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Shift in foraging grounds and diet broadening during ontogeny in southern elephant seals from Kerguelen Islands

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Abstract Highly dimorphic species like southern elephant seals (*Mirounga leonina*, SES hereafter) frequently exhibit resource partitioning according to sex and/or age classes. We measured carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) of 404 blood samples (136 males and 268 females from Kerguelen Islands, 49°21′S, 70°18′E) from 2004 to 2011. Assuming that the distribution of carbon isotopes ($\delta^{13}C$ value) reflects the two main foraging grounds (Polar Frontal and Antarctic Zones), we quantified the proportion of SES foraging within each zone in relation with size, a proxy for their age. We found a clear shift from Polar Frontal to Antarctic waters as male SES aged, but no relation as far as females is concerned. We also observed a widening range of nitrogen isotopic ($\delta^{15}N$) values, suggesting that both males and females expanded their diet spectra with age. Whereas males increased their trophic level, females remained constant on average, with some adult females feeding both at lower and at higher trophic levels than juveniles.

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Introduction

Age–body size structure has long been recognized as a major component of total niche width (Polis 1984). For species that grow through a large range of sizes, ontogenetic niche shifts in diet or habitat are common. There is generally an increase in the diversity of resources used and, therefore, an expanding niche width with age (Polis 1984). According to many authors, age-related shifts in diet composition lead to decreased potential intra-specific competition for resources (Dickman 1988; Field et al. 2007) and enhance population viability. For example, Polis (1984) proposed that exclusion from resources and habitats of young scorpions *Paruroctonus mesaensis* by older ones explained resource partitioning between age classes in this species. In most cases, however, it is unclear whether ontogenetic shifts are an adaptive consequence of population stability over evolutionary time (Polis 1984) or a direct consequence of body size changes (Bolnick et al. 2003).

The southern elephant seal (*Mirounga leonina*, SES hereafter), the largest of all pinnipeds, is a highly sexually dimorphic species that exhibits pronounced morphological and physiological differences with age. With an estimated worldwide population of 664,000 individuals (Laws 1994), SES are major consumers from Southern Ocean (Bradshaw et al. 2003; Hindell et al. 2003). Unsurprisingly, previous studies using various methods found evidence of habitat and resource partitioning between juveniles and adults (Field et al. 2005, 2007; Newland et al. 2009; Bailleul et al. 2010; Martin et al. 2011). This pattern is frequently observed when resources are patchy and when environment conditions are unpredictable (Bolnick et al. 2003; Field et al. 2005). In fact, there is a clear spatial separation between juvenile and adult SES foraging strategies: as seals age, they make fewer but longer trips at sea and move

further from their natal islands (Field et al. 2005). Diet differences between juveniles and adults were confirmed in recent studies comparing fatty acids in the blubber of juveniles and adults SES (Newland et al. 2009) and using stable isotopes (Bailleul et al. 2010; Newland et al. 2011). On Kerguelen Island (49°21′S, 70°18′E), nitrogen stable isotope analyses revealed a major change in the trophic level of males with size but not in females (Bailleul et al. 2010). Furthermore, carbon stable isotope analyses revealed that both males and females foraged over broader areas as they aged (Bailleul et al. 2010).

Over the past 50 years, the population size of a large number of seabirds and seals, including SES, has declined severely on several breeding localities (Hindell and Burton 1987; Guinet et al. 1999; Weimerskirch et al. 2003; McMahon and Burton 2005; Authier et al. 2011). These changes in population size or demographic parameters have been related to an ecosystem shift in the Southern Ocean (Weimerskirch et al. 2003), probably linked to a transient decrease in the carrying capacity of the ecosystem (Jaeger and Cherel 2011). The Kerguelen SES population decreased by about one-third over a 30-year period (Guinet et al. 1999), and a similar trend was observed on Macquarie Island due to a sharp decline in juvenile survival (Hindell and Burton 1987). Juveniles are indeed very sensitive to resource limitation (McMahon and Burton 2005). Weaning mass and juvenile foraging success were the two main factors influencing juvenile survival (McMahon et al. 2000, 2003). Thus, investigating mechanisms behind ontogenetic foraging shifts may provide insights into the consequences of Southern Ocean's resource depletion on SES population dynamics.

However, dealing with a species such as SES that spends extended periods at sea is challenging. Many of the difficulties encountered in the quantification of diet in marine mammals stem from the intrinsic limitations of traditional techniques (e.g., stomach content, fecal analysis). These methods are often representative of the last meal eaten and biased toward hard tissues such as cephalopod beaks. A recent isotopic investigation challenged the traditional view that SES are squid eaters and, instead, suggested that females from Kerguelen Islands mainly feed on myctophids (Cherel et al. 2008).

