

# Stable isotopes document winter trophic ecology and maternal investment of adult female southern elephant seals (*Mirounga leonina*) breeding at the Kerguelen Islands

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**Abstract** Individual specialisation is widespread and can affect a population's ecological and evolutionary dynamics. Whether intra-specific niche differences can influence reproductive investment was examined in a marine mammal, the southern elephant seal (*Mirounga leonina*), whose females were known to forage in two different areas during the austral winter. The study was conducted at Kerguelen Islands (49°21'S, 70°18'E), southern Indian Ocean, in late winter–early spring 2006. Pups were used as proxies of their mothers' biology and combined information on their weaning mass (a proxy of females' foraging success and short-term fitness) together with their blood  $\delta^{13}\text{C}$  value (a proxy of female foraging zone). First, the use of isotopic signature of pups was validated to study the female foraging ecology during their pre-breeding trip by demonstrating that  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of pups and their mothers were positively and linearly correlated. Then, blood samples were taken from a large number of newly-weaned pups, which were also weighed, to provide information at the population level. Estimated  $\delta^{13}\text{C}$  values of female seals encompassed a large range of values (from  $-23.7$  to  $-19.1\text{‰}$ ) with an unimodal frequency distribution, suggesting no contrasted foraging areas within the population. No significant relationship was found between pup weaning

mass and their carbon signature, indicating no link between female foraging areas and maternal foraging success and investment. Finally, blood  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values gave new insights into southern elephant seal ecology, suggesting that females mainly foraged north of the Polar Front where they preyed upon myctophid fish in late winter.

## Introduction

While inter-individual niche differences have been ignored in many studies, individual specialisation is widespread and it can profoundly affect a population's ecological and evolutionary dynamics (Bolnick et al. 2003). Within a population, individual foraging strategies can result in differential reproductive performance and survival (Stephens and Krebs 1986). Relationships between inter-individual niche differences and reproductive fitness have been investigated on both the short- and long-term in mammals and birds (Clutton-Brock et al. 1982; Bolnick et al. 2003). For example, pigeon guillemots *Cephus columba* with specialised diets had higher fledging rates than generalists (Golet et al. 2000), and western gulls, *Larus occidentalis*, that adopted a fish diet had higher long-term reproductive success than individuals specialising on human refuse (Annett and Pierotti 1999). Inter-individual niche differences also occur in several species of marine mammals (Hoelzel et al. 1989; Field et al. 2001; Staniland et al. 2004; Herman et al. 2005), but almost no information is available on their consequences for reproductive fitness (Georges and Guinet 2000).

The southern elephant seal (*Mirounga leonina*) is the largest phocid. Parental care is exclusively the responsibility of the female, which is a strict capital breeder relying on her energy reserves during the spring breeding fast including

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the 3-week lactation period of her pup (Costa 1993). Reserves are built-up during an extended (8-month) pre-breeding winter foraging trip. Female foraging choices made prior to breeding therefore have profound effects on their pups during and after the reproductive period. The resources a mother has stored during the pre-breeding trip determine the pup body mass at weaning, with no evidence that the mother's length (a condition-independent measure of size) is important. Moreover, the mass of a pup at weaning is positively related to the probability the pup survives its first year at sea. Consequently, pup body mass at weaning is a good proxy of both female foraging efficiency during the pre-breeding foraging trip and of female short-term reproductive fitness (McCann et al. 1989; Arnbohm et al. 1993, 1997; McMahon et al. 2000; McMahon and Bradshaw 2004). Satellite and geolocation tracking has shown that adult females winter in two distinct oceanic habitats, with some individuals migrating to high-latitude Antarctic waters while others favour the lower latitudes of the Polar Frontal Zone (Bradshaw et al. 2003, 2004; Biuw et al. 2007). The overall simplicity of its breeding biology (no paternal investment, capital breeder, a single offspring, two distinct foraging areas) together with the ease of handling pups make elephant seals an ideal marine mammal model for investigating whether foraging in different habitats leads to differences in foraging success and maternal investment. Elephant seals were studied at the Kerguelen Islands, where winter tracks of 18 seals previously indicated that females used the two habitats: 67% of individuals ( $n = 12$ ) foraged in the Polar Frontal Zone and the remaining 33% ( $n = 6$ ) migrated further south, into Antarctic waters (authors' unpublished data).

