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Foraging Strategies of Female Elephant Seals from Península Valdés, Patagonia, Inferred from Whisker Stable Isotope Signatures of Their Pups

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Abstract

The foraging strategies of gestating female elephant seals (*Mirounga leonina*) from Península Valdés, Patagonia, were assessed by analyzing the values of stable isotopes of carbon (C) and nitrogen (N) from whiskers of 60 weanlings as a proxy for maternal spatial niche utilization. The data were combined with isotopic values and at-sea satellite locations of juvenile seals and adult female satellite tracks to provide classifications of the likely foraging strategies of the mothers of the studied pups. Based on at-sea locations during the austral summer, females foraged in oceanic waters while juveniles foraged both in neritic and in oceanic habitats. Weanling isotopic values (n = 60 pups) ranged from -19.9 to -14.8‰ for C and from 10.6 to 18.9‰ for N. The degree of variation of spatial niche distribution exhibited individual patterns of habitat use over time and revealed significant intra-population differences. Ten percent of the individuals exhibited neritic maternal foraging ($\delta^{13}C$ = -15.6 ± 0.5‰, $\delta^{15}N$ = 17.3 ± 1.1‰) and high consistency, thus suggesting specialization (%CV $\delta^{13}C$ values = 0.3 to 2.2), while 90% of the individuals exhibited oceanic maternal foraging ($\delta^{13}C$ = -17.9 ± 0.7‰, $\delta^{15}N$ = 12.4 ± 0.5). Additionally, oceanic maternal foraging could be further classified to distinguish broader individual variability: 58% were specialists (%CV = 0.03 to 2.2), 30% were intermediate specialists-generalists (%CV = 2.5 to 4.5), and 12% were generalists (%CV = 5.0 to 7.3). The prevailing strategy for females was oceanic foraging as exhibited by location at sea and the greater extent of oceanic habitats (88%) potentially available for foraging. At the population level, the existence of both alternate foraging strategies and high individual variability exhibited by gestating females in a high-quality foraging area such as the oceanic environment of the Argentine Basin may confer an ecological edge to these females to succeed in a less predictable (although fairly rich) environment, thus influencing population trends.

Key Words: habitat use, neritic/oceanic foraging strategies, stable isotopes, individual specialization

Introduction

Southern elephant seals (*Mirounga leonina*) are important top predators in the Southern Ocean because of their large population (*ca*. 700,000) and prey biomass consumption (*ca*. 4-5 × 10^6 tons annually) (Le Boeuf & Laws, 1994). Foraging at sea makes up 80% of their annual cycle and can be divided into post-breeding and post-moulting periods (2 to 3 mo after breeding and 7 to 8 mo after moulting on land, respectively; Campagna et al., 1993, 1998, 1999, 2000; Le Boeuf & Laws, 1994; and references therein). Most of the information regarding the foraging ecology of southern elephant seals has come from bio-logging technologies and satellite tracking applied to sub-Antarctic breeding colonies. Males undertake foraging migrations to the pack ice and the Antarctic continental shelves where they remain throughout the winter (Hindell et al., 2001; Bailleul et al., 2007; Labrousse et al., 2017; Malpress et al., 2017). Females, in contrast, undertake long-distance, pole-ward migrations during the winter and forage at ocean frontal systems and within the marginal sea-ice extent over the Antarctic continental shelf (Jonker & Bester, 1998; Bailleul et al., 2007; van den Hoff et al., 2014; Hindell et al., 2016), although some have been reported foraging in the high-quality Antarctic shelf or shelf break of the Western Antarctic Peninsula during the summer months (Costa et al., 2010; Hückstädt et al., 2012; Muelbert et al., 2013).

Most of the key sub-Antarctic colonies are surrounded by deep water (1,000 m or more within 9 to 100 km from the coast) and are therefore characterized by narrow shelves (Campagna et al., 2007). In contrast, the Península Valdés colony is located next to one of the largest, shallowest (almost 1×10^6 km^2 and less than 150 m deep), and most productive continental shelves in the world (Bisbal, 1995; Croxall & Wood, 2002; Acha et al., 2004) (Figure 1). Satellite-tracked males forage over the Patagonian shelf or at its edge and tend to concentrate foraging on seasonal frontal areas (Campagna et al., 1998, 1999, 2006, 2007) or within areas where the productivity is associated with the bathymetry and, thus, is geographically predictable (Campagna et al., 2006; Romero et al., 2006). In contrast, females migrate widely far offshore to forage in deep waters of the Argentine Basin during their post-moulting trip, and their diving activity over the shelf suggests extensive travelling on their way to or returning from foraging grounds (Campagna et al., 1998, 2000).

Although satellite telemetry and bio-logging technologies have provided helpful information on the foraging behavior of elephant seals, sample sizes have been small in Península Valdés. Stable isotopes of carbon and nitrogen (δ^{13}C and δ^{15}N, respectively) provide another method to evaluate foraging ecology at a population scale and complement traditional methods of dietary analysis (stomach content and scat collection) in wide-ranging and deep-diving marine animals (Ducatez et al., 2008). Both carbon and nitrogen isotope values in the tissues of consumers reflect those of assimilated foods, characterized by a stepwise enrichment in the heavier isotope relative to prey (Kelly, 2000). This increase is more pronounced in δ^{15}N values (3 to -5‰); therefore, it is useful as an indicator of prey trophic level. In contrast, trophic enrichment in ^{13}C is usually small, and animal δ^{13}C values are more useful for identifying foraging areas at different

