Mar Biol (2012) 159:1317–1326
DOI 10.1007/s00227-012-1912-y

ORIGINAL PAPER

Stable isotopes identify age- and sex-specific dietary partitioning and foraging habitat segregation in southern giant petrels breeding in Antarctica and southern Patagonia

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Received: 9 November 2011 / Accepted: 29 February 2012 / Published online: 14 March 2012
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Abstract We examined the isotopic signatures ($\delta^{13}C$, $\delta^{15}N$) of adult body feathers from southern giant petrels *Macronectes giganteus* collected at two breeding colonies in Antarctica (Potter Peninsula and Cape Geddes) and one in southern Patagonia (Observatorio Island), as well as in whole blood collected from adults of both sexes at each Antarctic colonies and from chicks at Potter Peninsula. As body feather moult is a continuous process in giant petrels, feathers provide an integrated annual signal of an adult's diets and foraging habitats. In contrast, the stable isotope values of adult and chick blood are reflective of their diets during the breeding season. We found that sex-specific dietary segregation in adults breeding in Antarctica was notable during the breeding season (blood samples) but absent when examined across the entire year (feather samples). In addition, blood stable isotope values differed between chicks and adults, indicating that adults provision their offspring with a relatively higher amount of penguin and seal prey that what they consume themselves. This finding confirms previous work that suggests that chicks are preferentially fed with prey of presumably higher nutritional value such as carrion. Finally, based on isotopic differences between major oceanographic zones in the Southern Ocean, our data indicate population-specific differences in foraging distribution, with Antarctic populations move seasonally between Antarctic and subantarctic zones, while Patagonian populations likely forage in subtropical waters and in continental shelf habitats year-round.

Communicated by S. Garthe.

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Introduction

Knowledge of animal's dispersion is crucial for our understanding of their ecology, life history, and behaviour and is a prerequisite for their effective conservation (Rubenstein and Hobson 2004). Establishing patterns of movement of wild animals at various scales helps to understand the dynamic and trends of wildlife populations (Gonzalez Solís and Shaffer 2009). Knowledge about movements is useful to establish the effect of fisheries (Copello and Quintana 2009; Bartumeus et al. 2010), climate change (Croxall et al. 2002), and contamination (Ramos et al. 2009; Roscales et al. 2010) on seabirds' populations. Furthermore, the knowledge of seabirds' distribution during the breeding season as well as during the post-breeding or winter period is essential for the complete understanding of their biology, trends and for effective conservation measures (Cherel et al. 2006; Raya Rey et al. 2007; Phillips et al. 2009).

Intraspecific competition for food may play a significant role in structuring populations of animal communities

(Furness and Birkhead 1984) and thus influence the at-sea distribution (Forero et al. 2002; Grémillet et al. 2004; Forero et al. 2005; Weimerskirch et al. 2009). Sexual segregation by foraging habitat and/or diet is a common feature in seabirds and occurs at varying temporal and spatial scales (Catry et al. 2005, Phillips et al. 2011). It is generally considered to result from social dominance, competitive exclusion, and niche specialization arising from the difference in morphology or reproductive role (Gilardi 1992; Clarke et al. 1998; González-Solís et al. 2000; Cook et al. 2007; Quintana et al. 2011). In addition, the level of intraspecific competition is determined by colony and population size (Lewis et al. 2001; Ainley et al. 2003). Niche differentiation proved to be intensified during the breeding season as seabirds are central place foragers and also juveniles might be feeding in the same area (Forero et al. 2002). One more consideration is that growing chicks require more energy than adult subsistence (Ricklefs et al. 1998); thus, parents could be foraging on different prey items for themselves and to feed the offspring.

Levels of intraspecific niche differentiation may possibly be established through the assessment of stable isotopes on animal tissues. For seabirds, the isotopic signature of tissues is a powerful tool to investigate their trophic niche along two dimensions, with δ^{13}C and δ^{15}N values reflecting the consumers' foraging habitat and trophic level, respectively (Cherel et al. 2007). In particular, biogeochemical markers are particularly useful for studying animal movements, and they provide time-integrated information that can be linked directly to geographical regions, an approach that has recently been utilized in the last decade on a variety of animals (Rubenstein and Hobson 2004, Graham et al. 2009). In the southern hemisphere, the geographical δ^{13}C gradient is well defined in particulate organic matter from surface waters, ranging from high δ^{13}C values in warm subtropical waters in the north to low values in cold Antarctic waters in the south (François et al. 1993; Trull and Armand 2001), and thus suitable for studying the at-sea distribution of seabirds and marine mammals (Best and Schell 1996; Cherel et al. 2006).

