mm². After collection, all samples were stored at -20°C until analysis.

Skin and fur have different turnover rates and provide different dietary information over time. In our case, skin informs about the diet and the foraging grounds used a few months before the breeding season (approx. from June to September 2011), whereas fur informs about the diet and the foraging grounds used after the breeding season but before the moulting season (approx. from December to January 2010).

Stable isotope analyses

In the laboratory, the samples were thawed; fur and skin were then separated, dried at 60°C for 48 h and ground with a mortar. Lipids were extracted from all of the skin and fur samples using a chloroform:methanol (2:1) solution (Bligh & Dyer 1959) because they are depleted in ^{13}C compared to other molecules, and variability in lipid content may result in undesirable variability in $\delta^{13}\text{C}$ values (DeNiro & Epstein 1978, Caut et al. 2011, Giménez et al. 2016). Nevertheless, since chemical lipid extraction may lead to unpredictable changes in $\delta^{15}\text{N}$ values likely due to the inadvertent removal of amino acids (Sotiropoulos et al. 2004, Ryan et al. 2012), we extracted lipids for carbon isotope analysis and used a non-extracted subsample for nitrogen determination.

Approximately 0.3 mg of skin and 0.25 mg of fur, along with calibration standards, were weighed into tin cups (3.3×5 mm) and analysed by elemental analysis isotope ratio mass spectrometry (EA-IRMS) using an elemental analyser (model FlashEA 1112, ThermoFisher Scientific) coupled with a Delta C isotope ratio mass spectrometer (ThermoFinnigan). All

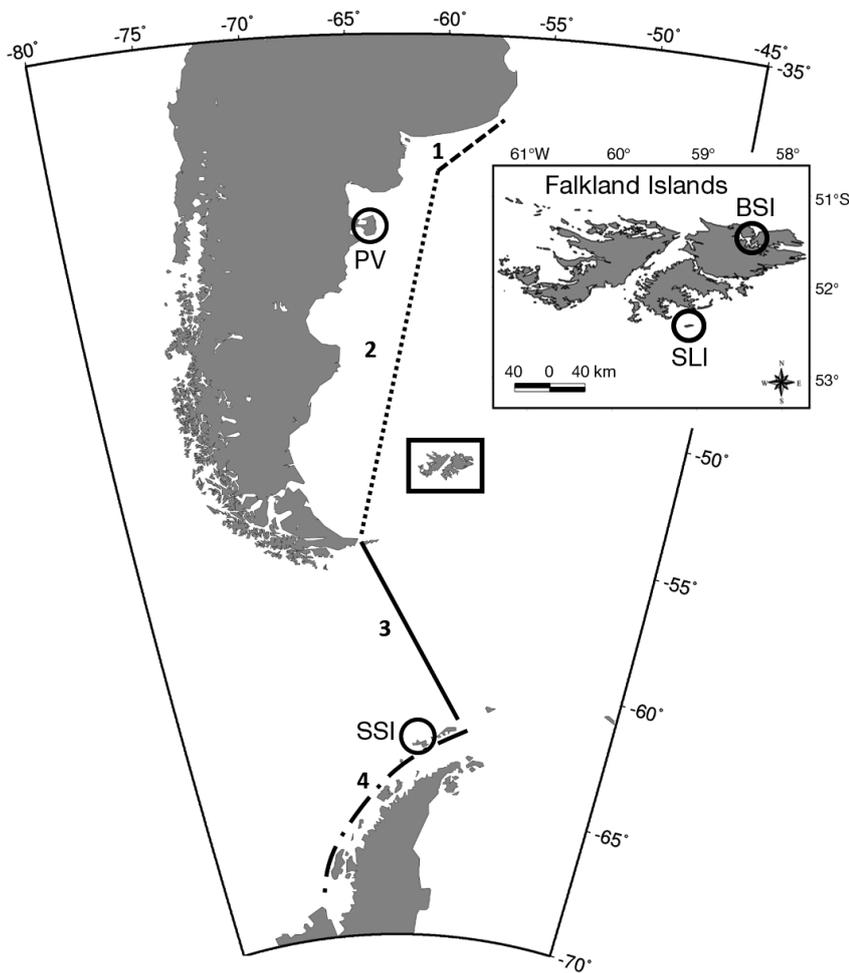


Fig. 2. Sampling locations. Abbreviations denote pinniped sampling areas and line transects for POM sampling. SLI: southern elephant seals *Mirounga leonina* from Sea Lion Island (Falkland Islands); PV: southern elephant seals from Peninsula Valdes (Argentinian Patagonia); SSI: southern elephant seals from the southern Shetland Islands; BSI: South American sea lions *Otaria flavescens* from Big Shag Island (Falkland Islands). 1: nearshore Patagonian shelf, 2: offshore Patagonian continental shelf, 3: Drake Passage, and 4: western Antarctic Peninsula

analyses were performed at the Scientific and Technological Centres (CCiT), University of Barcelona, Spain.

Stable isotope abundances are expressed in delta (δ) notation, with relative variations of stable isotope ratios expressed in per mil (‰) deviations from predefined international standards, and they were calculated as:

$$\delta^j X = \frac{(^j X / ^i X)_{\text{sample}}}{(^j X / ^i X)_{\text{standard}}} - 1 \quad (1)$$

where $^j X$ is the heavier isotope (^{13}C or ^{15}N) and $^i X$ is the lighter isotope (^{12}C or ^{14}N) in the analytical sample and in the international measurement standard (Bond & Hobson 2012); international standards were

Vienna Pee Dee Belemnite (VPDB) calcium carbonate for $\delta^{13}\text{C}$ and atmospheric nitrogen (air) for $\delta^{15}\text{N}$. However, data were normalized using commercially available laboratory reference materials. For carbon, isotopic reference materials of known $^{13}\text{C}:^{12}\text{C}$ ratios, as given by the International Atomic Energy Agency (IAEA), were used for calibration at a precision of 0.05‰. These include polyethylene (IAEA CH₇, $\delta^{13}\text{C} = -32.1\text{‰}$), L-glutamic acid (IAEA USGS₄₀, $\delta^{13}\text{C} = -26.4\text{‰}$) and sucrose (IAEA CH₆, $\delta^{13}\text{C} = -10.4\text{‰}$). For nitrogen, secondary isotopic reference materials of known $^{15}\text{N}:^{14}\text{N}$ ratios, namely (NH₄)₂SO₄ (IAEA N₁, $\delta^{15}\text{N} = 0.4\text{‰}$ and IAEAN₂, $\delta^{15}\text{N} = 20.3\text{‰}$), L-glutamic acid (IAEA USGS₄₀, $\delta^{15}\text{N} = -4.5\text{‰}$) and KNO₃ (IAEA NO₃, $\delta^{15}\text{N} = 4.7\text{‰}$), were used to a precision of 0.2‰. These isotopic reference materials were employed to recalibrate the system and compensate for any measurement of drift over time once every 12 analysed samples. The raw data were normalized by the multipoint normalization method based on linear regression (Skrzypek 2013). Furthermore, as a control for data quality after lipid extraction, we quantified the carbon to nitrogen (C:N) mass ratio of each delipidated sample to verify that it was within the standard protein range (i.e. between 3 and 4), thus ensuring an adequate lipid extraction (Newsome et al. 2010).

Data analyses

Prior to any statistical analysis, normality was tested by means of the Kolmogorov-Smirnov test and homoscedasticity by means of the Bartlett test. Although the data followed a normal distribution, males showed a higher variance than females in both tissues even when an outlier (a 13 yr old male) was removed, thus violating one of the assumptions required by parametric tests. For this reason, the general linear models run to assess the effect of tissue and age on stable isotope ratios were conducted for each sex independently, and their residuals were

also visually checked for homoscedasticity. Differences between the stable isotope ratios of the 2 sexes were tested for each tissue separately using Welch's *t*-test for samples with unequal variances. Cross-correlation between the tissues was also conducted for each sex independently. All statistical analyses were carried out using the free software R (R Core Team 2016).