Stable isotope (SI hereafter) ratios of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) are now increasingly used to investigate the feeding habits of major consumers (Kelly 2000). These methods are based on the principle that "you are what you eat" (DeNiro and Epstein 1977), that is, the biochemical compositions of molecules and tissues of consumers reflect that of their diet over the period of their synthesis. Consumers are typically enriched in ^{15}N relative to their food, and consequently, $\delta^{15}N$ values serve as indicators of a consumer's trophic position (McCutchan et al. 2003). In contrast, $\delta^{13}C$ values vary little along the food chain and are mainly used to

determine carbon sources in a trophic network (Kelly 2000; McCutchan et al. 2003) and foraging habitats in the marine environment (Cherel and Hobson 2007).

SES from Kerguelen Islands exhibit two main foraging grounds (Bailleul et al. 2007, 2010; Dragon et al. 2010): the Antarctic and the Interfrontal zones, which are defined as the zones in the south of the southern boundary of the Antarctic Circum-Polar Front (PF), and between PF and the subtropical front (STF), respectively. Juveniles and adult females favor oceanic waters in both zones, while subadult males forage almost exclusively over the Antarctic and Kerguelen shelves (Bailleul et al. 2010). There is a latitudinal gradient in $\delta^{13}C$ values of particulate organic matters at the base of the food chain within the Southern Ocean (Rau et al. 1983; Trull and Armand 2001) that is reflected in organisms at higher trophic levels (Cherel and Hobson 2007; Jaeger et al. 2010). Assuming that the distribution of $\delta^{13}C$ values accurately reflects the two main foraging grounds, the foraging strategy of a broad number of animals can be inferred from SI (Ducatez et al. 2008). Indeed, Authier et al. (2012a) showed that blood SI value was indicative of the seal foraging zone visited at least 4 months prior to its return to the colony.

Using mixture models, we first estimated the proportion of individuals feeding in the Interfrontal versus Antarctic zones. Secondly, we investigated whether foraging strategy depended on age. And finally, we aimed to investigate changes in trophic levels by sex and foraging location according to age. Our study will thus clarify whether females SES change their diet as they grow (e.g., on Macquarie Islands: Field et al. 2007; Newland et al. 2009), or not (e.g., on Kerguelen Islands: Bailleul et al. 2010).

Body length is used as a proxy for SES age (McLaren 1993; Bell et al. 2005). Males and females exhibit a similar growth until the age of 4 when they reach a body size of ca. 250 cm. Females growth rate then decreases after maturity (ca. 4 years: McMahon et al. 2003; Bell et al. 2005), whereas males undergo another period of growth until maturity (ca. 7 years: Bell et al. 2005; McLaren 1993). Therefore, juvenile refers to individuals under a body size of 250 cm (ca. 4 years), and adults/subadults refer to females/males over a body size of 250 cm. We hypothesized that as SES age and grow (1) they forage more frequently in Antarctic waters and (2) they feed on larger prey items at higher trophic levels and/or on a wider range of trophic levels.

Materials and methods

Sample collection

Field work was carried out between 2004 and 2011 at Kerguelen Islands (49°21′S, 70°18′E), a major breeding

ground for SES. Blood samples (whole blood) were collected year round from randomly chosen animals hauling out on beaches along the Courbet Peninsula. All animals were caught with a canvas head-bag and anaesthetized. Blood was collected from the dorsal venous sinus using 90×1.2-mm needles, and 70 % ethanol was added for sample preservation before laboratory analysis. Animals were also sexed, and snout-to-tail length (hereafter body length) was measured. For practical reasons, we sampled animals only up to 4 m long, which excluded fully adult males.

Before isotopic analysis, blood was oven dried at 50–60 °C and powdered. Subsamples were weighed (0.3–0.4 mg) with a microbalance and packed in tin containers prior to combustion in an elemental analyzer (Thermo Fisher, Flash EA 1112, Waltham, MA, USA) coupled to a continuous flow mass spectrometer (Thermo Fisher, Delta V Advantage). Lipids are depleted in ^{13}C relative to proteins and carbohydrates, but the low lipid content of whole blood does not typically necessitate lipid extraction (Cherel et al. 2005). We nevertheless carefully checked the C/N mass ratios of the samples, and when above 3.7, lipids were extracted using cyclohexane (<5 % of the samples). Stable isotopic values are presented in the usual δ notation (in ‰) relative to Vienna Pee Dee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$ values, respectively. Typical precisions for isotopic measurement were 0.15 ‰ and 0.20 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Measurement errors were accounted for in subsequent statistical analyses.