Investigating relationships between foraging ecology and maternal investment necessitates determination of the foraging areas of a large number of individuals, which is obviously out of reach using the costly method of satellite tracking. At a broader spatial scale, the stable isotope method appears particularly suitable for defining foraging areas of top predators in the Southern Ocean at a population scale. The stable isotopic ratio of carbon ( $\delta^{13}\text{C}$ ,  $^{13}\text{C}/^{12}\text{C}$ ) in tissues varies little along the food chain and is mainly used to determine sources of primary production. In the Southern Hemisphere, the geographical  $\delta^{13}\text{C}$  gradient is well defined in particulate organic matter at the base of the food web, ranging from high  $\delta^{13}\text{C}$  values in warm subtropical waters to low values in cold Antarctic waters (Trull and Armand 2001). This latitudinal gradient is reflected in organisms at higher trophic levels (Quillfeldt et al. 2005; Cherel and Hobson 2007), hence, its use for investigating foraging areas of seabirds and marine mammals (Cherel et al. 2006, 2007). We therefore made the two following predictions about the carbon signature of female elephant seals. First, females foraging in Antarctic and Polar Frontal Zone

waters should have lower and higher  $\delta^{13}\text{C}$  values, respectively, with their overall carbon signature encompassing a large range of values (from about  $-25$  to  $-20\text{‰}$ ). Second, the frequency distribution of  $\delta^{13}\text{C}$  values should be bimodal, thus reflecting the two different foraging habitats.

The capture and handling of numerous female elephant seals can be dangerous and arduous work in the field. Since pups are easier to access and handle, an effective way to overcome this problem is to use pups as proxies for maternal foraging success and investment (see above). Pup tissues theoretically have an isotopic composition that is related to female foraging ecology over the preceding months, because the exclusive diet of a suckling pup is its mother's milk, which, in turn will reflect the female's energy reserves (Aurioles et al. 2006). The relationship between foraging habitats and maternal investment in elephant seals was thus investigated in the present work by measuring blood isotopic signature and body mass of a large sample size (over 200) of newly weaned pups allowing statistical testing at the population level. Blood was the targeted tissue, because it can be sampled easily and non-destructively in the field.

A second, but preliminary goal of this work was to validate the assumption that isotopic signatures of pups reflect the isotopic signature of their mothers in a predictable manner. The blood of adult females and their pups was sampled at weaning to compare their  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ( $^{15}\text{N}/^{14}\text{N}$ ) values. We predicted little difference in  $\delta^{13}\text{C}$  values, because there is no or minimal enrichment in  $^{13}\text{C}$  between food and consumer (Kelly 2000). In contrast, consumer tissues are enriched in  $^{15}\text{N}$  relative to their food and  $\delta^{15}\text{N}$  measurements thus serve as indicators of consumer trophic position (Kelly 2000). We consequently predicted significant  $^{15}\text{N}$  enrichment between females and their pups at weaning, because the nursing pup is "consuming its mother" and, therefore, would be theoretically a trophic level higher than the female (Jenkins et al. 2001). Finally, since female elephant seals fast ashore, and thus literally "feed on themselves" for about 3 weeks during the lactating period, we looked at possible fasting-related changes in their isotopic signatures by comparing blood  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values at birth and weaning. We predicted no changes in  $\delta^{13}\text{C}$  values and no or very little  $^{15}\text{N}$  enrichment in whole blood, because blood integrates a period of 2–3 months in large mammals (Hilderbrand et al. 1996), thus buffering the short-term fasting effect found in tissues with high rates of protein turnover (Cherel et al. 2005a).