The oldest male in the samples (age 13) was excluded from the general linear models and Welch's *t*-test because its $\delta^{15}\text{N}$ values were more than 4 standard deviations higher than average value for both tissues. Although extreme, the consistency of the results between the 2 tissues, which were analysed independently, confirm that the data obtained from this individual are correct and not an analytical error. However, the inclusion of this animal in the models could hide subtle patterns for the rest of the population.

Stable isotope ratios from different tissues cannot be compared directly to infer environmental information because trophic discrimination factors (TDFs or Δ) from prey to predator are tissue-specific. The TDFs of skin and fur have not been determined in elephant seals, so we used those reported by Hobson et al. (1996) for other pinnipeds: $\Delta_{\text{skin}}^{13}\text{C} = 2.8\text{‰}$, $\Delta_{\text{skin}}^{15}\text{N} = 2.3\text{‰}$, $\Delta_{\text{fur}}^{13}\text{C} = 2.8\text{‰}$, $\Delta_{\text{fur}}^{15}\text{N} = 3\text{‰}$. After subtracting the corresponding TDFs, the stable isotope values from our study (skin and fur) could be compared, and we denote these by $\delta^{15}\text{N}_{\text{corr}}$ and $\delta^{13}\text{C}_{\text{corr}}$. Furthermore, we compared them to the stable isotope ratios reported previously for the western South Atlantic and the Antarctic Peninsula to identify potential foraging grounds. The stable isotope data sets used for this comparison were: POM from the Patagonian Continental Shelf, Drake Passage and the western Antarctic Peninsula (Lara et al. 2010), stable isotope ratios in the vibrissae of southern elephant seals from Argentinean Patagonia (Lewis et al. 2006, Eder et al. 2010), and South American sea lions *Otaria flavescens* from the Falkland Islands (Baylis et al. 2015), and stable isotope ratios in the fur of southern elephant seals from the Antarctic Peninsula (Hückstädt et al. 2012). We corrected the stable isotope ratios in vibrissae according to the vibrissa TDF ($\Delta_{\text{vibrissae}}^{15}\text{N} = 2.8\text{‰}$, $\Delta_{\text{vibrissae}}^{13}\text{C} = 3.2\text{‰}$) reported by Hobson et al. (1996). Although there are more recently published TDF values for vibrissae (Beltran et al. 2016), we used those reported by Hobson et al. (1996) to ensure consistency with the TDF values used for skin and fur. When comparing our data with the POM isotopic data, we shifted our data -7.5‰ of $\delta^{13}\text{C}$ and -12‰ of $\delta^{15}\text{N}$. This would approximately account for the

trophic level discrimination between POM and southern elephant seals (Kelly 2000), thus allowing the comparison between the 2 geographical patterns. This shift is not meant to be a precise correction of the trophic discrimination, but an approximation for visual comparison.

The individual specialization index (*S*) was calculated for each individual following the approach developed by Bearhop et al. (2004) and used in other marine mammal studies (Newsome et al. 2009, Hückstädt et al. 2012). Accordingly, the TNW was calculated as the standard deviation of the whole $\delta^{13}\text{C}$ data set (both skin and fur) and the WIC was calculated for each individual as the standard deviation of its fur and skin $\delta^{13}\text{C}$ values. Following Hückstädt et al. (2012), we split the population into extreme specialists ($S < 0.2$), specialists ($0.2 \leq S \leq 0.5$) and generalists ($S > 0.5$).

Since the individual component of *S* was calculated using only 2 points, we performed a bootstrap analysis to assess the probability that the observed pattern of specialization in the population might have emerged just by chance. We created 1000 simulated populations of elephant seals each by randomly resampling 100 pairs of $\delta^{13}\text{C}$ values from the original data set. Later, we computed *S* for each simulated individual and the population median. The null hypothesis was that a non-specialist population would present a median individual specialization index within the 95% confidence interval of the simulated population medians. Only $\delta^{13}\text{C}$ values were used, since the $\delta^{15}\text{N}$ values could be influenced by trophic level, fasting and other confounding factors independent of the foraging strategy (Hobson et al. 1993, Cardona et al. 2017b).

RESULTS

The C:N mass ratio of all samples ranged from 3.3 to 3.4%, well within the theoretical range that characterizes unaltered protein (Newsome et al. 2010). The mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the Falkland Islands elephant seals population were, respectively, -18.6 ± 1.97 and $15.1 \pm 1.8\text{‰}$ in skin and -18.23 ± 2.03 and $14.2 \pm 1.9\text{‰}$ in fur (Table 1). In both tissues, the variability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was extremely high (Table 1). The variability of $\delta^{13}\text{C}$ values was 2-fold higher in males than in females in both tissues, while the variability of $\delta^{15}\text{N}$ values was similar in both sexes. The average $\delta^{15}\text{N}$ values for both tissues were statistically higher in males than in females (Table 2). The effect of sex on average $\delta^{13}\text{C}$

Table 1. Isotopic values (mean \pm SD) obtained in this study and adapted from other studies. Patagonian southern elephant seal adult males were divided into 3 groups (Males 1, 2 and 3) in accordance with Lewis et al. (2006), who described them as 3 separate clusters that possibly feed in different locations and/or have different diet. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$: values not corrected for isotope discrimination factors; $\delta^{13}\text{C}_{\text{corr}}$ and $\delta^{15}\text{N}_{\text{corr}}$: values corrected for isotope discrimination factors

Population	Age class	Sex	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}_{\text{corr}}$ (‰)	$\delta^{15}\text{N}_{\text{corr}}$ (‰)	Source
<i>Mirounga leonina</i>								
Falkland Is.	Adult/juvenile	Male	Fur	-17.8 ± 2.4	15.3 ± 1.7	-20.6 ± 2.4	12.3 ± 1.7	Present study
	Adult/juvenile	Male	Skin	-18.1 ± 2.3	16.1 ± 1.7	-20.9 ± 2.3	13.8 ± 1.7	Present study
	Adult/juvenile	Female	Fur	-18.7 ± 1.5	13.2 ± 1.3	-21.5 ± 1.5	10.2 ± 1.3	Present study
	Adult/juvenile	Female	Skin	-19.1 ± 1.4	14.1 ± 1.3	-21.9 ± 1.4	11.8 ± 1.3	Present study
Antarctica	Adult	Female	Fur	-21.3 ± 0.3	11.5 ± 0.5	-24.1 ± 0.3	8.5 ± 0.5	Hückstädt et al. (2012)
Patagonia	Adult	Male 1	Vibrissae	-20.7 ± 0.7	12.7 ± 0.7	-23.9 ± 0.7	9.9 ± 0.7	Lewis et al. (2006)
	Adult	Male 2	Vibrissae	-14.8 ± 0.5	15.0 ± 0.8	-18.0 ± 0.5	12.2 ± 0.8	Lewis et al. (2006)
	Adult	Male 3	Vibrissae	-13.2 ± 0.4	19.1 ± 0.3	-16.4 ± 0.4	16.3 ± 0.3	Lewis et al. (2006)
	Adult	Female	Vibrissae	-16.7 ± 0.5	11.4 ± 0.7	-19.9 ± 0.5	8.6 ± 0.7	Lewis et al. (2006)
	Juvenile	Male/female	Vibrissae	-17.0 ± 1.3	14.2 ± 2.2	-20.2 ± 1.3	11.4 ± 2.2	Eder et al. (2010)
<i>Otaria flavescens</i>								
Falkland Is.	Adult	Female	Vibrissae	-14.2 ± 0.9	16.3 ± 0.5	-17.4 ± 0.9	13.5 ± 0.5	Baylis et al. (2015)

values of both tissues was smaller, but still significant (Table 2).