$\delta^{13}C$ mixture modelling

Mixture models are useful whenever the data are heterogeneous and composed of several hidden clusters or groups. Carbon isotopic values were assumed to follow a bimodal distribution (Bailleul et al. 2010). Assuming that a bimodal distribution reflects the two identified strategies, we used a Bayesian mixture model to discriminate individuals foraging north (that is, within the Interfrontal zone) or south (the Antarctic Zone) from their $\delta^{13}C$ values.

We modelled $\delta^{13}C$ value of individual i as a mixture of two Gaussian distributions:

$$\delta^{13}C_i = p_i \times \left(\delta^{13}C_{North} + \varepsilon_{North}\right) + (1 - p_i)$$
$$\times \left(\delta^{13}C_{South} + \varepsilon_{South}\right) \quad (1)$$

where p_i is the probability for the ith animal to have foraged in the southern zone ($p_i = 0$) versus the northern zone ($p_i = 1$) and ε, the residuals, are assumed to follow a normal distribution with mean 0 and variance σ^2_{North} and σ^2_{South}. From the documented latitudinal gradient in $\delta^{13}C$ across the Southern Ocean (Trull and Armand 2001), we used the following identification constraint:

$$\delta^{13}C_{North} > \delta^{13}C_{South} \quad (2)$$

The foraging strategy (S) of each animal can be conceptualized as missing data to be estimated:

$$S_i \sim \text{Bernoulli}(p_i), \text{for } i = 1, \ldots, n \quad (3)$$

The variable S_i indicates if the ith animal has foraged in the southern zone ($S_i = 0$) versus the northern zone ($S_i = 1$). We used two multilevel hierarchical models (Table 2) with p_i (on a logit scale) as the dependent variable, and standardized body length (BL) as a covariate to assess any effect of size on foraging location. For clarity, all modelling details are provided as supplementary material for interested readers (Online Resource 3).

Because of their different foraging ecology (Newland et al. 2009; Authier et al. 2012b), we analyzed males and females independently.

Modelling $\delta^{15}N$ conditionally on $\delta^{13}C$

We used another multilevel hierarchical model to test the effect of body length on the mean $\delta^{15}N$ value within estimated foraging groups. The two submodels (one for $\delta^{13}C$ and one for $\delta^{15}N$) were then linked in a single overarching model. $\delta^{13}C$ values first allowed us to estimate foraging groups (the latent variables S_i). We modelled the $\delta^{15}N$ conditional of the foraging strategy identified on the sole basis of the carbon isotopic values (Online Resource 4). That is, we did not allow in our models for $\delta^{15}N$ to inform on foraging strategy assignment. Then, conditionally on foraging strategy, we tested for differences in the mean $\delta^{15}N$ value in relation to BL. Because we wanted to investigate interactions of the foraging groups with the trophic level, we considered a multilevel model in which intercepts and slopes can vary by group:

$$\delta^{15}N_i \sim N(\alpha_{S[i]} + \beta_{S[i]}BL_i, \sigma_i^2), \text{for } i = 1, \ldots, n \quad (4)$$

where N refers to a normal distribution with a mean and a variance, BL refers to standardized body length and S_i is the foraging strategy of the ith animal. Variable S_i is estimated for each individual (see above) from $\delta^{13}C$ values, thus the uncertainty in assigning a seal to a southern or northern strategy is taken into account. We used six different models in overall (Table 3) with or without the variable S_i.

We further allowed the residual $\delta^{15}N$ variance (σ_i) to vary with body length because exploratory analyses revealed a funnel-shaped scatter plot of $\delta^{15}N$ values against BL (Online Resource 1):

$$\sigma_i = \exp(a + bBL_i) \quad (5)$$

In other words, the submodel for $\delta^{15}N$ values was heteroscedastic. Residual variances were modelled on a log scale to guarantee positive values.

Statistical analyses

We pooled data from all years. Gibbs sampling was performed for each mixture model using 3 parallel Markov chains with WinBUGS 1.4 (Lunn et al. 2000) called from R 2.12.0 (R Development Core Team, 2010) with the package R2WinBUGS (Sturtz et al. 2005). Following a burn-in phase of 25,000 iterations, we further sampled for 25,000 more iterations (retaining every 10th sample). Convergence and diagnostic statistics were performed using the CODA package in the R environment (Plummer et al. 2006).