## Materials and methods

Field work was carried out at the Kerguelen Islands ( $49^{\circ}21'\text{S}$ ,  $70^{\circ}18'\text{E}$ ), a major breeding ground for elephant

seals (*M. leonina*), which is located in the southern part of the Polar Frontal Zone, in the immediate vicinity of the Polar Front (Fig. 1) (Park and Gambéroni 1997). The study was conducted at two haul out sites near the scientific station (Port-aux-Français, Courbet Peninsula), during the 2006 breeding season (from mid-September to mid-November). Adult female elephant seals from the Courbet Peninsula are counted every year and include the majority of seals breeding at Kerguelen (Guinet et al. 1999). Elephant seals were randomly chosen for each of the following three groups.

Fasting group (females on arrival and at weaning,  $n = 15$ ). To quantify potential differences in blood  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values due to fasting between arrival at the colony and weaning, 15 adult females were sampled twice, at birth and shortly before weaning (on the 18th day of lactation).

Lactation group (females and pups at weaning,  $n = 17$ , including 14 females from the group above). To quantify potential differences in blood  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values between pups and their mothers, blood was sampled from 17 pup–mother pairs. Pups and females were captured at weaning and shortly before weaning (on the 18th day of lactation), respectively.

Weaning group (pups at weaning,  $n = 209$ , including 16 pups from the group above). The two haul out sites were visited daily from the first birth onward. Pups leaving the harems were considered to have completed the suckling period (precision 1 day). The blood of each newly weaned pup was sampled; the pups were measured from nose to tail (standard length), weighed, and marked with a hind-flipper tag.

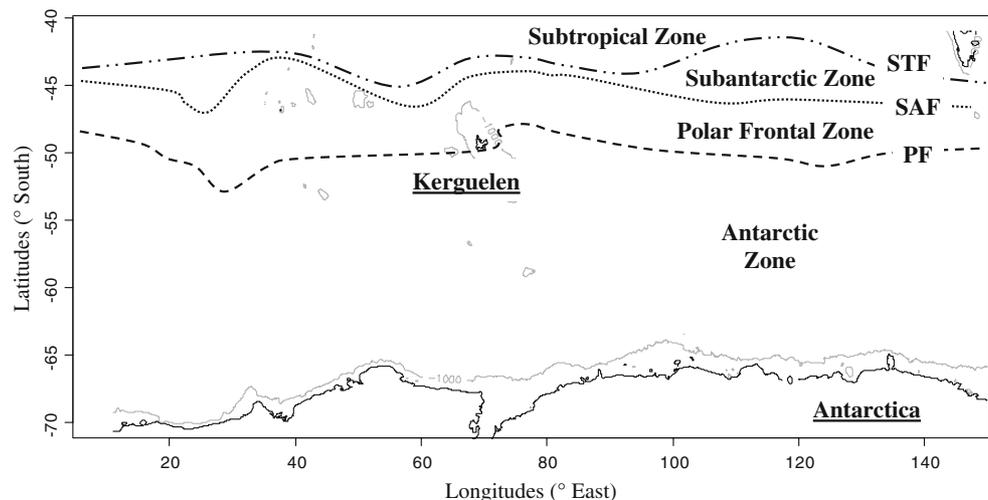
All adult females, but not pups, were caught with a canvas head-bag to avoid bites (Bailleul et al. 2007a). Seals were not anaesthetized. Once females and pups were immobilised, blood was sampled and seals were measured and tagged. Pups were then rolled in a net stretcher and

weighed to the nearest kg using a balance attached to an aluminium tripod. Blood was collected from the dorsal venous sinus of both pups and female seals using  $90 \times 1.2$  mm needles. Seventy percent ethanol was added to whole blood, because this preservation method does not alter the isotopic composition of tissues (Hobson et al. 1997a).