The linear models showed that seal age had no effect on the tissue isotopic values (Table 3). On the other hand, the tissue type, and therefore the period over which the seals foraged (i.e. skin: pre-breeding period; fur: pre-moulting period), affected the $\delta^{15}\text{N}_{\text{corr}}$ but not the $\delta^{13}\text{C}_{\text{corr}}$ values in both sexes (Table 3). The linear regressions (Fig. 3) showed that the skin and fur corrected values were strongly correlated, with higher R^2 values in males than in females for both $\delta^{13}\text{C}_{\text{corr}}$ and $\delta^{15}\text{N}_{\text{corr}}$ (Table 4).

The degree of specialization of Falkland elephant seals was very high in most cases (Fig. 4): 51% of the animals were extreme specialists, occupying less than 20% of the population isotopic niche; 45.8% were specialists, occupying less than 50% of the population isotopic niche; and only 3.2% of the animals were generalists (Fig. 4). The population median for S was 0.21, a value well below the 95% confidence interval of the simulated populations (0.54–0.88).

Table 2. Results of Welch's test for samples with unequal variances. Each group of southern elephant seals was tested independently against the variable sex. Significant values ($p < 0.05$) are shown in **bold**

Variable	Para-meter	Fur		Skin	
		$\delta^{13}\text{C}_{\text{corr}}$	$\delta^{15}\text{N}_{\text{corr}}$	$\delta^{13}\text{C}_{\text{corr}}$	$\delta^{15}\text{N}_{\text{corr}}$
Sex	t	2.01	6.87	2.32	6.72
	df	81.91	92.64	78.46	92.87
	p	0.047	<0.001	0.0226	<0.001

Compared to other pinniped populations (Fig. 5), the distribution of the Falkland Islands elephant seals in the regional isospace was very close to that of males and juveniles of elephant seals from Patagonia and between those of elephant seals from the Antarctic Peninsula and South American sea lions *Otaria flavescens* from the Falkland Islands. These results stand for both the corrected values of fur and skin, although the skin values of the Falkland Islands elephant seals were slightly displaced from the rest. A similar geographical pattern emerged when the stable isotope ratios of elephant seals from the Falkland Islands were compared to those reported for POM across the western South Atlantic (Fig. 6). POM from the Patagonian continental shelf was characterized by high levels of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, while that from the Antarctic Peninsula and the Drake Passage was more depleted in both heavy isotopes. The difference between these 2 water masses is quite similar to the

Table 3. Results of the general linear model for southern elephant seals. Each isotope and sex was tested independently against the variables age and tissue. Significant values ($p < 0.05$) are shown in **bold**

Variable	Para-meter	Males		Females	
		$\delta^{13}\text{C}_{\text{corr}}$	$\delta^{15}\text{N}_{\text{corr}}$	$\delta^{13}\text{C}_{\text{corr}}$	$\delta^{15}\text{N}_{\text{corr}}$
Age	t	-1.09	1.18	-0.31	0.18
	df	95	95	93	93
	p	0.28	0.24	0.76	0.85
Tissue	F	-0.684	2.76	-1.358	3.36
	df	95	95	93	93
	p	0.49	0.007	0.760	0.001

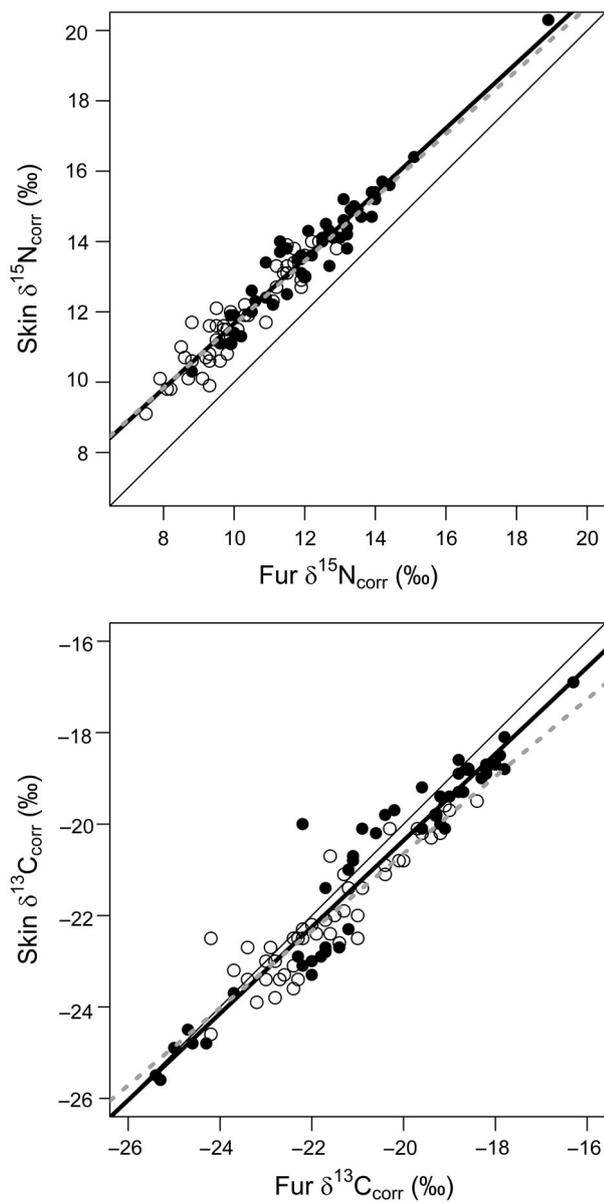


Fig. 3. Correlation of nitrogen and carbon corrected isotopic values between the 2 tissues (fur and skin) sampled from southern elephant seal males (filled circles) and females (open circles). The linear regressions are shown as a thick black line (males) and dashed grey line (females). The 1:1 line (thin black line) is also shown as a reference of a perfect correlation

Table 4. Results of the linear regression between tissues of southern elephant seals. All tests were highly significant ($p < 0.001$)

Parameter	Males		Females	
	$\delta^{13}\text{C}_{\text{corr}}$	$\delta^{15}\text{N}_{\text{corr}}$	$\delta^{13}\text{C}_{\text{corr}}$	$\delta^{15}\text{N}_{\text{corr}}$
R ²	0.92	0.93	0.85	0.86
Slope	0.95	0.93	0.84	0.90

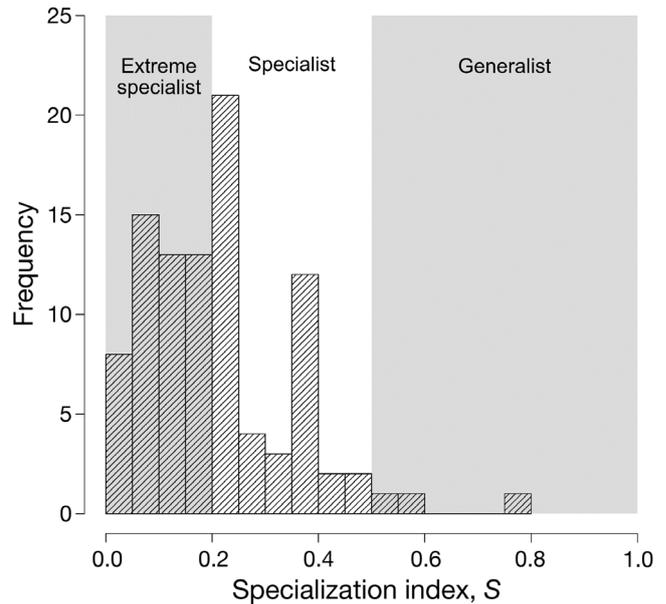


Fig. 4. Frequency distribution of the specialization index (S) calculated as the ratio between the within-individual component and the total niche width, both measured using the $\delta^{13}\text{C}$ values. Southern elephant seal individuals ($n = 96$) are classified as extreme specialists ($S < 0.2$), specialists ($0.2 \leq S \leq 0.5$) or generalists ($S > 0.5$)

range of our data set. The stable isotope ratios in the 13 yr old male (skin: -14.1‰ $\delta^{13}\text{C}$ and 22.6‰ $\delta^{15}\text{N}$; fur: -13.5‰ $\delta^{13}\text{C}$ and 21.9‰ $\delta^{15}\text{N}$), considered an outlier, were compatible with those of the northernmost zone of the Patagonian Shelf.