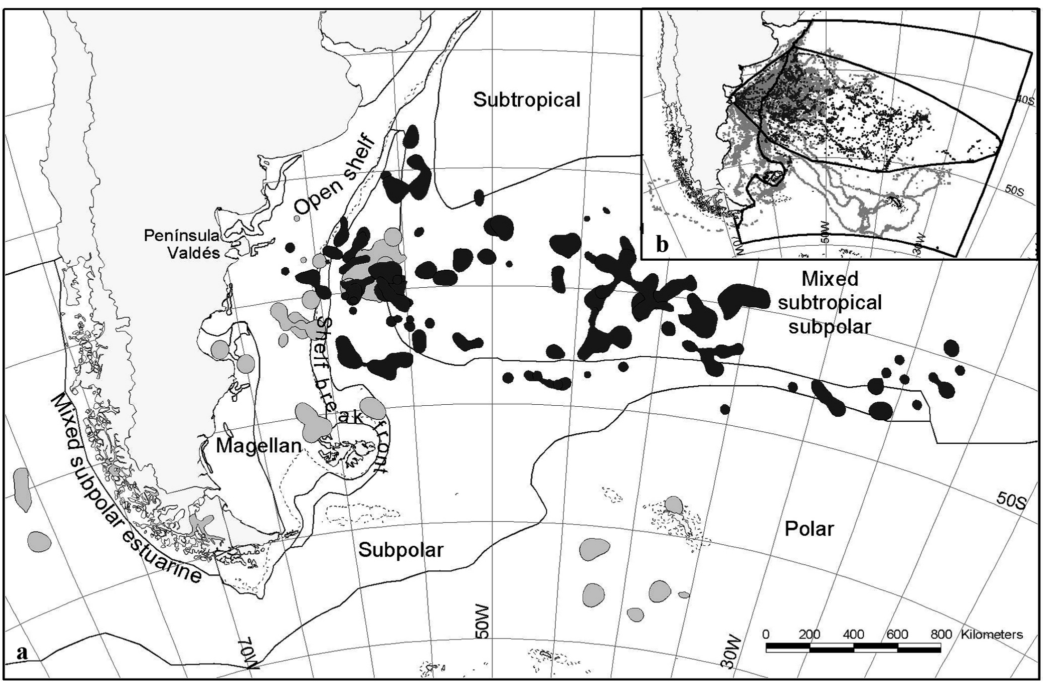

Figure 1. (a) Kernel analysis of satellite data resulted in the identification of foraging areas for individual females (in black) and individual juveniles (in grey) from Península Valdés; use frequency estimated by Kernel technique (contours representing 75% of the satellite localizations) and the oceanographic regimes for the region are adapted from Piola & Matano (2001); and (b) total available area (box enclosing 99.1% of the locations) and explored area defined by the locations of the post-moulting female trips.

geographic scales. In the southern hemisphere, $\delta^{13}C$ values of plankton and particulate organic matter are higher in warm subtropical waters than in cold Antarctic waters (Trull & Armand, 2001; Cherel & Hobson, 2007). In addition, more productive neritic coastal/inshore or benthic habitats have higher food web $\delta^{13}C$ values than oceanic offshore or pelagic food webs (reviewed in Koch, 2007). This spatial variation is reflected in organisms at higher trophic levels (Quillfeldt et al., 2005; Cherel & Hobson, 2007).

Previous reports of stable isotopes of carbon and nitrogen along the whiskers of subadult and adult elephant seals from Península Valdés were consistent with neritic and oceanic foraging strategies of males and females, respectively (Lewis et al., 2006). However, it is difficult to obtain a large sample of adult female elephant seals for population-scale analyses (Ducatez et al., 2008; Hindell et al., 2012). In contrast, pups are easier to access and handle and have proven to be an effective proxy for maternal foraging since their isotopic compositions derive from those of their mothers (Ducatez et al., 2008; Habran et al., 2010; Authier et al., 2012; Velazquez-Castillo & Elorriaga-Verplancken, 2017; Gallon et al., 2018).

In the present study, the foraging spatial niche of female southern elephant seals from Península Valdés was described by using the stable isotope values of C and N along the whiskers of newly weaned pups (weanlings). The previously reported stable isotope values of satellite-tracked juveniles, obtained during the same months in which females are foraging at sea, were used as an isotopic reference to classify the foraging strategies of the gestating females as either neritic or oceanic. In addition, the relationship between available foraging habitats and those targeted by females were assessed from satellite tracks of females in relation to neritic and oceanic domains and oceanographic regimes. While it is unclear if oceanic foraging of females from Península Valdés results from differences in spatial range and trophic niche among conspecifics (sexual/age segregation) or from a small sample size (or possibly both), their transit through the productive continental shelf to reach distant oceanic foraging habitat is noteworthy. The evaluation of the female foraging strategies using stable isotope analysis to provide a sufficiently large sample size may give insight in this regard.

Methods

The present study was carried out at Península Valdés, Patagonia, Argentina (Figure 1), over a number of field seasons from 1997 to 2014. Data from different seasons were used to describe foraging habitat and strategies of southern elephant seal females using satellite tracking and stable isotopes. Our study encompassed data from three separate datasets that were combined to better portray foraging strategies of gestating females: (1) the satellite tracks of six adult females instrumented at the end of the moulting seasons (January) in 1997 (Campagna et al., 1998), 2008, 2013, and 2014; (2) stable isotope values of C and N from the whiskers of six satellite-tracked juveniles instrumented at the end of the moulting season (late November/ early December) in the years 2005 (three females and one male) and 2006 (two males), previously reported by Eder et al. (2010); the tracks of these juveniles were reanalyzed to assess their spatial use related to their foraging habitats and the oceanographic regimes; and (3) the stable isotope values of C and N from the whiskers of 60 weanlings selected at random in late October of the 2011 breeding season, the time when most of the pups are weaned (Campagna et al., 1993).