Before isotopic analysis, blood was dried in an oven at  $+40^\circ\text{C}$  and powdered. Sub-samples were then weighed (from 0.3 to 0.4 mg) with a microbalance, packed in tin containers, and nitrogen and carbon isotope ratios were subsequently determined by a continuous flow mass spectrometer (Micromass Isoprime) coupled to an elemental analyser (Euro Vector EA 3024). Lipids are depleted in  $^{13}\text{C}$  relative to proteins and carbohydrates (Post et al. 2007), but the low lipid content of whole blood does not typically necessitate lipid extraction (Cherel et al. 2005b). We nevertheless carefully checked C:N ratios of the samples (Table 1), and lipids were extracted using cyclohexane from nine blood samples with a C:N ratio  $>3.7$  to avoid bias in the interpretation of  $\delta^{13}\text{C}$  values due to varying lipid contents among samples. Results are presented in the usual  $\delta$  notation relative to PeeDee Belemnite (PDB) and atmospheric  $\text{N}_2$  (Air) for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors  $<0.15$  and  $<0.20\text{‰}$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively.

Data were analysed using R (R Development Core Team 2005). Values are mean  $\pm$  SD. Normality and homoscedasticity were tested using the Shapiro test and residual analysis, respectively. Different linear models were used with  $\delta^{13}\text{C}$  values as the independent variable, and sex, weaning mass, weaning length, weaning day and capture site as dependent variables. The most parsimonious model was then selected according to the Akaike's information criteria.

**Fig. 1** Location of Kerguelen Islands and oceanographic fronts and zones in the Indian Ocean. *PF* Polar Front; *SAF* Subantarctic Front; *STF* Subtropical Front



## Results

### Fasting group

No fasting effect was observed in either blood  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  values of female elephant seals (*M. leonina*) between birth and weaning ( $n = 15$ , paired-samples  $t$  tests,  $t = 1.96$  and  $0.06$ ,  $P = 0.071$  and  $0.951$ , respectively) (Table 1).

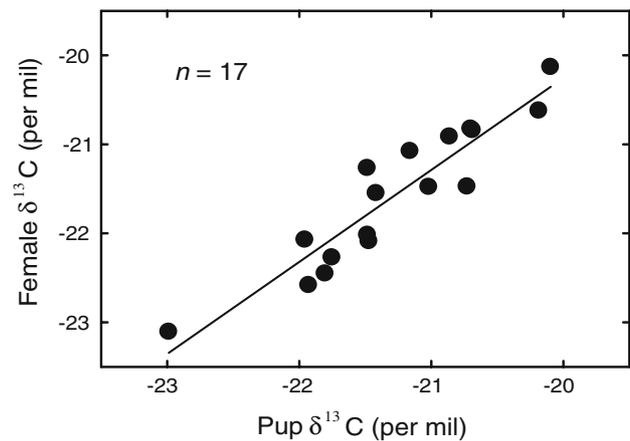
### Lactation group

At weaning, both blood  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were significantly higher in pups than in their mothers ( $n = 17$ , paired-samples  $t$  tests,  $t = 4.15$  and  $16.87$ ,  $P = 0.001$  and  $<0.0001$ , respectively) (Table 1). Carbon and nitrogen signatures of pups and their mothers were positively and linearly correlated (Fig. 2) ( $\delta^{13}\text{C}$ :  $y = 1.04x + 0.45$ ,  $r^2 = 0.87$ ,  $P < 0.0001$ ;  $\delta^{15}\text{N}$ :  $y = 0.48x + 4.71$ ,  $r^2 = 0.33$ ,  $P = 0.016$ ).