We monitored convergence with the potential scale reduction factor (R-hat) for each parameter (Gelman and Hill 2006). We ran simulations until R-hat was no greater than 1.1. We also assessed the effective sampling size (n-eff) due to autocorrelation: n-eff was at least around 500. We retained mean value and 95 % credibility interval (noted 95 % CI) of each estimated parameters calculated from Markov chains.

Mixture model selection

Determining the number of components in a finite-mixture model is still a challenge despite a lot of research (Fruhwirth-Schnatter and Pyne 2010). The deviance information criterion (Spiegelhalter et al. 2002) is a popular tool for Bayesian model selection (Barnett et al. 2010). Yet, its use with mixture models is problematic (Celeux et al. 2006). Information theoretic criteria that have been found to empirically work well are the approximate weight of evidence (AWE) and the integrated complete likelihood-Bayesian information criterion (ICL-BIC) (Fruhwirth-Schnatter and Pyne, 2010). The formulae to compute these criteria for two-component mixture models such as considered in our work are detailed in supplementary material (Online Resource 5).

The ICL-BIC penalizes not only model complexity but also the failure of the model to provide a classification into well-separated clusters (Fruhwirth-Schnatter and Pyne 2010). For both AWE and ICL-BIC, a lower value also means a better fit.

Results

Foraging groups prediction

Blood samples were collected from 404 SES including 268 females and 136 males of various sizes (127–287 cm and 149–380 cm, respectively). Isotopic signatures range from −24.0 to −18.1 ‰ and from 9.3 to 13.6 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Males' and females' carbon isotopic values exhibited a mixture of two Gaussian distributions

(Fig. 1; Table 1). The mean $\delta^{13}C$ value corresponding to the south strategy was lower for males than for females: the 95 % credibility interval excluded 0 (Table 1). However, the mean $\delta^{13}C$ value corresponding to the north strategy tended to be higher for males than for females, but the 95 % credible interval of this difference included 0 (Table 1; Fig. 1).

Whereas males' foraging group probabilities were mainly close to the upper or lower limit ($p = 0$ or $p = 1$) with a small standard error, most of the females had in-between probabilities and high standard error (Online Resource 2). This result underlines that we obtained a good prediction of foraging group for males but not so good for females.

In males, exploratory analyses with linear penalized splines (Gurrin et al. 2005) revealed that $\delta^{15}N$ value and body length varied in a non-monotonic way in relation to $\delta^{13}C$ value: both increased at lower and at higher $\delta^{13}C$ values (Fig. 2). This pattern was not observed for females.

Body length and foraging location

For males, a model with body length fitted the data better than a model without (Table 2). The proportion of animals foraging in the northern zone decreased sharply with body length (Fig. 3). For 250-cm males (ca. 4 years, McLaren 1993), this proportion was 0.69, 95 % CI = [0.57, 0.89]. For 350-cm males, this proportion was down to 0.22, 95 % CI = [0.10, 0.48].
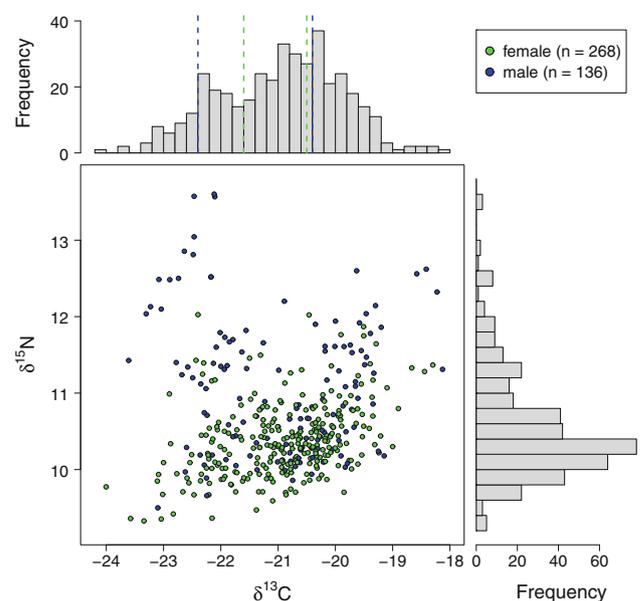

Fig. 1 *Mirounga leonina* blood $\delta^{13}C$ and $\delta^{15}N$ values of 268 females and 126 males. Frequency distributions are drawn in the margin. *Dashed lines* indicate posterior carbon mixture mean values by sex