DISCUSSION

The Falkland Islands southern elephant seal *Mirounga leonina* subpopulation has some of the greatest isotopic individual variability ever reported in any southern elephant seal population (Ducatez et al. 2008, Eder et al. 2010, Newland et al. 2011, Walters et al. 2014) and is only comparable to the neighbouring population breeding in Argentinean Patagonia (Lewis et al. 2006, Eder et al. 2010). This great variability was probably caused by the heterogeneity of foraging locations which this population uses, as supported by the variability observed in POM across the western South Atlantic. On the other hand, the individual variation in the stable isotope ratios between the 2 feeding periods considered is rather small, as expected for an individual specialist species (Bolnick et al. 2003, Vander Zanden et al. 2010, Hückstädt et al. 2012, Terraube et al. 2014, Paganin-Núñez et al. 2015). The high levels of individual specialization revealed by the specialization index, in

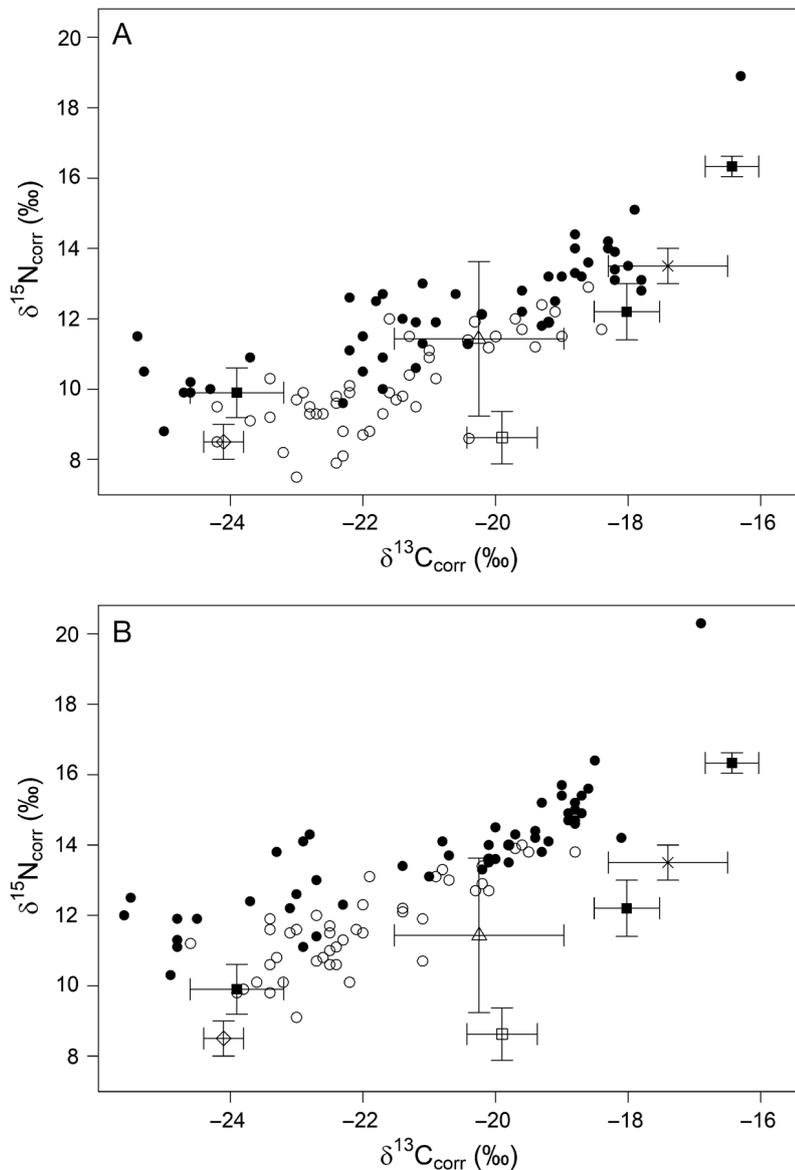


Fig. 5. Comparison (mean \pm SD) among the different populations of southern elephant seals *Mirounga leonina* of the South Atlantic and Peninsular Antarctica, and the Falkland Islands population of South American sea lions *Otaria flavescens*. Filled and open circles show, respectively, corrected isotopic values of male and female Falkland Islands elephant seal (A) fur and (B) skin. Other corrected isotopic data shown are: whiskers from Patagonian elephant seal adult males (filled squares), adult females (open squares) and juveniles (open triangles); whiskers from Falkland Islands adult female southern sea lions (\times symbol); and fur from Antarctic Peninsula elephant seal adult females (open rhombus)

conjunction with the high correlation between skin and fur stable isotope ratios, suggest that each animal feeds in the same region and on similar prey in both feeding seasons (pre-breeding and pre-moulting). This does not imply that each animal has a narrow feeding zone or feeds on few species, but rather that its feeding strategy is consistent over time and differs from that of other individuals.

The main difference between the 2 feeding periods was caused by a slight decrease in the $\delta^{15}\text{N}$ after the breeding period. Multiple reasons could explain this $\delta^{15}\text{N}$ shift. It could be caused by internal factors (fasting and lactation), behavioural factors (change in prey/location) or external factors (seasonal change of the ecosystem baseline). Fasting and lactation affect $\delta^{15}\text{N}$ values in multiple species (Hobson et al. 1993, Kurle & Worthy 2001, Polischuk et al. 2001, Cardona et al. 2017b); however, due to their abundant lipid reserves, capital breeders mobilise energy from their lipid reserves during fasting and limit the catabolism of proteins, thus reducing the fasting effect on $\delta^{15}\text{N}$ (Habran et al. 2010, Aguilar et al. 2014). Nevertheless, the energy expenditure of the breeding season could have an indirect impact on southern elephant seal behaviour. We hypothesize that the nutritional stress of breeding leaves the elephant seals in poor body condition (Boyd et al. 1993), which, in turn, could lead to a behavioural change (Frid et al. 2006) and a reduction in prey selectivity. Thus, elephant seals may temporarily feed on suboptimal prey at a lower trophic level until they recover part of their lipid reserves. Whether this reduction of selectivity also occurs after moulting is unclear since the skin only integrates information for a few months, when the animals have recovered their lipid reserves. It is unlikely that the difference in $\delta^{15}\text{N}$ was caused by a change on the feeding grounds or in the ecosystem baseline, as both would have a greater effect on $\delta^{13}\text{C}$ than the one we detected (Lara et al. 2010, Quillfeldt et al. 2010).