### Weaning group

At weaning, elephant seal pups weighed  $104 \pm 20$  kg ( $n = 209$ ) with a total length of  $1.4 \pm 0.1$  m, and their blood  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values averaged  $-21.2 \pm 0.9$  and  $11.4 \pm 0.4\text{‰}$ , respectively (Table 1). Using the above linear regressions, estimated blood  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of adult females averaged  $-21.5 \pm 0.9$  and  $10.1 \pm 0.2\text{‰}$ , respectively, encompassing a large range of  $\delta^{13}\text{C}$  (4.6‰, from  $-23.7$  to  $-19.1\text{‰}$ ), but not  $\delta^{15}\text{N}$  (1.1‰, from 9.6 to  $10.7\text{‰}$ ) values. Surprisingly, the frequency distribution of pup  $\delta^{13}\text{C}$  values and, accordingly that of female values, was not bimodal, but, instead showed a single broad mode at  $-22.5$  to  $-20.5\text{‰}$  (Fig. 3).

Potential effects of sex, weaning mass, weaning length, weaning day and capture site on blood  $\delta^{13}\text{C}$  values of pups were tested using a linear model and a backward stepwise procedure. Importantly, weaning mass was not significantly related to  $\delta^{13}\text{C}$  values, weaning day being the only variable that was significantly but weakly correlated with the carbon signature (LM:  $n = 209$ , adjusted  $r^2 = 0.02$ ,  $P = 0.040$ ) (Fig. 4). Since weaning mass was found to be related to



**Fig. 2** Relationship between blood  $\delta^{13}\text{C}$  values of female elephant seals and their pups at weaning

weaning date (adjusted  $r^2 = 0.17$ ,  $P < 0.0001$ ) (Fig. 4), we tested (ANOVA) a  $\delta^{13}\text{C}$  effect on residuals of the regression between weaning mass and weaning date and found no significant relationship ( $P = 0.210$ ).

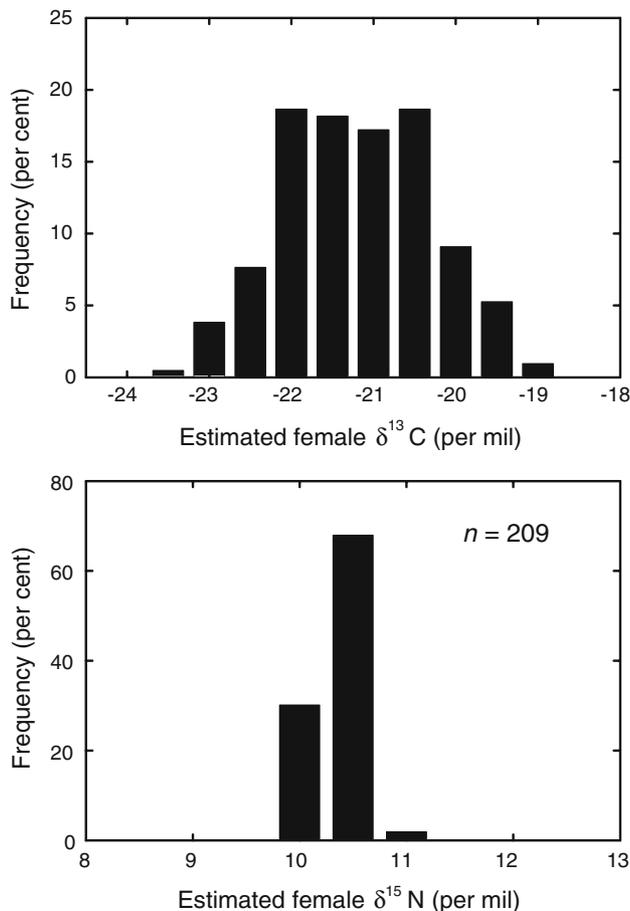
## Discussion

Using pups as proxies of their mothers' biology, this study investigates whether intra-specific niche differences can influence short-term reproductive fitness in a marine mammal. It is the first, to our knowledge, to combine information on pup weaning mass (a proxy of females' foraging success and maternal investment) together with the pup blood  $\delta^{13}\text{C}$  value (a proxy of female foraging zone) to investigate intra-specific and geographic variation in the behaviour of female phocid seals and its biological consequences. Isotopic signatures of pups were unexpected in some ways, giving new insights into the winter ecology of female elephant seals (*M. leonina*) during the pre-breeding foraging trip.