The southern giant petrel *Macronectes giganteus* is an important scavenger in the South Atlantic Ocean (González-Solís et al. 2000; Copello et al. 2008). This species shows a noticeable sexual segregation in diet and foraging areas (González-Solís et al. 2000, 2005; Forero et al. 2005; Phillips et al. 2009; Copello et al. 2011). Segregation in diet and foraging areas among individual seabirds from different colonies and sex and age classes within a colony for the southern giant petrel has been proved for some locations during the breeding period (Forero et al. 2005) and throughout the year (Phillips et al. 2009). Knowledge of the at-sea distribution is key in this species given the high overlap with fisheries (Otley et al. 2007; Copello and Quintana 2009) and the low but present mortality associated with this interaction (Gonzalez-Zevallos and Yorio 2006; Sullivan et al. 2006).

In this context, the purpose of this study was to add the information about trophic position and foraging habitat of southern giant petrels breeding at two colonies in Antarctica and Observatorio Island, southern Patagonia, Argentina. To achieve this aim, we assess the differences in the isotopic signature (δ^{13}C and δ^{15}N) by sex, age, and locality in two tissues: whole blood and body feathers. The isotopic composition of whole blood represents 3–4 weeks of diet during the breeding season, while a pooled sample of body feathers provides an integrated annual signature as southern giant petrels moult body feathers throughout the year (Hunter 1984a; Forero et al. 2005; Phillips et al. 2009).

Methods

Sample collection

Fieldwork was carried out at Observatorio Island, Tierra del Fuego, Argentina, in southern Patagonia and on two colonies in Antarctica: Cape Geddes, Laurie Island, South Orkney Islands and Potter Peninsula, 25 de Mayo/King George Island, South Shetland Islands (Fig. 1) during January (Antarctic colonies) and March (Patagonia colony) of the 2008/2009 breeding season. We collected five body feathers from the mantle region of adult southern giant petrels, and sex was determined through bill measurements when possible; otherwise, birds were marked as unknown sex. In Antarctica, we caught adults and chicks (50–60 days old) on their nests, took about 0.3 ml of whole blood from the foot vein, and transferred it to 2 different vials containing 1.5 ml of 70 % ethanol from a common source and stored for later analysis. Storage in 70 % ethanol has been generally found to not affect the stable isotope values of whole blood (Hobson et al. 1997; Halley et al. 2008; Therrien et al. 2011; though see Bugoni et al. 2008).

We collected representative samples of the most common southern giant petrel prey species identified by a study examining chick regurgitations at Cape Geddes and King George Island in 1998/1999 (N. Coria, unpublished data). These samples include Antarctic Krill (*Euphausia superba*, $n = 20$), one squid (*Psychroteuthis glacialis*, $n = 12$), and two fish species (*Pleuragramma antarcticum*, $n = 8$; *Gymnoscopelus nicholsi*, $n = 6$) collected during trawls conducted around the South Shetland and South Orkney Islands from 2006 to 2009. These samples were kept frozen prior to sample preparation and stable isotope analysis. Unfortunately, we were not able to collect muscle tissues from penguins and seals in this region, which are commonly consumed by southern giant petrels. Instead. we