Table 1 Posterior estimated mixture mean values and differences between mixture mean values (noted Δ)

	Males	Females	Δ (Males–Females)
Mean ($\delta^{13}C_{North}$) (‰)	−20.4	−20.5	*0.1*
	95 % CI = [−20.7, −20.1]	95 % CI = [−20.8, −20.3]	*95 % CI = [0.5, −0.3]*
Mean ($\delta^{13}C_{South}$) (‰)	−22.4	−21.6	−0.7
	95 % CI = [−22.7, −22.1]	95 % CI = [−22.1, −21.1]	95 % CI = [−1.4, −0.2]
Δ (North–South) (‰)	2.0	1.2	
	95 % CI = [1.7, 2.3]	95 % CI = [0.3, 1.7]	

95 % CI is the 95 % posterior credibility interval

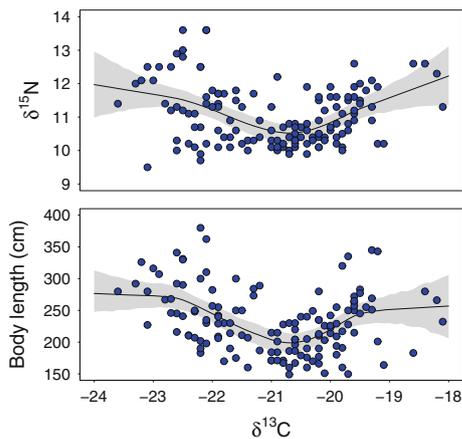Values not significantly different from null are in italics

Fig. 2 Relation between males' δ^{15}N and δ13C values (*top*) and males' body length and δ13C values (*bottom*). We fitted linear penalized splines (*black curves*, Gurrin et al. 2005) to uncover the pattern as this analysis is exploratory. Gray envelopes correspond to a 95 % credibility interval

Table 2 Linear model selection on the estimated foraging strategy probability (*p*) results from δ^{13}C values for both males (M) and females (F)

Model		k	Sex	N	AWE	ICL-BIC
Model1	logit(p) ∼ 1	5	M	136	556.4	625.1
Model2	logit(p) ∼ 1 + body length	6	M	136	**503.8**	**570.5**
Model1	logit(p) ∼ 1	5	F	268	1151.0	1152.9
Model2	logit(p) ∼ 1 + body length	6	F	268	NC	NC

Best AWE and ICL-BIC values are in bold

k number of parameters, *NC* not converged

We excluded the model with body length for females since it did not converge: there was no relationship between BL and foraging strategy in females. The proportion of females foraging in the Interfrontal zone was constant (0.46, 95 % CI = [0.10, 0.88]).
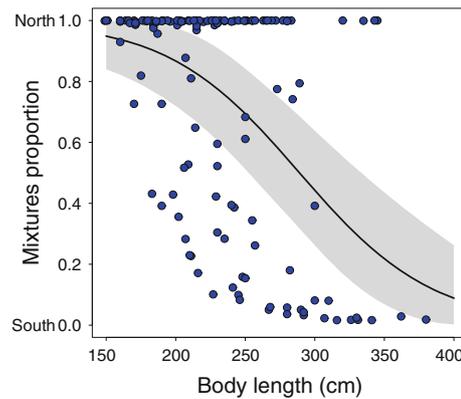

Fig. 3 Relation between males' mixture proportion and body length. The *black curve* corresponds to the posterior mean, and the gray envelope corresponds to a 95 % credibility interval. Each individual is represented by a *dot* with the probability to have foraged in the northern zone versus southern zone in ordinate

Body length and trophic level

AWE and ICL-BIC values decreased in the model for males as we introduced body length as a covariate (Table 3), indicating that this variable best described the observed asymmetrical distribution (Fig. 2). Both AWE and ICL-BIC suggested no effect of foraging strategy on trophic level (Table 3). Males' nitrogen values increased with body length (Fig. 4). At the same time, the range of δ^{15}N values widened.

Regarding females, we selected the simplest model because of its lowest AWE and ICL-BIC values (Table 3). Thus, with our dataset, we could not detect any effect of foraging strategy nor body length on females' δ^{15}N values. Although δ^{15}N values did not increase, we observed a broadening range of δ^{15}N values with size.