All elephant seals were randomly selected, and a sampling protocol was performed in accordance with animal ethics standards and permits. Female and juvenile deployment procedures for satellite tracking were reported previously (Campagna et al., 2006, 2007), as well as the juvenile stable isotope data sampling (Eder et al., 2010). For the weanling stable isotope sampling, animals were restrained with a customized canvas head bag, and a single whisker was clipped from its root during the 2011 breeding season.

Satellite Tracking and Foraging Habitat

The configuration of satellite telemeters and the location data analyses were described in Campagna et al. (2006, 2007). Satellite telemeters transmitted as soon as the animals entered the water, 24 h/d, with sampling rates of 40 ± 6 s. The estimated accuracy of each location was provided by the Argos system. The iterative forward/backward averaging filter was applied to reject unrealistic uplinks (based on travel rate greater than 2.8 m/s [10 km/h]; McConnell et al., 1992). To avoid any bias introduced by variation in sampling frequency, the first location recorded per day was used to compute the density contours using a Kernel technique (bandwidth = 30 km) with the *ArcView GIS* software and the Animal Movement extension in order to estimate individual foraging areas. The *individual foraging area* was defined as the area within the 75% Kernel where each elephant seal concentrated activity based on the percentage of the total time at sea (high location rate; Campagna et al., 2006; Eder et al., 2010; Figure 1).

Foraging habitat was defined based on the individual percentage of time at sea within the main oceanographic regimes for the region (defined below), as well as either neritic or oceanic habitats (defined as *shallower* or *deeper* than 200 m, respectively). The main oceanographic regimes for the region were classified according to their physical characteristics and water masses as adapted from Piola & Matano (2001). These regimes are located in association with neritic and oceanic habitats and were used to characterize the foraging strategies of females within the local environmental context (Figure 1a). The Minimum Convex Polygon method was used to define the total area explored (see polygon line around female's locations in Figure 1b) and to estimate the extent of neritic and oceanic habitats. Spatial analysis was performed using *Spatial Analyst 2.04* beta and Animal Movement extension which defined the potential foraging area (the big box in Figure 1b) considering the overall distribution of locations of all the satellite-tracked elephant seals (Campagna et al., 2009) and estimating the extent of neritic and oceanic habitats available.

The oceanographic regimes considered for the region are those adapted from Piola & Matano (2001): "Open Shelf," characterized by sub-Antarctic waters diluted by the influence of continental runoff (temperature ranges from 6º to 10ºC and low surface salinity < 30 PSU); "Magellan Straits" is notable for the introduction of a tongue of low salinity water and tidal mixing, which promotes coastal fronts; "Shelf-Break Front" is a narrow transition region between subpolar (temperature < 15ºC; salinity < 34.2 PSU) and shelf waters characterized by high chlorophyll-a (> 4 mg/m^3); "Subtropical" regime is characterized by high surface temperature (10º to 20ºC) and salinity (> 34.8 PSU) and low nutrient concentrations; "Mixed Subtropical-Subpolar" waters are a wide transition zone between the Subtropical and Subpolar regimes characterized by high eddy variability (surface temperature up to 16ºC) and moderate surface chlorophyll-a concentrations (~1 mg/m^3); "Subpolar" regime is characterized by relatively cold and high nutrient–low chlorophyll waters; and "Polar" regime is characterized by low temperature (< 4°C) and relatively high nutrient concentration waters derived from the Antarctic Circumpolar Current.

Stable Isotopes of Weanling Whiskers as a Proxy for Female Foraging Strategies

Whiskers are metabolically inactive tissues soon after synthesis, which approximates a long timeline of stable isotope values derived from food sources (Hobson et al., 1996; Lewis et al., 2006; Newsome et al., 2009; Eder et al., 2010; Newland et al., 2011; Hückstadt et al., 2012). Isotopic values along the whisker of elephant seals were assumed to represent tissue synthesized during a previous period that would not extend for longer than a year (Newland et al., 2011; Hückstadt et al., 2012). However, there is no reference for temporal isotopic integration in whiskers of pre-partum (mother-to-offspring transfer of matter directly during gestation) or nursing elephant seal pups (mother-to-offspring transfer of nutrients into pup tissues after assimilation of milk). The closest estimate is an average growth rate of 0.22 mm/d in newly weaned pups during their first months foraging at sea (Hindell et al., 2012) which, if applied to the pup whiskers of this study, would equal a time period longer than the gestating plus nursing periods. Regardless, the tip of the whisker clearly represents the oldest growth, and the root represents the most recent growth. Thus, the isotopic composition of a pup's whisker represents the foraging strategy of its mother over the preceding months during their post-moulting trip under the following assumptions: (1) whiskers appear early in the embryonic development (Berta & Sumich, 1999), at least 2 mo after the implantation of the blastocyst during the moult (Crocker et al., 2001) as noted in studies carried out in grey seal (*Halichoerus grypus*) embryos (Hewer & Backhouse, 1968), and that this is a period of rapid somatic growth (Hindell et al., 2012); (2) whiskers yield longer-term integrated isotopic composition than other tissues like blood components (Habran et al., 2010) and reflect a significant part of the female foraging; and (3) there is no or very little enrichment in the isotope values of the pup's tissues relative to its mother during gestation. The isotopic composition of a tissue type in the pup ($\delta^{13}C$ values) remains similar to that of their mother (Habran et al., 2010), or slightly enriched after weaning (~0.3‰; Ducatez et al., 2008). So, $\delta^{13}C$ values in pup tissue are useful in evaluating gestating female foraging strategies because enrichment is not expected to have any effect except during lactation when pups ingest their own food and integrate it in the recent growth.