It must be pointed out that the magnitude of the tissue isotopic shift, and therefore the shift in the foraging strategy, varies depending on the accuracy of TDFs. TDFs have a high standard deviation even within the same species, easily exceeding 0.5‰, (Hobson et al. 1996, Borrell et al. 2012, Beltran et al. 2016, Giménez et al. 2016) and may change among species of similar taxa (Beltran et al. 2016) or among

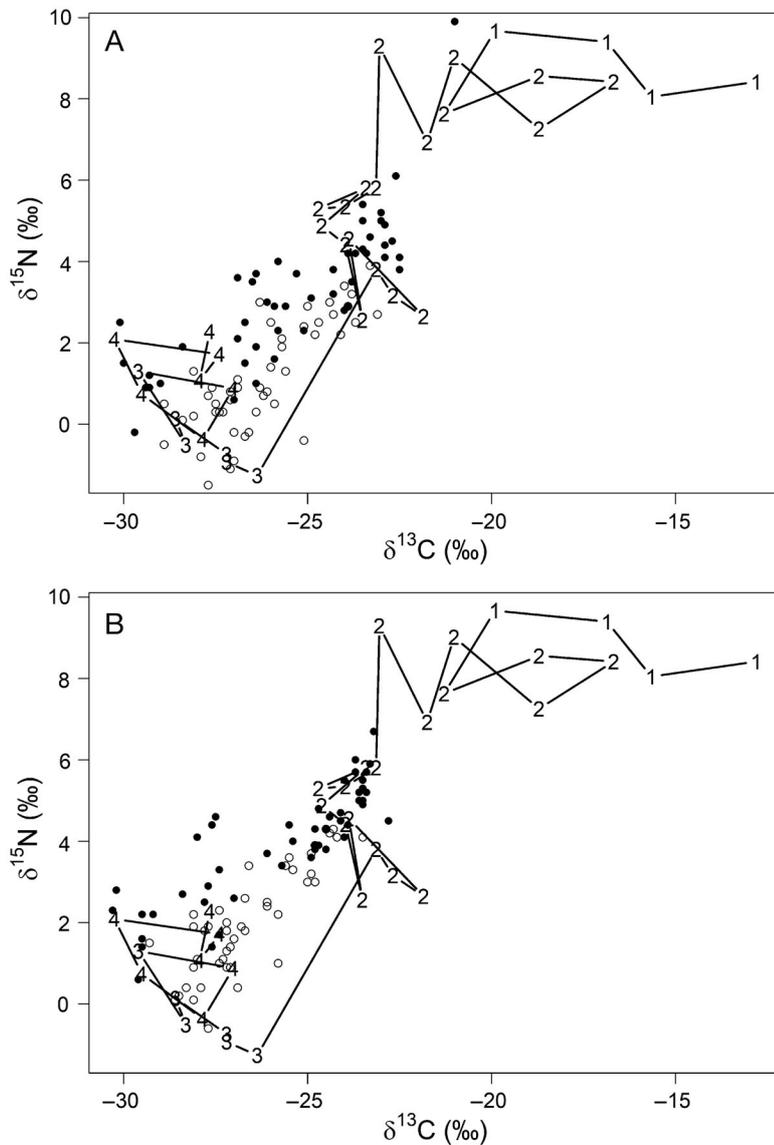


Fig. 6. Comparison between the Falkland Islands southern elephant seal results (males represented as filled circles and females as open circles) and the particulate organic matter (POM) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the Patagonian Continental Shelf nearshore (1) and offshore (2), Drake Passage (3) and western Antarctic Peninsula (4). Elephant seal isotopic values are given for (A) fur and (B) skin. Elephant seal isotopic values have been corrected -7.5‰ for $\delta^{13}\text{C}$ and -12‰ for $\delta^{15}\text{N}$

diets (Tyrrell et al. 2013). In this study, we used discrimination factors derived experimentally from other pinnipeds (Hobson et al. 1996), and the differences reported between tissues were greater than the possible error in the discrimination factors. Nevertheless, we remain uncertain about the absolute values of the diet presented here for elephant seals because of the absence of species-specific TDF values. Sample processing resulted in additional uncertainty, because the epidermis was not separated

from the dermis. The superficial layer of the epidermis (stratum corneum) is shed during the catastrophic moult and may contain some hairs. Thus, our skin samples may integrate some material synthesised immediately before moulting, although the inter-digital membrane has a very thin epidermis layer and therefore most of the sample tissue corresponded to the dermis.

A closer look at the variation between individuals shows that, while other subpopulations of southern elephant seals seem to segregate by age class (Slip 1995, Field et al. 2005, Walters et al. 2014), the Falkland Islands subpopulation only presents differences between sexes. The values of both tissue stable isotope ratios were higher in males than in females; the difference was particularly large (2‰) for $\delta^{15}\text{N}$. Dietary differences, previously reported for other populations (Rodhouse et al. 1992, Daneri et al. 2000, 2015), likely caused this difference, since a change in foraging ground location would have had a simultaneous and great effect on $\delta^{13}\text{C}$ values (Lara et al. 2010, Quillfeldt et al. 2010). However, we cannot rule out a simultaneous difference in foraging grounds and diet, as these 2 features are linked in other populations of northern and southern elephant seals (Le Boeuf & Crocker 2000, Lewis et al. 2006, Muelbert et al. 2013).

When compared with those of other southern elephant seal subpopulations and pinniped species from the western South Atlantic, the corrected isotopic values from the Falkland Islands elephant seal subpopulation overlapped with those of juveniles and some males of the Patagonian population (Lewis et al. 2006, Eder et al. 2010) and the Falkland Islands sea lions (Baylis et al. 2015). While elephant seal adult males from Argentinean Patagonia fed near the shelf break (Campagna et al. 1995, 1999), juveniles foraged on and off the Patagonian continental shelf, and a few took longer trips to the Pacific Ocean or the waters around South Georgia (Eder et al. 2010). The Falkland Islands population of South American sea lion *Otaria flavescens*, on the other hand, fed near the

shelf break north of the Falkland Islands (Baylis et al. 2016). Given the level of overlap between the stable isotope ratios in our data and the ratios of these 3 groups, we can assume that some Falkland Islands elephant seals migrated northward after both fasting seasons, and fed between the shelf break and mainland across the Patagonian Shelf break. Those individuals that do not overlap with the south American seals have intermediate isotopic values between the Patagonian and the Antarctic elephant seals (Hückstädt et al. 2012), suggesting that they feed south of the Falkland Islands, and some of them may reach the Antarctic Peninsula.

Our data also showed a strikingly similar pattern to that of the stable isotope ratios in POM reported by Lara et al. (2010), once the stable isotope ratios in elephant seal values were corrected according to TDF (12‰ for $\delta^{15}\text{N}$ and 7.5‰ for $\delta^{13}\text{C}$; Kelly 2000). This correction, although approximate, fits well the trophic levels reported for other elephant seal populations (Cherel et al. 2008). Such similarity supports our previous conclusions and show that Falkland Islands elephant seals feed across the Patagonian Shelf and Drake Passage. Setting the southern limit of the foraging grounds used by Falkland Islands elephant seals from stable isotope ratios is hard, because the isotopic baseline of the Drake Passage and the Southern Shetland Islands are very similar (Lara et al. 2010, Quillfeldt et al. 2010), although preliminary telemetry tagging results confirm that some seals reach the Antarctic Peninsula during their feeding trips (F. Galimberti unpubl. data).

Several studies have shown that elephant seals from other populations breed and moult within the same rookery (Lewis et al. 1996, Hofmeyr 2000, Le Boeuf & Crocker 2000). According to this model, Falkland Islands elephant seals that feed in the Southern Ocean or in the Pacific Ocean have to perform a >1000 km return trip twice every year. Such a migration pattern would have a high energy cost and seems unnecessary given that there are suitable breeding and moulting grounds near the feeding zones (McMahon et al. 2005, Hückstädt et al. 2012, Bogdanowicz et al. 2013) and, complementary, suitable feeding grounds near the Falkland Islands (Lewis et al. 2006, Eder et al. 2010). Philopatry can be evolutionarily beneficial due to the gregarious reproductive strategy of this species, but moulting has fewer requirements and can be performed on other beaches. Thus, it is plausible that some Falkland Islands individuals migrate to the Southern Ocean and stay there throughout the year, moulting on the closest beach (Bogdanowicz et al. 2013) and increas-

ing the difference between the moulting and the breeding cost. Further research is required to assess this issue, since it has important implications in those studies conducted during the moulting season if individuals are assigned to the incorrect population.