Discussion

In spite of the rising number of available telemetry data, SI remains a powerful tool to infer population pattern of

Table 3 Linear model selection on $\delta^{15}N$ values for both males (M) and females (F)

Model		k	Sex	N	AWE	ICL-BIC
Model 1	$\delta^{15}N \sim 1$	3	M	136	348.4	343.9
Model 2	$\delta^{15}N \sim 1|S$	4	M	136	512.9	475.5
Model 3	$\delta^{15}N \sim 1 + body\ length$	4	M	136	**274.6**	**270.1**
Model 4	$\delta^{15}N \sim 1|S + body\ length$	5	M	136	460.6	422.3
Model 5	$\delta^{15}N \sim 1 + body\ length|S$	5	M	136	458.3	421.7
Model 6	$\delta^{15}N \sim 1|S + body\ length|S$	6	M	136	471.2	426.8
Model 1	$\delta^{15}N \sim 1$	3	F	268	**372.6**	**368.1**
Model 2	$\delta^{15}N \sim 1|S$	4	F	268	777.0	745.7
Model 3	$\delta^{15}N \sim 1 + body\ length$	4	F	268	374.6	368.6
Model 4	$\delta^{15}N \sim 1|S + body\ length$	5	F	268	785.9	746.2
Model 5	$\delta^{15}N \sim 1 + body\ length|S$	5	F	268	794.5	749.6
Model 6	$\delta^{15}N \sim 1|S + body\ length|S$	6	F	268	799.4	752.1

PPC was calculated on the $\delta^{15}N$ distribution. $1|S$, body length$|S$: varying intercept or slope by foraging strategy. The smallest AWE and ICL-BIC values are in bold. See supplementary materials for details about the models (Online Resource 4)

k number of estimated parameters

foraging behavior at a broad scale (Ducatez et al. 2008). With a cross-sectional approach, it can indeed be applied in a cost-efficient way to a large number of individuals (Cherel et al. 2012). The main aim of this study was (1) to quantify the proportion of SES feeding in two main foraging grounds using $\delta^{13}C$ values, and (2) to assess how this proportion varied with the size and sex of sampled individuals. This study thus provides new information on an ontogenetic shift in foraging location in SES. It also uncovers a broadening of trophic niche width: both males and females were likely to feed on a greater diversity of prey species within a given foraging habitat as they grew.

Assessment of foraging location

The bimodal distribution of male and female blood $\delta^{13}C$ values (a proxy for their foraging habitats) reflects that at least two main foraging regions are used by both male and female SES from Kerguelen Islands. Since $\delta^{13}C$ values are decreasing with increasing latitude (Rau et al. 1983; Trull and Armand 2001), we can attribute, respectively, lower values to the consumption of mainly Antarctic prey and higher values to prey mainly found in Polar Frontal waters. We therefore assigned the northern-most and the southern-most strategy to animals mainly feeding in the Interfrontal and Antarctic zones, respectively.

However, isotopic values characteristic of the southern strategy was higher than expected for animals feeding in truly Antarctic waters (e.g., Adélie penguin *Pygoscelis adeliae,* ca. −25 to −24 ‰, Cherel and Hobson 2007; Cherel et al. 2008), while isotopic value for the northern strategy coincided well with expected values for Polar Frontal waters (ca. −21.50 to −19.50 ‰, Cherel and Hobson 2007). The apparent mismatch between the larger than expected $\delta^{13}C$ values and the satellite tracking data, which documented the importance of foraging in Antarctic waters (Bailleul et al. 2007; Biuw et al. 2007), is likely to be the result of whole blood protein turnover. Moreover, there is evidence supporting that SES are feeding continuously along their tracks, and therefore, SES that foraged in Antarctic waters are likely to also feed on their way back to Kerguelen Islands (Bailleul et al. 2007; Thums et al. 2011), thus diluting their low Antarctic blood $\delta^{13}C$ values by an enrichment of ^{13}C from lower-latitude prey.