Isotope Analysis

Weanling whiskers were washed in methanol in an ultrasonic bath for 15 min and measured to the nearest centimeter. Two subsamples of 1 ± 0.2 mg were cut from the whisker and sealed in tin cups for isotope analysis—one segment was from the proximal end of the tip and one segment from the middle (at half of the whisker total length). Given that pup isotope values increase during lactation, especially for $\delta^{15}N$ values (Ducatez et al., 2008; Habran et al., 2010), the recent growth of the whisker (root) representing lactation was not included in the analysis. Carbon and nitrogen isotope ratios were analyzed at the Stable Isotope Facility of the University of California at Davis. Results are presented in the usual delta (δ) notation relative to PeeDee Belemnite (PDB) and atmospheric N^2 (air) for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Female Foraging Strategies and Individual Variability

Data from juvenile seals were used as a reference to support the classification of the weanling isotopic values as representative of neritic or oceanic maternal foraging because the mean isotopic values of their whiskers, as reported in Eder et al. (2010), were representative of their feeding areas and trophic level (with shelf foragers associated to neritic prey with higher $\delta^{13}C$ and $\delta^{15}N$ values), and given that juveniles foraged at the same time of the year as gestating females. Therefore, isotopic values above -16.1‰ $\delta^{13}C$ and 15.4‰ $\delta^{15}N$ were considered as representative of neritic shelf foraging, while values below -16.9‰ $\delta^{13}C$ and 14‰ $\delta^{15}N$ were considered representative of oceanic foraging.

The percentage variation of $\delta^{13}C$ values along the whisker (% coefficient of variation [%CV]) was calculated to assess the individual variability of weanlings and juveniles and the specialization based on the spatial niche width as

$$\%CV\ \delta^{13}C = SD\ \delta^{13}C/(\delta^{13}C \times 100)$$

where

SD $\delta^{13}C$: standard deviation of $\delta^{13}C$ values along the whisker

$\delta^{13}C$: mean of $\delta^{13}C$ values along the whisker

Given that the geographic $\delta^{15}N$ distribution is variable (Bowen, 2010) and less predictable (Graham et al., 2010), only $\delta^{13}C$ values were used for this analysis.

Statistical Analysis

Isotopic data were tested for normality and homogeneity of variance, and non-parametric statistics were used when assumptions were not satisfied and transformations did not improve the data. Multivariate methods (cluster analysis) were employed to explore the intrinsic pattern of $\delta^{13}C$ and $\delta^{15}N$ values of pup whiskers, including the isotope values of juvenile whiskers. Statistical analyses and graphics were conducted using *Statistica* (*StatSoft*) and *Infostat* softwares. The level of significance was set at $p < 0.05$. The means are reported with SD unless otherwise stated.

Results

Satellite Tracking and Foraging Habitat

During the post-moulting pelagic phase (February and August), female locations obtained in 1997, 2008, 2013, and 2014 covered an area of 3,118,834 km², which is only 35% of the total potentially available foraging area (denoted by the overall locations of animals at sea, comprising 12% of neritic and 88% of oceanic habitats). They only used 15.6% of this area for foraging, including 2% of neritic and 98% of oceanic habitats (Figure 1a and associated data in Table 1). Tracked females focused foraging mainly in mixed subtropical-subpolar waters and, to a lesser extent, subpolar waters, spending 98% of their foraging time in the deep waters of the Argentine Basin (oceanic habitat; Figures 1a & 2).

Juvenile locations obtained in 2005 and 2006 suggest they were foraging in subpolar and polar waters, but they also foraged in open shelf and shelf-break front waters. Nearly 50% of their foraging time was both in neritic and oceanic habitats (Figures 1a & 2). Individual time spent foraging in neritic and oceanic habitats for all individuals show a wide range (Table 1).

Isotope Analysis

Whisker length of weaned pups averaged 8.5 ± 1.3 cm (range = 5.3 to 11.4 cm). Mean isotopic values along the whiskers (n = 120 segments) were -17.7 ± 1.0‰ for $\delta^{13}C$ and 12.9 ± 1.6‰ for $\delta^{15}N$, encompassing a broad range (from -19.9 to -14.8‰ $\delta^{13}C$ and 10.9 to 18.9‰ $\delta^{15}N$; Figure 3).