The variability in feeding behaviour of southern elephant seals seems to be related to a trade-off between the highly productive but distant feeding grounds of the Southern Ocean and the less productive but closer feeding grounds of the Patagonian shelf (McIntyre et al. 2015). These 2 strategies seem to be linked to the fitness of the individuals (Hindell et al. 2016), but the causes of individual specialization, such as culture (Harrison et al. 2010), genetics or ocean conditions during their first foraging trip (Ascani et al. 2016), are unknown. A high level of isotopic specialization does not imply that each individual feeds on a very few prey species or in a very specific location. Instead, it means that each individual always exploits the same resources, despite the variety of strategies shown by the rest of the population. Individual specialization is expected to be irreversible when based on morphological traits that cannot be modified at advanced life stages (Svanbäck & Bolnick 2007), but could be reverted in other cases (Mery & Burns 2010). There is no reason to believe that foraging specialization in elephant seals has a morphological basis, but learning has costs derived from the development and maintenance of the neural structures (Mery & Kawecki 2003, Mery & Burns 2010). Those costs explain why birds and mammals can learn certain tasks only during a critical or sensitive period early in their life (Brainard & Doupe 2002) and why spatial learning starts to decline immediately after adulthood in rats (Fischer et al. 1992). There is evidence that fidelity to foraging grounds in hard-shelled turtles is developed at the end of the juvenile stage and that they are unlikely to change during adulthood, even when foraging grounds are sub-optimal (Vander Zanden et al. 2016, Cardona et al. 2017a). The southern elephant seal is capable, as a species, of colonizing new areas (Acevedo et al. 2016) and maintaining gene flow between populations (Fabiani et al. 2003), despite its philopatry. However, the capacity of the adult elephant seals to revert the individual specialization is unclear. The results reported here reveal a high degree in individual specialization and high consistency in seasonal use of resources despite contrasting nutritional requirements. This could, potentially, indicate a reduced capacity to change their feeding grounds or diet and to use the most optimal foraging strategy for each situation. Sampling over multiple

years is needed to assess the long-term reversibility of foraging specialization. Further research is required to understand how and when individual specialization emerges in marine predators and hence better predict their adaptability to changing oceans.

In conclusion, the Falkland Islands elephant seals disperse over long distances both after breeding and moulting, but the tissues synthesised during the pre-moulting and pre-breeding foraging periods had similar $\delta^{13}\text{C}$ values, which suggests a high degree of individual specialization and fidelity to the same foraging grounds year round. The higher energetic cost of the breeding period could explain why all individuals consistently foraged at a lower trophic level after the breeding season. However, this last conclusion depends on the TDF used here, which can be inaccurate. Further research is needed to assess the capacity of highly specialized individuals to change their foraging tactics as a response to environmental change.

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LITERATURE CITED

- ✦ Acevedo J, Aguayo-Lobo A, Brito J, Torres D and others (2016) Review of the current distribution of southern elephant seals in the eastern South Pacific. *NZJ Mar Freshw Res* 50:240–258
- ✦ Aguilar A, Giménez J, Gómez-Campos E, Cardona L, Borrell A (2014) $\delta^{15}\text{N}$ value does not reflect fasting in mysticetes. *PLOS ONE* 9:e92288
- ✦ Alves-Stanley CD, Worthy GAJ (2009) Carbon and nitrogen stable isotope turnover rates and diet-tissue discrimination in Florida manatees (*Trichechus manatus latirostris*). *J Exp Biol* 212:2349–2355
- ✦ Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual specialisation. *Ecol Lett* 14:948–958
- ✦ Ascani F, Van Houtan KS, Di Lorenzo E, Polovina JJ, Jones TT (2016) Juvenile recruitment in loggerhead sea turtles linked to decadal changes in ocean circulation. *Glob Change Biol* 22:3529–3538
- ✦ Ayliffe LK, Cerling TE, Robinson T, West AG and others (2004) Turnover of carbon isotopes in tail hair and breath CO_2 of horses fed an isotopically varied diet. *Oecologia* 139:11–22
- ✦ Bahar B, Moloney AP, Monahan FJ, Harrison SM and others (2009) Turnover of carbon, nitrogen, and sulfur in bovine longissimus dorsi and psoas major muscles: implications for isotopic authentication of meat. *J Anim Sci* 87: 905–913
- ✦ Bailleul F, Charrassin JB, Monestiez P, Roquet F, Biuw M, Guinet C (2007) Successful foraging zones of southern elephant seals from the Kerguelen Islands in relation to oceanographic conditions. *Philos Trans R Soc B* 362: 2169–2181
- ✦ Baylis AMM, Orben RA, Arnould JPY, Peters K, Knox T, Costa DP, Staniland IJ (2015) Diving deeper into individual foraging specializations of a large marine predator, the southern sea lion. *Oecologia* 179:1053–1065
- ✦ Baylis AMM, Orben RA, Costa DP, Arnould JPY, Staniland IJ (2016) Sexual segregation in habitat use is smaller than expected in a highly dimorphic marine predator, the southern sea lion. *Mar Ecol Prog Ser* 554:201–211
- ✦ Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *J Anim Ecol* 73:1007–1012
- ✦ Beltran RS, Connolly Sadou M, Condit R, Peterson SH, Reichmuth C, Costa DP (2015) Fine-scale whisker growth measurements can reveal temporal foraging patterns from stable isotope signatures. *Mar Ecol Prog Ser* 523:243–253
- ✦ Beltran RS, Peterson SH, McHuron EA, Reichmuth C, Hückstädt LA, Costa DP (2016) Seals and sea lions are what they eat, plus what? Determination of trophic discrimination factors for seven pinniped species. *Rapid Commun Mass Spectrom* 30:1115–1122
- ✦ Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. *Can J Biochem Physiol* 37: 911–917
- ✦ Bogdanowicz W, Pilot M, Gajewska M, Suchecka E, Gola-chowski M (2013) Genetic diversity in a moulting colony of southern elephant seals in comparison with breeding colonies. *Mar Ecol Prog Ser* 478:287–300
- ✦ Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R (2002) Measuring individual-level resource specialization. *Ecology* 83:2936–2941
- ✦ Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulseley CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. *Am Nat* 161:1–28
- ✦ Bond AL, Hobson KA (2012) Reporting stable-isotope ratios in ecology: recommended terminology, guidelines and best practices. *Waterbirds* 35:324–331
- ✦ Borrell A, Abad-Oliva N, Gómez-Campos E, Giménez J, Aguilar A (2012) Discrimination of stable isotopes in fin whale tissues and application to diet assessment in cetaceans. *Rapid Commun Mass Spectrom* 26:1596–1602
- ✦ Bost CA, Cotté C, Bailleul F, Cherel Y and others (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J Mar Syst* 78:363–376
- ✦ Boyd I, Arnobom T, Fedak M (1993) Water flux, body composition, and metabolic rate during molt in female southern elephant seals (*Mirounga leonina*). *Physiol Zool* 66: 43–60
- ✦ Boyd IL, Walker TR, Poncet J (1996) Status of southern elephant seals at South Georgia. *Antarct Sci* 8:237–244
- ✦ Brainard MS, Doupe AJ (2002) What songbirds teach us about learning. *Nature* 417:351–358
- ✦ Campagna C, Lewis MN, Baldi R (1993) Breeding biology of southern elephant seals in Patagonia. *Mar Mamm Sci* 9: 34–47
- ✦ Campagna C, Le Boeuf BJ, Blackwell SB, Crocker DE, Quintana F (1995) Diving behaviour and foraging location of female southern elephant seals from Patagonia. *J Zool (Lond)* 236:55–71