A crucial methodological issue was to validate use of the blood isotopic signature of weaned pups to investigate female foraging ecology during their pre-breeding trip.

**Table 1** Blood  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values and C/N mass ratio of females and pups of elephant seals during the 2006 breeding season at Kerguelen Islands. Values are mean  $\pm$  SD

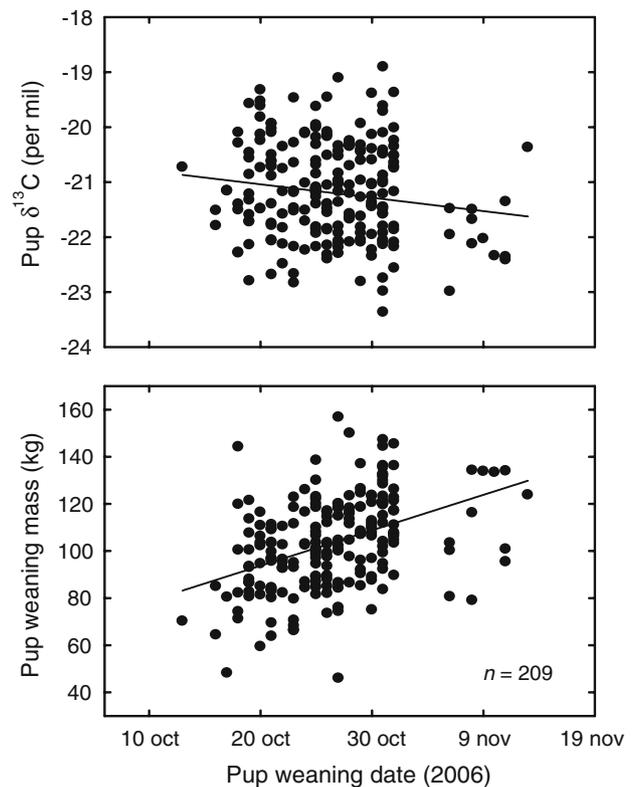
Status	<i>n</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C/N mass ratio
Fasting group				
Females on arrival	15	$-21.3 \pm 0.7$	$10.1 \pm 0.3$	$3.42 \pm 0.08$
Females at weaning	15	$-21.4 \pm 0.8$	$10.1 \pm 0.3$	$3.39 \pm 0.03$
Lactation group				
Females at weaning	17	$-21.6 \pm 0.8$	$10.1 \pm 0.3$	$3.38 \pm 0.03$
Pups at weaning	17	$-21.3 \pm 0.7$	$11.4 \pm 0.4$	$3.49 \pm 0.06$
Weaning group				
Pups at weaning	209	$-21.2 \pm 0.9$	$11.4 \pm 0.4$	$3.44 \pm 0.06$



**Fig. 3** Frequency distribution of estimated blood  $\delta^{13}\text{C}$  (upper panel) and  $\delta^{15}\text{N}$  (lower panel) values of female elephant seals at weaning at Kerguelen Islands in 2006

A first step was to investigate whether female signatures changed or not between birth and weaning, a 3-week period during which females rely exclusively on their energy reserves. As predicted, both blood  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of breeding females did not vary significantly over the lactating period (fasting group), which is in agreement with limited fasting-induced changes in isotopic signature of tissues with medium to low rates of protein turnover, including whole blood (Cherel et al. 2005a). Consequently, blood  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values at weaning were representative of the signatures of the females at their arrival to the colony to breed.