Fig. 4 Relation between nitrogen value and body length for females (left) and males (right). The *black line* corresponds to the posterior mean, and the *gray* envelope corresponds to an associated error (± 1 standard error). Each observation is represented by a *dot* with a symbol related to the corresponding foraging strategy (foraging strategy was assigned with a cutoff of 50 %)
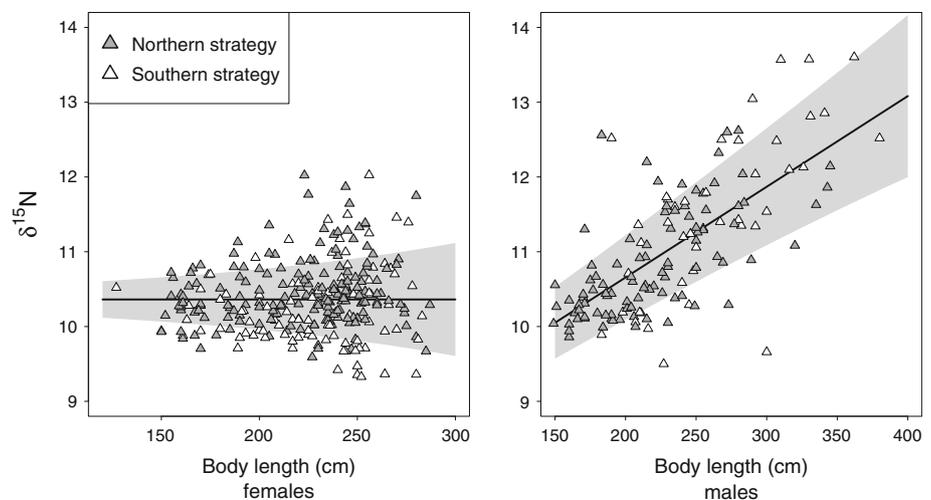
The Kerguelen Plateau (defined as bathymetry less than 1,000 m) is characterized by a food web enriched in ^{13}C compared to offshore food webs (Trull et al. 2008). Satellite tracking data revealed that subadult males highly depend on the Kerguelen and Antarctic Plateaus for feeding, whereas females and juvenile males forage to a very large extent in oceanic waters (Bailleul et al. 2007, 2010; Dragon et al. 2010). We indeed observed with our isotopic dataset that juvenile males and females exhibited similar δ^{13}C values indicative of the oceanic Polar Frontal zone (ca. −21.50 to −19.50 ‰, Cherel and Hobson 2007). Small males have middle δ^{13}C values. Some large males have larger δ^{13}C values than small ones, whereas the other large males have smaller δ^{13}C values (Fig. 2). An increase in δ^{13}C values may result from foraging into subtropical waters (e.g., female subantarctic fur seal, *Arctocephalus tropicalis* had δ^{13}C values of -18.1 ‰ ± 0.2, $n = 10$, Cherel et al. 2008). However, among 45 tracked males from Kerguelen Islands, none went into subtropical waters (Guinet unpubl data). This suggests a neritic origin for the observed enrichment in ^{13}C. We may interpret the increase of δ^{13}C value with size in males as indicative of the ontogenetic foraging shift from oceanic to neritic waters over the Kerguelen shelf (Fig. 2).

Foraging strategy shift

Our study provides new information on the proportion of individuals using the two main foraging habitats. We found that males foraged mainly within the Interfrontal zone when they were juvenile. As male SES aged, they foraged further south, in Antarctic waters (Fig. 3). Such changes may be explained either by a shift in seals foraging grounds as they age, in relation to the foraging conditions encountered and/or by a differential survival rate of subadults/adults according to the chosen and fixed foraging strategy. Recent works on male SES teeth revealed that by 4-year-old, males became faithful for the rest of their lives to a given foraging habitat (Martin et al. 2011; Authier et al. 2012b). At this age, our study suggested that about 70–30 % of males were assigned to the Interfrontal and the Antarctic foraging strategies, respectively. These proportions are close to those found by Authier et al. (2012b) who used teeth SI data collected on 47 male SES. However, for males longer than 350 cm (ca. 6 years and older, McLaren 1993), this proportion was only 20 % for the Interfrontal zone but increased to 80 % for the Antarctic zone (Fig. 5). We may interpret this result as the Kerguelen Plateau being associated with an increased mortality rate compared to the Antarctic shelf. Future studies should address this hypothesis by investigating foraging performances and/or predation risks experienced by male SES according to their foraging habitat (Kerguelen Plateau vs. Antarctic shelf).
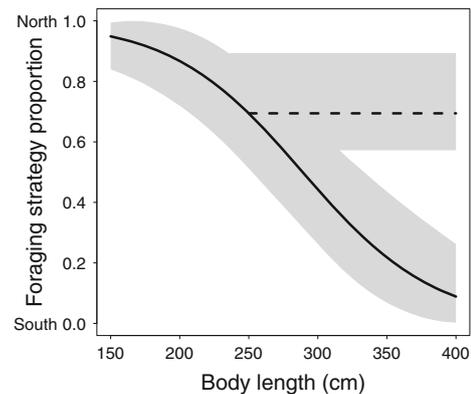

Fig. 5 Relationship between the proportion of males foraging in the Interfrontal zone versus Antarctic zone and body length. The *black curve* corresponds to the observed proportion, and the *dashed line* corresponds to the expected stabilized proportion after 4 years (69 %). *Gray* envelopes correspond to 95 % credibility intervals

Blood SI data on female SES suggested an even mixture between foraging strategies, but the estimated proportions were not precisely estimated. In a previous study, Bailleul et al. (2010) estimated from tracking data that about 70 % of Kerguelen female SES foraged within the Interfrontal zone in winter, a result which is consistent with ours. Unlike males, we did not find any relationship between foraging strategy and body length in females.