- Campagna C, Quintana F, le Boeuf BJ, Blackwell S, Crocker DE (1998) Diving behaviour and foraging ecology of female southern elephant seals from Patagonia. *Aquat Mamm* 24:1–11
- Campagna C, Fedak MA, McConnell BJ (1999) Post-breeding distribution and diving behavior of adult male southern elephant seals from Patagonia. *J Mammal* 80: 1341–1352
- Campagna C, Piola AR, Marin MR, Lewis MN, Zajaczkowski U, Fernández T (2007) Deep divers in shallow seas: southern elephant seals on the Patagonian shelf. *Deep Sea Res I* 54:1792–1814
- Cardona L, Martins S, Uterga R, Marco A (2017a) Individual specialization and behavioural plasticity in a long-lived marine predator. *J Exp Mar Biol Ecol* 497:127–133
- Cardona L, Vales D, Aguilar A, Crespo E, Zenteno L (2017b) Temporal variability in stable isotope ratios of C and N in the vibrissa of captive and wild adult South American sea lions *Otaria byronia*: more than just diet shifts. *Mar Mammal Sci* 33:975–990
- Caut S, Laran S, García-Hartmann E, Das K (2011) Stable isotopes of captive cetaceans (killer whales and bottlenose dolphins). *J Exp Biol* 214:538–545
- Cherel Y, Ducatez S, Fontaine C, Richard P, Guinet C (2008) Stable isotopes reveal the trophic position and mesopelagic fish diet of female southern elephant seals breeding on the Kerguelen Islands. *Mar Ecol Prog Ser* 370: 239–247
- Cherel Y, Kernaléguen L, Richard P, Guinet C (2009) Whisker isotopic signature depicts migration patterns and multi-year intra- and inter-individual foraging strategies in fur seals. *Biol Lett* 5:830–832
- Clarke MR, MacLeod N (1982) Cephalopods in the diet of elephant seals at Signy Island, South Orkney Islands. *Br Antarct Surv Bull* 57:27–31
- Daneri GA, Carlini AR (2002) Fish prey of southern elephant seals, *Mirounga leonina*, at King George Island. *Antarct Sci* 1248:739–743
- Daneri GA, Carlini AR, Rodhouse PGK (2000) Cephalopod diet of the southern elephant seal, *Mirounga leonina* at King George Island, South Shetland Islands. *Antarct Sci* 72:76–79
- Daneri GA, Carlini AR, Marschoff ER, Harrington A, Negrete J, Mennucci JA, Márquez MEI (2015) The feeding habits of the Southern elephant seal, *Mirounga leonina*, at Isla 25 de Mayo/King George Island, South Shetland Islands. *Polar Biol* 38:665–676
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–506
- Dragon AC, Monestiez P, Bar-Hen A, Guinet C (2010) Linking foraging behaviour to physical oceanographic structures: southern elephant seals and mesoscale eddies east of Kerguelen Islands. *Prog Oceanogr* 87:61–71
- Ducatez S, Dalloyau S, Richard P, Guinet C, Cherel Y (2008) Stable isotopes document winter trophic ecology and maternal investment of adult female southern elephant seals (*Mirounga leonina*) breeding at the Kerguelen Islands. *Mar Biol* 155:413–420
- Eder EB, Lewis MN, Campagna C, Koch PL (2010) Evidence of demersal foraging from stable isotope analysis of juvenile elephant seals from Patagonia. *Mar Mammal Sci* 26: 430–442
- Eder E, Ceballos A, Martins S, Pérez-García H, Marín I, Marco A, Cardona L (2012) Foraging dichotomy in loggerhead sea turtles *Caretta caretta* off northwestern Africa. *Mar Ecol Prog Ser* 470:113–122
- Fabiani A, Hoelzel AR, Galimberti F, Muelbert MMC (2003) Long-range paternal gene flow in the southern elephant seal. *Science* 299:676
- Field IC, Bradshaw CJA, Burton HR, Sumner MD, Hindell MA (2005) Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals (*Mirounga leonina*). *Oecologia* 142:127–135
- Fischer W, Chen KS, Gage FH, Björklund A (1992) Progressive decline in spatial learning and integrity of forebrain cholinergic neurons in rats during aging. *Neurobiol Aging* 13:9–23
- Frid A, Baker GG, Dill LM (2006) Do resource declines increase predation rates on North Pacific harbor seals? A behavior-based plausibility model. *Mar Ecol Prog Ser* 312:265–275
- Galimberti F, Boitani L (1999) Demography and breeding biology of a small, localized population of southern elephant seals (*Mirounga leonina*). *Mar Mammal Sci* 15: 159–178
- Galimberti F, Sanvito S, Boitani L, Fabiani A (2001) Viability of the southern elephant seal population of the Falkland Islands. *Anim Conserv* 4:81–88
- Giménez J, Ramírez F, Almunia J, Forero MG, de Stephanis R (2016) From the pool to the sea: applicable isotope turnover rates and diet to skin discrimination factors for bottlenose dolphins (*Tursiops truncatus*). *J Exp Mar Biol Ecol* 475:54–61
- Grant BR, Grant PR (1996) High survival of Darwin's finch hybrids: effects of beak morphology and diets. *Ecology* 77:500–509
- Habran S, Debier C, Crocker DE, Houser DS, Lepoint G, Bouquegneau JM, Das K (2010) Assessment of gestation, lactation and fasting on stable isotope ratios in northern elephant seals (*Mirounga angustirostris*). *Mar Mamm Sci* 26:880–895
- Harrison XA, Tregenza T, Inger R, Colhoun K and others (2010) Cultural inheritance drives site fidelity and migratory connectivity in a long-distance migrant. *Mol Ecol* 19: 5484–5496
- Hilderbrand GV, Farley SD, Robbins CT, Hanley TA, Titus K, Servheen C (1996) Use of stable isotopes to determine diets of living and extinct bears. *Can J Zool* 74: 2080–2088
- Hindell MA, McMahon CR (2000) Long distance movement of a southern elephant seal (*Mirounga leonina*) from Macquarie Island to Peter 1 Øy. *Mar Mammal Sci* 16:504–507
- Hindell MA, McMahon CR, Bester MN, Boehme L and others (2016) Circumpolar habitat use in the southern elephant seal: implications for foraging success and population trajectories. *Ecosphere* 7:e01213
- Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120:314–326
- Hobson KA, Alisauskas RT, Clark RG (1993) Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *Condor* 95:388–394
- Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63:786–798
- Hobson KA, Schell DM, Renouf D, Noseworthy E (1996) Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive seals: implications for dietary reconstruction. *Can J Zool* 78:848–852