The second step was to test the assumption that pup tissue isotopic compositions reflect those of their mothers in a predictable manner (Aurioules et al. 2006). Indeed, highly significant positive and linear relationships were found between blood  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of newly-weaned pups and those of their mothers (lactation group). This is in agreement with the positive correlations between maternal and nursing offspring isotopic signatures previously found



**Fig. 4** Relationships between blood  $\delta^{13}\text{C}$  values (upper panel), weaning mass (lower panel) and weaning date of elephant seal pups. Pup  $\delta^{13}\text{C}$  value and weaning mass are negatively and positively related to pup weaning date, respectively ( $n = 209$ ,  $r^2 = 0.021$  and  $0.177$ ,  $P = 0.038$  and  $<0.0001$ )

in a study on 11 mammal species (Jenkins et al. 2001). As expected, small (but significant) changes in  $\delta^{13}\text{C}$  and larger increases in  $\delta^{15}\text{N}$  values were observed between pups and female elephant seals. The increase in  $\delta^{15}\text{N}$  ( $1.3 \pm 0.3\text{‰}$ ,  $n = 17$ ) was within the range of published values and consistent with fractionation between mother and nursing offspring (including marine mammals) being less than one trophic level (Hobson et al. 1997b; Jenkins et al. 2001; Das et al. 2003). This fractionation between offspring and mother is species-specific and no generalisation can be made (Jenkins et al. 2001). Importantly, however, the present study showed that the isotopic signatures of female elephant seals can be estimated using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of their pups. Using suckling offspring as proxies of female trophic ecology is theoretically a powerful tool that can be applied to many mammal species, for example in capital and income breeders, to investigate female foraging ecology during the costly pre-lactation and lactation period, respectively.

Our prediction that female elephant seals would show a large range in  $\delta^{13}\text{C}$  values indicating foraging grounds encompassing a wide latitudinal isotopic gradient was verified (weaning group). When compared to the blood carbon

signatures of marine mammals and seabirds from the Southern Ocean (Cherel and Hobson 2007; Cherel et al. 2007, 2008), the carbon signature of the female elephant seal was more negative than that of subtropical fur seals and more positive than those of high-Antarctic penguins and petrels. The majority of the females had  $\delta^{13}\text{C}$  values suggesting foraging north of the Polar Front, in the Polar Frontal Zone (Fig. 1). However, a significant number of females (31%) had relatively low carbon signatures ( $<-22\text{‰}$ ) indicative of the Polar Front and south of it, in low-Antarctic waters. The unimodal frequency distribution with a continuum of female  $\delta^{13}\text{C}$  values was not in agreement with the two main distinct foraging zones showed by satellite-tracked individuals (Bailleul et al. 2007b). This discrepancy is likely to be a consequence of the two methods per se and gives new insights about the female winter foraging ecology. The first issue is that isotopes and tracking did not integrate the same temporal scale. Most females were tracked during the first part of their 8-month, pre-breeding foraging trip with almost no complete recording of the whole trip (Bailleul et al. 2007b). On the other hand, since the stable isotope method is based on time-integrated assimilated food and blood of large mammals integrates a period of 2–3 months (Hilderbrand et al. 1996), blood  $\delta^{13}\text{C}$  values here correspond to the foraging ecology of female elephant seals at the end of winter, during the last part of the trip. A second issue is that the blood isotopic signature was a single value integrating a long foraging period. Consequently, the value can be indicative of a given foraging zone, or, more likely, it was an average of different feeding zones according to the migration pathway of the seals. Hence, on their way back to Kerguelen, foraging individuals that were in Antarctica progressively diluted their low  $\delta^{13}\text{C}$  values by the input of higher  $\delta^{13}\text{C}$  values from lower-latitude prey. In any case, however, the complete lack of very low Antarctic  $\delta^{13}\text{C}$  values pointed out for the first time the importance of feeding and building up energy stores in northern waters at the end of winter for all female elephant seals. Their foraging strategy thus contrasts with that of some male Antarctic fur seals, *Arctocephalus gazella*, whose very low blood carbon signatures ( $<-25\text{‰}$ ) indicate feeding at high latitudes during the Austral winter (Cherel et al. 2007).