Female Foraging Strategies and Individual Variability

Mean isotopic values of weanlings and juveniles were clustered in two main groups (Figure 4). Cluster 1 had $\delta^{13}C$ values above -16.2‰, and Cluster 2 had $\delta^{13}C$ values below -16.5‰. Values of $\delta^{13}C$ and $\delta^{15}N$ of weanlings were significantly different between those clusters (Wilcoxon Mann-Whitney $W_{6, 54} = 345.0$, $p < 0.05$; Figure 5). Ten percent ($n = 6$) of the weanlings had mean values consistent with neritic foragers ($\delta^{13}C$ = -15.6 ± 0.5‰ and $\delta^{15}N$ = 17.3 ± 1.4‰), and the remaining 90% ($n = 54$) had mean values consistent with oceanic foragers (-17.9 ± 0.7‰ $\delta^{13}C$ and 12.4 ± 0.5‰ $\delta^{15}N$; Figure 5). Within Cluster 2, there was a single weanling individual with the lowest isotopic values (-19.8 ± 1.4‰ $\delta^{13}C$ and 10.9 ± 0.5‰ $\delta^{15}N$; individual "E" in Figure 4). This single individual is very distant from the other two subgroups of weanlings ($2_{2\text{-}1}$ and $2_{2\text{-}2}$ in Figure 4) that differed significantly in their $\delta^{13}C$ values (-17.4 ± 0.4 vs -18.6 ± 0.3‰; $W_{30, 23} = 276.0$, $p < 0.05$) and $\delta^{15}N$ (12.7 ± 0.4 vs -12.2 ± 0.2‰; $W_{30, 23} = 363.5$, $p < 0.05$).

Table 1. Summary data from satellite-tracked females and juveniles at sea during the same season (different years), including the percent time spent (foraging time) in each foraging habitat (foraging strategy). All females were known to have returned to Península Valdés (PV) for the breeding season (September) and to give birth, except Females 2 and 5 whose satellite devices stopped transmitting positions after 2 and 4 mo at sea, respectively. Juveniles returned to the colony to rest on land and were recovered between 2 and 7 mo after deployment.

	Date of deployment	Duration of the trip (d)	Estimated total travel distance (km)	Max distance from PV (km)	% neritic strategy	% oceanic strategy
Females						
1	15 Jan 1997	232	11,427	2,342	0	100
2	15 Jan 1997	42	2,276	936	12	88
3a	17 Jan 2008	51	3,449	700	4	96
3b*	15 March 2008	183	11,699	2,145		
4	16 Jan 2008	230	16,495	2,525	0	100
5	10 Jan 2013	74	5,441	3,371	3	97
6	10 Jan 2014	236	9,394	1,403	0	100
Juveniles						
RUS2	30 Nov 2005	74	3,070	742	1	99
RON6	1 Dec 2005	81	2,346	521	100	0
BUC10	9 Dec 2005	171	3,290	1,182	85	15
FAR11	10 Dec 2005	228	7,969	1,689	36	64
1LID	28 Dec 2006	210	22,595	2,769	12	88
2LID	28 Dec 2006	171	16,873	2,274	49	51

*Female 3a returned to the colony 2 mo after deployment and spent a week on land before embarking on a new foraging trip (3b) that ended in September when she returned to the colony for the breeding season.

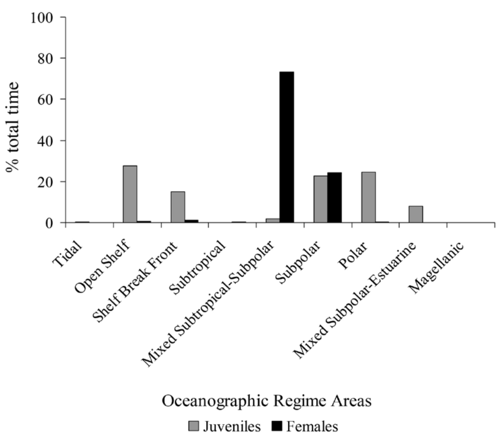

Figure 2. Individual percent total time spent by post-moulting adult elephant seal (*Mirounga leonina*) juveniles ($n = 6$) and females ($n = 6$) in each oceanographic regime

According to the %CV analysis, 62% of the individuals from both clusters had a low variability along their whiskers (%CV < 2.2; Figure 6), suggesting individual specialization within the spatial habitat. Of the remaining, 27% of the individuals had an intermediate variability (%CV between 2.5 to 4.5), and 11% had a high variability (%CV > 5; Figure 6), suggesting more generalist foraging. Individuals in Cluster 1, classified as neritic foragers ($n = 7$; Figure 4), were all specialists according to their within-whisker variability (%CV = 1.4 ± 0.6), showing high consistency in their $\delta^{13}C$ values. This cluster included one juvenile that spent 100% of its foraging time in neritic habitat (RON6; Table 1). Animals in Cluster 2 ($n = 59$) had broader variability: 58% were specialists (%CV = 0.9 ± 0.6) showing high consistency in their $\delta^{13}C$ values, 30% were intermediate between specialists and generalists (%CV = 3.4 ± 0.7), and 12% were generalists (%CV = 6.3 ± 0.8). The specialist group included two juveniles (RUS2 and BUC10; Table 1); and the intermediate group included two juveniles which, despite clustering with oceanic foragers, spent considerable time in both neritic and oceanic habitats (Juveniles FAR11 and 2LID; Table 1). The generalist group included a juvenile that spent most of its foraging time in distant oceanic polar regime (> 50° S; 1LID; Table 1).