- Hobson KA, Barnett-Johnson R, Cerling T (2010) Using isoscapes to track animal migration. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) *Isoscapes: understanding movement, pattern, and process on Earth through isotope mapping*. Springer Science + Business Media, Dordrecht, p 273–298
- Hofmeyr GJG (2000) Dispersal and dispersion of southern elephant seals at Marion Island. MSc thesis, University of Pretoria
- Hückstädt LA, Koch PL, McDonald BI, Goebel ME, Crocker DE, Costa DP (2012) Stable isotope analyses reveal individual variability in the trophic ecology of a top marine predator, the southern elephant seal. *Oecologia* 169: 395–406
- Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Can J Zool* 78:1–27
- Kernaléguen L, Cazelles B, Arnould JPY, Richard P, Guinet C, Cherel Y (2012) Long-term species, sexual and individual variations in foraging strategies of fur seals revealed by stable isotopes in whiskers. *PLOS ONE* 7: e32916
- Kurle CM, Worthy GAJ (2001) Stable isotope assessment of temporal and geographic differences in feeding ecology of northern fur seals (*Callorhinus ursinus*) and their prey. *Oecologia* 126:254–265
- Labrousse S, Vacquie-Garcia J, Heerah K, Guinet C and others (2015) Winter use of sea ice and ocean water mass habitat by southern elephant seals: the length and breadth of the mystery. *Prog Oceanogr* 137:52–68
- Lara RJ, Alder V, Franzosi CA, Kattner G (2010) Characteristics of suspended particulate organic matter in the southwestern Atlantic: influence of temperature, nutrient and phytoplankton features on the stable isotope signature. *J Mar Syst* 79:199–209
- Le Boeuf BJ, Crocker DE (2000) Foraging ecology of northern elephant seals. *Ecol Monogr* 70:353–382
- Le Boeuf BJ, Gantt RF, Whiting RJ (1973) Perinatal behavior of northern elephant seal females and their young. *Behaviour* 43:121–156
- Lewis MN, Campagna C, Quintana F (1996) Site fidelity and dispersion of southern elephant seals. *Mar Mamm Sci* 12: 138–147
- Lewis R, O'Connell TC, Lewis MN, Campagna C, Hoelzel AR (2006) Sex-specific foraging strategies and resource partitioning in the southern elephant seal (*Mirounga leonina*). *Proc R Soc B* 273:2901–2907
- Ling J (2012) The skin and hair of the southern elephant seal, *Mirounga leonina* (Linn.). I. The facial vibrissae. *Aust J Zool* 60:259–271
- Massie PP, McIntyre T, Ryan PG, Bester MN, Bornemann H, Ansorge IJ (2016) The role of eddies in the diving behaviour of female southern elephant seals. *Polar Biol* 39: 297–307
- McIntyre T, Donaldson A, Bester MN (2015) Spatial and temporal patterns of changes in condition of southern elephant seals. *Antarct Sci* 10:1–10
- McMahon CR, Bester MN, Burton HR, Hindell MA, Bradshaw CJA (2005) Population status, trends and a re-examination of the hypotheses explaining the recent declines of the southern elephant seal *Mirounga leonina*. *Mammal Rev* 35:82–100
- Mery F, Burns JG (2010) Behavioural plasticity: an interaction between evolution and experience. *Evol Ecol* 24: 571–583
- Mery F, Kawecki TJ (2003) A fitness cost of learning ability in *Drosophila melanogaster*. *Proc R Soc B* 270:2465–2469
- Muelbert MMC, de Souza RB, Lewis MN, Hindell MA (2013) Foraging habitats of southern elephant seals, *Mirounga leonina*, from the Northern Antarctic Peninsula. *Deep Sea Res II Top Stud Oceanogr* 88–89:47–60
- Narita R, Sasaki K, Goda K, Maeda N, Takayanagi A (2006) Turnover of stable isotopes in Hokkaido brown bear (*Ursus arctos yesoyensis*). *Mammal Study* 31:59–63
- Newland C, Field IC, Cherel Y, Guinet C, Bradshaw CJA, McMahon CR, Hindell MA (2011) Diet of juvenile southern elephant seals reappraised by stable isotopes in whiskers. *Mar Ecol Prog Ser* 424:247–258
- Newsome SD, Tinker MT, Monson DH, Oftedal OT and others (2009) Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology* 90:961–974
- Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. *Mar Mamm Sci* 26:509–572
- Pagani-Núñez E, Valls M, Senar JC (2015) Diet specialization in a generalist population: the case of breeding great tits *Parus major* in the Mediterranean area. *Oecologia* 179:629–640
- Polischuk SC, Hobson KA, Ramsay MA (2001) Use of stable-carbon and -nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. *Can J Zool* 79:499–511
- Quillfeldt P, Masello JF, McGill RA, Adams M, Furness RW (2010) Moving polewards in winter: a recent change in the migratory strategy of a pelagic seabird? *Front Zool* 7:15
- R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Reich KJ, Bjørndal KA, Bolten AB (2007) The 'lost years' of green turtles: using stable isotopes to study cryptic life-stages. *Biol Lett* 3:712–714
- Riedman M (1990) *The pinnipeds: seals, sea lions and walruses*. University of California Press, Berkeley, CA
- Rodhouse PG, Arnborn TR, Fedak M, Yeatman J, Murray AWA (1992) Cephalopod prey of the southern elephant seal, *Mirounga leonina* L. *Can J Zool* 70:1007–1015
- Ryan C, McHugh B, Trueman CN, Harrod C, Berrow SD, O'Connor I (2012) Accounting for the effects of lipids in stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) analysis of skin and blubber of balaenopterid whales. *Rapid Commun Mass Spectrom* 26:2745–2754
- Scott R, Marsh R, Hays GC (2014) Ontogeny of long distance migration. *Ecology* 95:2840–2850
- Skrzypek G (2013) Normalization procedures and reference material selection in stable HCNOS isotope analyses: an overview. *Anal Bioanal Chem* 405:2815–2823
- Slip DJ (1995) The diet of southern elephant seals (*Mirounga leonina*) from Heard Island. *Can J Zool* 73:1519–1528
- Sotiropoulos MA, Tonn WM, Wassenaar LI (2004) Effects of lipid extraction on stable carbon and nitrogen isotope analyses of fish tissues: potential consequences for food web studies. *Ecol Freshw Fish* 13:155–160
- Sponheimer M, Robinson TF, Cerling TE, Tegland L and others (2006) Turnover of stable carbon isotopes in the muscle, liver, and breath CO_2 of alpacas (*Lama pacos*). *Rapid Commun Mass Spectrom* 20:1395–1399
- Svanbäck R, Bolnick DI (2007) Intraspecific competition drives increased resource use diversity within a natural population. *Proc R Soc B* 274:839–844

- ✦ Svanbäck R, Eklöv P (2002) Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. *Oecologia* 131:61–70
- ✦ Terraube J, Guixé D, Arroyo B (2014) Diet composition and foraging success in generalist predators: Are specialist individuals better foragers? *Basic Appl Ecol* 15:616–624
- ✦ Tyrrell LP, Newsome SD, Fogel ML, Viens M, Bowden R, Murray MJ (2013) Vibrissae growth rates and trophic discrimination factors in captive southern sea otters (*Enhydra lutris nereis*). *J Mammal* 94:331–338
- ✦ Valenzuela LO, Sironi M, Rowntree VJ, Seger J (2009) Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). *Mol Ecol* 18:782–791
- ✦ Vales DG, Cardona L, García NA, Zenteno L, Crespo EA (2015) Ontogenetic dietary changes in male South American fur seals *Arctocephalus australis* in Patagonia. *Mar Ecol Prog Ser* 525:245–260
- ✦ Vander Zanden HB, Bjorndal KA, Reich KJ, Bolten AB (2010) Individual specialists in a generalist population: results from a long-term stable isotope series. *Biol Lett* 6:711–714
- ✦ Vander Zanden HB, Bolten AB, Tucker AD, Hart KM and others (2016) Biomarkers reveal sea turtles remained in oiled areas following the Deepwater Horizon oil spill. *Ecol Appl* 26:2145–2155
- ✦ Walters A, Lea MA, Van Den Hoff J, Field IC and others (2014) Spatially explicit estimates of prey consumption reveal a new krill predator in the Southern Ocean. *PLOS ONE* 9:e86452
- ✦ Yurkowski DJ, Ferguson SH, Semeniuk CAD, Brown TM, Muir DCG, Fisk AT (2016) Spatial and temporal variation of an ice-adapted predator's feeding ecology in a changing Arctic marine ecosystem. *Oecologia* 180:631–644
- ✦ Zenteno L, Borella F, Otero JG, Piana E and others (2015) Shifting niches of marine predators due to human exploitation: the diet of the South American sea lion (*Otaria flavescens*) since the late Holocene as a case study. *Paleobiology* 41:387–401

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