In the present work, a remarkable consistency in estimated  $\delta^{15}\text{N}$  values (encompassing 1.1‰) was observed over a wide range of  $\delta^{13}\text{C}$  values (4.6‰), indicating slight inter-individual differences in diet and suggesting that all female seals fed at the same trophic level whatever their oceanic foraging zones. In the Southern Ocean where epipelagic schooling fish are absent, the main pelagic elephant seal prey are likely to be euphausiids (krill), mesopelagic myctophid fishes and the poorly known oceanic squids. The nitrogen isotopic signature of crustaceans is, however, too

low, that of squids is generally too high, and that of myctophids fits well when compared to the theoretical  $\delta^{15}\text{N}$  value of elephant seal prey (Cherel et al. 2008). Our large data set thus contrasts with the traditional view that elephant seals are squid consumers (Rodhouse et al. 1992; Slip 1995) and is consistent with female seals feeding on mesopelagic fish during their pre-breeding winter trip (see details in Cherel et al. 2008).

No significant relationship was found between weaning mass of pups and their carbon signature, suggesting no strong link between foraging areas and maternal investment and foraging success in the female southern elephant seal. Correcting pup body mass according to their weaning date showed no significant relationships between the residuals and pup  $\delta^{13}\text{C}$  values, which again suggests no link between foraging areas of the females and their foraging success. The lack of an obvious foraging advantage with feeding area specialisation has also been reported for female Antarctic fur seals, whose trip duration (and hence foraging location) has no effect on pup mass prior to weaning (Staniland et al. 2004), and for Adélie penguins, *Pygoscelis adeliae*, with no effect of chick feeding frequency and meal size (Watanuki et al. 2003). Since pup weaning mass is a good proxy of individual quality of female elephant seals, the large range in pup weaning mass for a given  $\delta^{13}\text{C}$  value suggests large inter-individual differences in foraging success within the same feeding areas. Therefore, the primary variable in the foraging success of females is likely to be how to forage rather than about where to forage. The lack of short-term advantage of individual specialisation does not preclude, however, that this behaviour may serve to maximize energy gain and reproductive output over an individual's lifetime (Annett and Pierotti 1999). Moreover, pup weaning mass in seals is not only related to female quality but also to environmental factors that influence ocean productivity and hence the availability of resources (Proffitt et al. 2007; de Little et al. 2007). Consequently, disentangling relationships between varying foraging areas and individual specialisation and quality in elephant seals would greatly benefit from investigations conducted over several winters and including years with contrasting oceanographic conditions affecting the Southern Ocean and its trophic web.

Pup  $\delta^{13}\text{C}$  value was weakly and negatively correlated to pup weaning date, indicating a tendency for females foraging in more southern waters to arrive on average later at the colony to give birth than individuals foraging further north. As recently shown, seals foraging in Antarctic waters spend a much longer time in transit (as much as one extra month) compared with those foraging in the Polar Frontal Zone (Biuw et al. 2007). More distant wintering zones, and thus a longer time to return to Kerguelen, were therefore the likely explanation for the later arrival of females with lower  $\delta^{13}\text{C}$

values. We also found that weaning mass of pups was positively correlated to their weaning date, suggesting that heavier (better quality) females arrived later on the breeding grounds. Since female mass increases with age and adult females return to breed later in the season as they age (McMahon and Bradshaw 2004), our data overall suggest that older and heavier experienced females favoured foraging in colder waters when compared to younger individuals, and consequently that a shift to more southern foraging grounds might occur with age. During the juvenile years, younger elephant seals remain closer to the breeding grounds, and, as they age and grow, they travel farther and spend more time in more southerly regions (Field et al. 2005). The hypothesis of an adult shift in foraging areas, however, is not in agreement with breeding females using the same preferred regions year after year (Bradshaw et al. 2004), and it thus needs further investigation on adult females of known-age.

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