Dietary shift

A new finding from this study was how females, as they age and grow, gradually feed on a broadening range of trophic levels whatever their foraging ground. Moreover, no increase in their δ^{15}N values in relation to size (i.e., age) was observed. However, as female SES growth slows down by 4 years of age (Bell et al. 2005), the large-sized individuals are likely to encompass individuals of very different ages, and this could partly mask a shift in relation to the exact age of the individuals.

Previous studies conducted in Kerguelen Islands on blood samples (Bailleul et al. 2010) failed to identify any significant change of δ^{15}N value with female size, although diet studies (Field et al. 2007) and fatty acids studies (Newland et al. 2009) on SES from Macquarie Islands suggested ontogenetic shifts. Our study partly addresses this apparent discrepancy. Indeed, our results indicated no major dietary shifts on average, but a broadening range of the trophic niche with age. Some females decreased their trophic level, others increased it, possibly by consuming a greater proportion of squids as suggested by Newland et al. (2009), while others maintained a trophic level identical to juveniles. These results would have been probably undetected using other dietary analyses. Diet analyses based on hard remains found in stomach content would have

probably suggested an increase in trophic level with size. Indeed, undigested squid beaks, more likely to be found in female increasing their trophic level, are also more likely to be detected compared to the small and fragile otoliths of myctophids. Furthermore, while fatty acid analyses can be powerful to determine the main categories of prey, this technique does not provide direct indications of the trophic level occupied by the individual.

Males SES were found to exhibit both a progressive increase and a widening of their $\delta^{15}N$ values in relation to size (i.e., age) as suggested by previous studies (Bailleul et al. 2010; Martin et al. 2011). Our study shows that this shift in trophic level is observed regardless of foraging strategy. As underlined by Bailleul et al. (2010), it is unclear whether this increase of $\delta^{15}N$ values reflects a shift in prey species, because large fish and squid have higher trophic positions than small mesopelagic fish (Cherel et al. 2008), and/or in foraging habitat, because the $\delta^{15}N$ baseline level is higher over the Kerguelen Plateau than in the adjacent oceanic waters (Trull et al. 2008). Recent studies on teeth (Martin et al. 2011; Authier et al. 2012b) provide information throughout the whole life of the individuals. Dentin $\delta^{13}C$ values had a unimodal distribution for young males and a clear bimodal distribution when they age, with older individuals being faithful to their foraging strategies while progressively increasing their $\delta^{15}N$ values. According to the teeth analysis, we thus interpret our blood isotopic data as an indication of a progressive change in males' prey consumed (widening of the range of $\delta^{15}N$ values) concomitant with a shift from oceanic to neritic waters over the Kerguelen Plateau and Antarctic shelf.

Our analysis of $\delta^{15}N$ values supports the idea that juveniles SES exploit a narrower range of prey than adults, possibly due to higher constraints in foraging abilities or experience (Field et al. 2005, 2007). This age-related spatial and dietary resource partitioning is consistent with large metabolic and physiological differences arising with age. Reproductive females, highly constrained by large energetic requirement related to lactation, may be feeding opportunistically on prey items with higher energetic content (e.g., myctophids, Newland et al. 2009; Cherel et al. 2008).

Finally, the large inter-individual variability of the $\delta^{15}N$ value for a given size and sex category indicates some levels of individual dietary specialization, suggesting that SES from Kerguelen may be a population of individual specialists.

Conclusion

Our study presents a novel use of hierarchical models to study ontogenetic foraging shifts with SI values. Using mixture models, we quantified the proportion of SES feeding in either the Interfrontal or the Antarctic zones.

Our analysis yielded a proportion of males foraging in the Interfrontal zone lower than expected from teeth SI studies (Martin et al. 2011). It is currently unknown if the change in the proportion of males foraging in Interfrontal versus Antarctic waters is related to a behavioral shift in foraging habitat (within-individual process) or a differential survival (between individual process). Additional studies targeting explicitly breeding males may help clarify this point and refine our understanding of the mechanisms driving the demography of a top marine predator under climate change (Trathan et al. 2007).

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