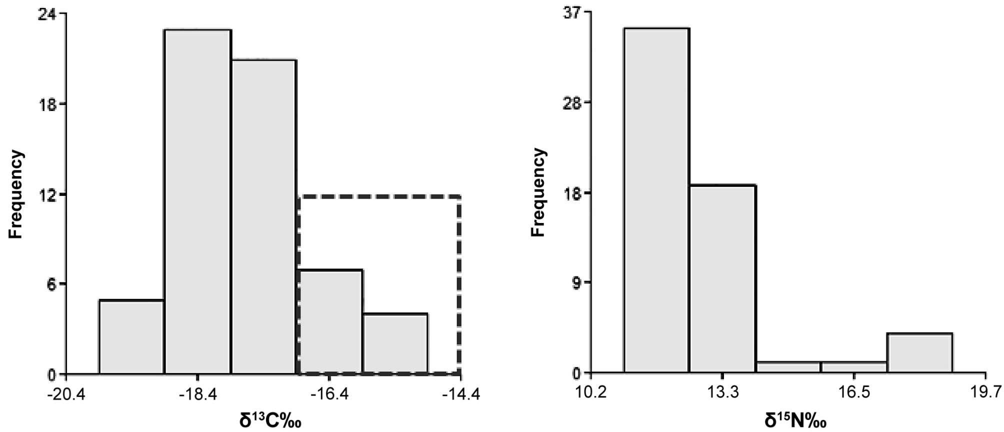

Figure 3. Frequency distribution of mean isotope values of $\delta^{13}C$ and $\delta^{15}N$ along whiskers of weanlings; dotted line represent the isotopic limit between neritic and oceanic habitat.

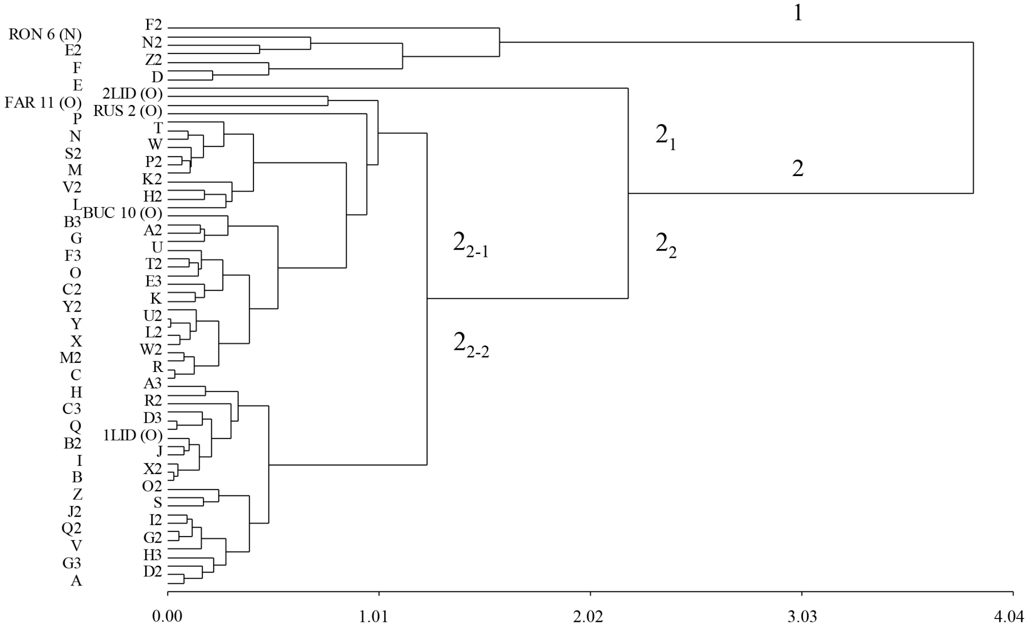

Figure 4. Cluster analysis using mean isotope values of C and N along whiskers of weanlings and juveniles from Península Valdés. Isotope values from satellite-tracked juveniles were used as a reference for neritic (N) and oceanic (O) foraging. Euclidean distances, averaged linkage method, and cophenetic correlation factor: 0.923. Cluster 1 includes weanlings enriched in both ^{15}N and ^{13}C (likely reflecting neritic female foragers); and Cluster 2 includes weanlings depleted in ^{15}N and ^{13}C (likely reflecting oceanic female foragers).

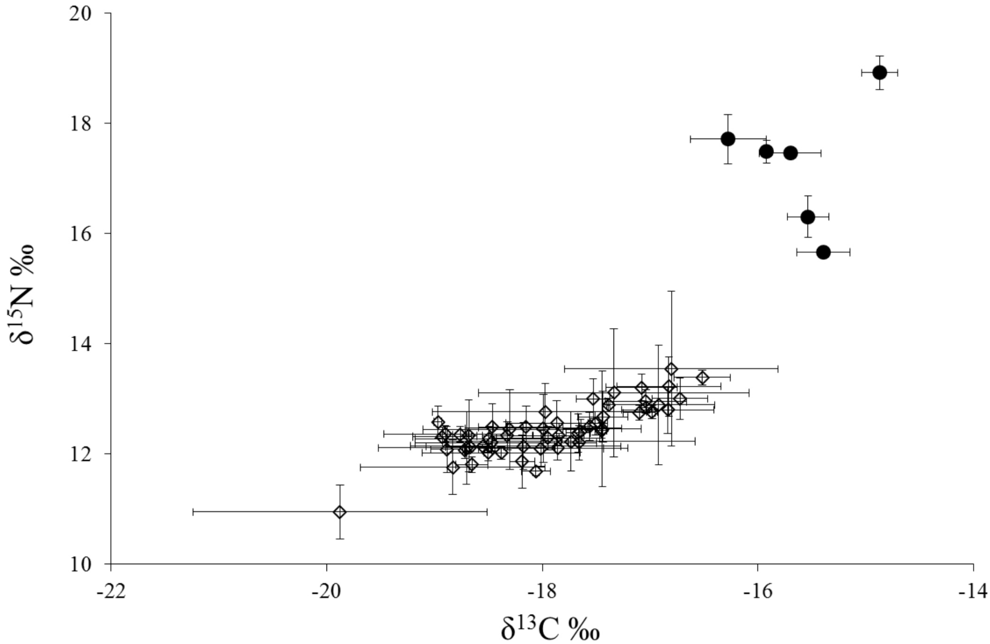

Figure 5. $\delta^{13}C$ and $\delta^{15}N$ mean values along whiskers of weanlings used to differentiate the foraging strategies of gestating females (mean and SD are plotted for each weanling). Filled symbols are neritic foragers (*n* = 6; overall mean values = -15.6 ± 0.5‰ $\delta^{13}C$ and 17.3 ± 1.1‰ $\delta^{15}N$), while empty symbols are oceanic foragers (*n* = 54; overall mean values = -17.9 ± 0.7‰ $\delta^{13}C$ and 12.4 ± 0.5‰ $\delta^{15}N$).

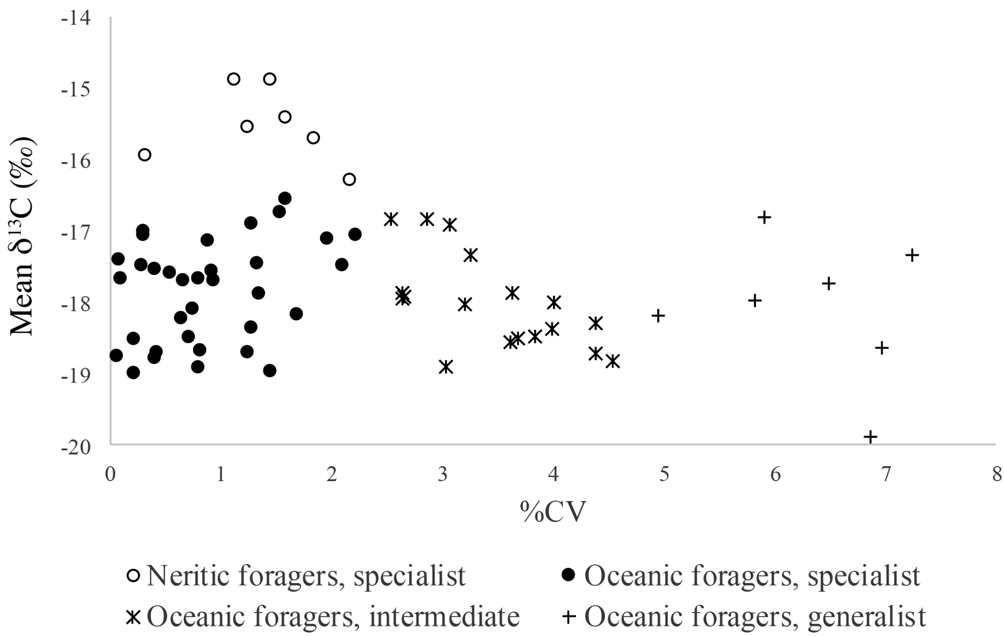

Figure 6. Individual variability of the weanlings according to the % coefficient of variation (%CV) distribution

Discussion

This study assessed the foraging strategies of female southern elephant seals from Península Valdés on a population scale using pups as proxies of their mother's biology and combining different datasets of local female and juvenile foraging ecology based on satellite tracking and stable isotopes of C and N. This type of information is particularly valuable for the Península Valdés colony because studies using satellite tracking have been limited. Until this study, there was no evidence to suggest neritic foraging in gestating females. Combining satellite-tracking data with stable isotope studies, despite the temporal mismatching between the approaches used herein (tracking and isotopic analysis), made it possible to overcome the limits of both methodologies when they are utilized independently. This may encourage similar studies in other southern breeding groups to analyze relations between foraging aspects and population trends over the last few decades.

Stable Isotopes of Weanling Whiskers as a Proxy for Female Foraging Strategies

A key aspect to being able to evaluate the adult female foraging strategies using stable isotope analysis on a large sample was the use of the $\delta^{13}C$ values of a pup's whisker as a proxy for the foraging strategy of its mother. For this assumption, it would be optimal to consider the variation of $\delta^{13}C$ values specifically in whiskers between pups and adult females, but these data are not available for elephant seals. The use of different tissues has provided similar variation values between pups and adult females for other pinnipeds (Velazquez-Castillo & Elorriaga-Verplancken, 2017), and the available $\delta^{13}C$ values from the blood of southern elephant seals indicate that variation between pups and adult females is small even after weaning (Ducatez et al., 2008; Habran et al., 2010). If this variation (0.3‰; Ducatez et al., 2008) was applied to the whisker values in this study (which have a much lower metabolic rate than blood; Habran et al., 2010), the classification into neritic and oceanic groups would have been maintained, and the difference between them would have also remained significant, *ca.* 2.3‰ ($\delta^{13}C$). Nonetheless, the use of values from directly sampled female elephant seals, or the between group variation specific to the particular tissue, would strengthen future research.

Female Foraging Strategies and Individual Variability

The main foraging area of females from the Patagonian colony during the gestation period is the Argentine Basin under mixed subtropical-subpolar waters (oceanic habitat and strategy), according to the satellite tracking of six adult females (7 records). However, the isotopic composition of the 60 pup whiskers analyzed in our study identified both neritic and oceanic foraging strategies for gestating females, with an overall high consistency in the individual spatial niche. According to the $\delta^{13}C$ values from our larger sample (weanlings), it can be estimated that at least 10% of the females would have neritic strategies likely associated with the continental shelf or shelf break. These values aligned to shelf forager values (Lewis et al., 2006; Eder et al., 2010) and neritic waters of the Patagonian area during the study period (Quillfeldt et al., 2010). Moreover, females with neritic foraging strategies were specialists according to the low intra-individual variability in the $\delta^{13}C$ values along the weanling whiskers, indicating that foraging related to the Patagonian shelf or shelf-break waters was not just opportunistic (Campagna et al., 1998) but a distinct strategy as seen in other colonies (Hückstädt et al., 2012; Muelbert et al., 2013; van den Hoff et al., 2014; Hindell et al., 2016). For females that exhibited oceanic foraging (90%), there may be alternative foraging strategies within this general classification given 26 individuals had low isotopic values (one of them was extremely depleted in ^{13}C and ^{15}N); hence, they were likely reaching distant and high latitude feeding grounds. Fifty-eight percent of these females were specialists, while 42% showed intermediate and high individual variability in the spatial niche used.

Foraging in neritic habitats may yield some advantages for gestating females from Patagonia. The Península Valdés colony is located in a temperate latitude, and females could easily forage over the Patagonian shelf without running the risks of their counterparts for getting trapped while the pack ice expands, with the resulting high fitness cost if they fail to return to the colony to breed (Biuw et al., 2010). Moreover, frontal systems and productivity are tied to bathymetry and food distribution, and are therefore more predictable in the shelf than in the open ocean (Campagna et al., 2006, 2007). Nevertheless, only a small proportion of the gestating females in this study (10%) exhibited a neritic foraging strategy. A possible explanation is that the shelf and shelf-break areas in Patagonia are used by many predators, which likely produces high intra- and interspecific competition. The competition pressure would be greatest when most of the elephant seals (subadult and adult males and juveniles; Campagna et al., 1995, 1998, 1999; Eder et al., 2010), as well as other species such as the dusky dolphin (*Lagenorhynchus obscurus*; Crespo et al., 1997) and the South American sea lion (*Otaria flavescens*), are foraging in the shelf waters at the same time (Campagna et al., 1998, 2001). This may be the reason why most of the females avoid the predictable and potentially advantageous resources of the Patagonian shelf and move to more distant oceanic foraging areas in the Argentine Basin. This hypothesis that oceanic foraging is a mechanism to deal with high competition is also supported by the high specialization (low intra-individual variability in the weanling $\delta^{13}C$ values) of the neritic gestating females.

The competition (intra- and interspecific) over the Patagonian shelf, however, might not be the only explanation for disregarding this habitat considering the fact that Antarctic female counterparts appear to withstand competition over the Antarctic shelf (Hückstädt et al., 2012). The oceanic habitat in the deep waters of the Argentine Basin, where the main foraging ground of tracked females from Península Valdés is found, is an area of eddy fields characterized by mixed subtropical-subpolar waters (Campagna et al., 2006). This area is included in the Subtropical Front Zone (STFZ) within the Sub-Antarctic Water Ring, which accounts for most of the total primary production within the Southern Ocean during all seasons (Moore & Abbot, 2000). Therefore, the high quality of the mixed subtropical-subpolar waters likely offers good conditions for foraging that may overcome the large distances to the preferred Argentine Basin, in contrast to the higher cost of competition that feeding in the nearer Patagonian Shelf would imply. Foraging conditions in the Argentine Basin may likely be better than in the oceanic habitat for their sub-Antarctic counterparts. Total annual primary production of the southern Atlantic Ocean (oceanic regions > 200 m) is higher than that of the Southern Ocean (> 50º S; 5.0 and 3.5 Gt C yr-1, respectively; Uitz et al., 2010). In contrast, at higher latitudes, negligible primary production in oceanic areas during austral winter (Moore & Abbot, 2000) is likely to force females to feed closer to more productive continental margins (with the known associated risks) or to feed in low-quality areas.

Foraging Strategies and Implications to Population Trends

Given the large size of the Península Valdés colony (50,700 individuals; Lewis & Campagna, 2002), analysis at the population scale provides an insight into the mechanisms to minimize competition with conspecifics in the foraging grounds such as individual consistency within the population resource niche (Newsome et al., 2009; McClellan et al., 2010; Vander Zanden et al., 2010; Hückstädt et al., 2012). Although similar studies in other breeding groups and foraging environmental contexts are needed for general statements, individual specialization and different foraging strategies of gestating females may contribute to the increasing population of Península Valdés. This colony is part of the South Georgia stock—the largest stock of the species (54% of the world population; Laws, 1994; Boyd et al., 1996) that has been recently stable (McMahon et al., 2005)—and it includes the colony of Livingston Island in which high specialization in the spatial niche and different foraging strategies were detected among the females (Hückstädt et al., 2012). The causes of different population trends among colonies are still uncertain. However, broad- and local-scale physical characteristics in the foraging habitats, which are not consistent across the Southern Ocean, may have an impact since they affect food availability and the individual's ability to amass reserves for breeding (Bester & Wilkinson, 1994; Pistorius et al., 1999; van den Hoff et al., 2014; McMahon et al., 2015). It is not clear how individuals cope with less predictable environments, but oceanic females in this study were able to narrow their spatial niche, were likely to deal with intraspecific competition in easily detected feeding patches (those associated with mesoscale features; Campagna et al., 2006), and were able to broaden their spatial niche and foraging strategies, possibly to buffer against environmental changes or lower predictability by moving to areas with better conditions.

Since primary production of the Patagonian shelf is higher than that of the oceanic regions (Longhurst, 1998), foraging in neritic habitats may reward some gestating female elephant seals from Patagonia, possibly by increasing their short-term reproductive success, with potential effects on the population trend. However, this would need to be tested in further studies, including pup mass at weaning and its comparison among different foraging strategies.

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