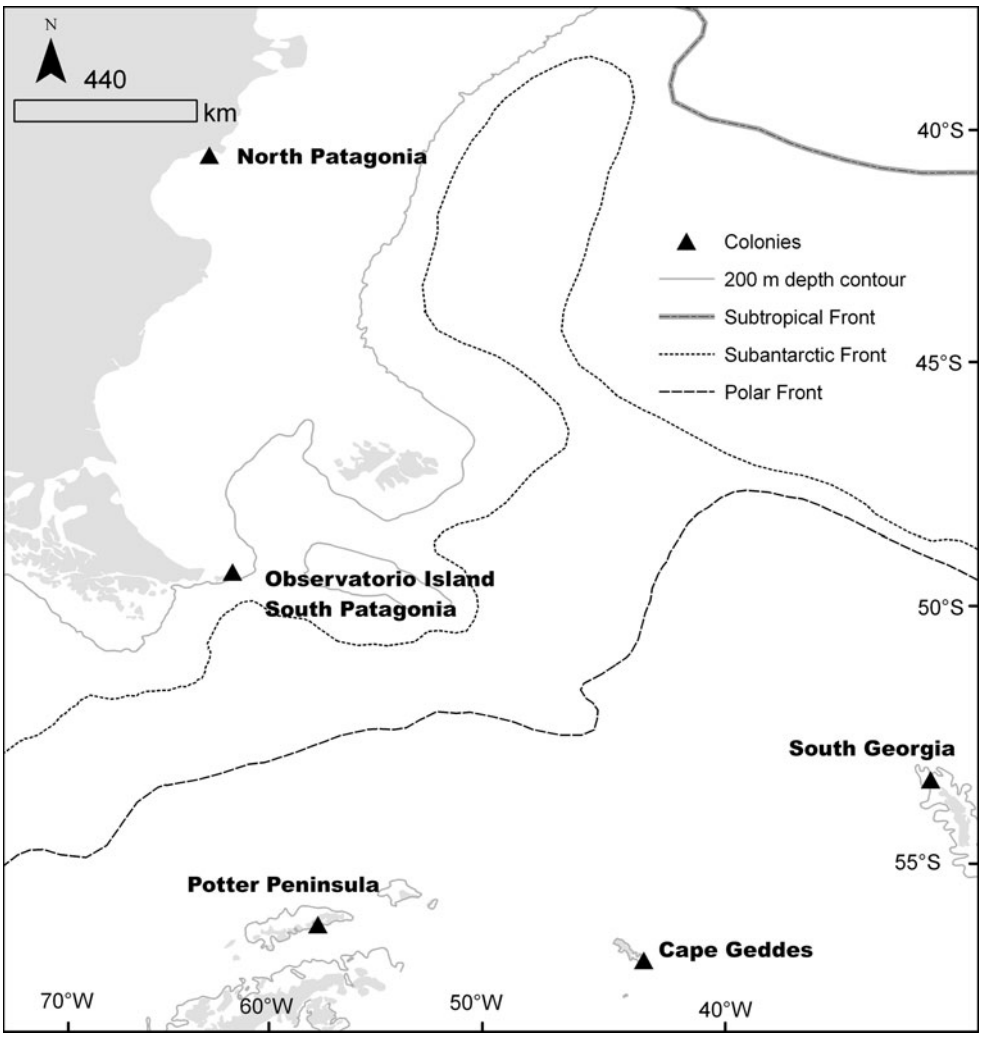

Fig. 1 Study area in the southwest Atlantic and Southern Ocean. Colony sites from Antarctica (Cape Geddes and Potter Peninsula) and southern Patagonia (Observatorio Island) are indicated. Also, location of colonies with data from previous studies at South Georgia and northern Patagonia is shown (Forero et al. 2004; Anderson et al. 2009). The location and boundaries of major oceanographic zones are identified following Belkin and Gordon (1996)

collected down feathers from Chinstrap penguins chicks (*Pygoscelis antarctica*, $n = 16$) at Admiralty Bay on 25 de Mayo/King George Island during January 2009 and used published isotopic values of lipid-extracted milk from Antarctic Fur Seal (*Arctocephalus gazella,* $n = 31$) at Livingston Islands, South Shetland Islands in December to February of 2007/2008 (Polito and Goebel 2010). We then adjusted penguin down δ^{13}C (−0.1 ‰) and δ^{15}N (+1.6 ‰) values to reflect the isotopic signature of penguin muscle tissue based on a controlled study on ring-billed gulls on a piscivorous diet (*Larus delawarensis*; Hobson and Clark 1992). While no comparative studies between milk and muscle are available in pinnipeds, previous studies suggest that the isotopic composition of milk is similar to that of blood tissues after correction for lipid content (Stegall et al. 2008; Habran et al. 2010). Therefore, we adjusted lipid-extracted milk δ^{13}C and δ^{15}N values using the mean difference between muscle and whole blood values derived from a captive study of pinnipeds (Hobson et al. 1996; δ^{13}C: −0.04 ‰; δ^{15}N: +0.7 ‰).

Sample preparation and stable isotope analysis

Petrel blood and whole prey samples were dried in an oven at 60 °C and then ground to a fine powder using a quartz mortar and pestle. We extracted lipids from prey samples using a Soxhlet apparatus with a 1:1 petroleum–ether: ethyl–ether solvent mixture for 8 h (Seminoff et al. 2007). Lipid-extracted prey items were not acidified prior to isotopic analysis. Petrel feathers and penguin chick down were cleaned of surface contaminants using a 2:1 chloroform–methanol rinse, air-dried, and then cut with stainless steel scissors into small fragments of multiple feathers that were pooled by individual. We loaded approximately 0.5 mg of each blood, feather, and prey tissue samples into tin cups that were flash-combusted (Costech ECS4010 elemental analyzer) and analysed for carbon and nitrogen isotopes (δ^{13}C and δ^{15}N) through an interfaced thermo delta V plus continuous flow stable isotope ratio mass spectrometer (CFIRMS) at the University of North Carolina Wilmington. Raw δ values were normalized on a

two-point scale using depleted and enriched glutamic acid reference materials USGS-40 and -41. Sample precision based on repeated sample and reference material was 0.1 and 0.2 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Stable isotope abundances are expressed in δ notation in per mil units (‰), according to the following equation:

$$\delta X = \left[\left(R_{\text{sample}}/R_{\text{standard}}\right) - 1\right] \cdot 1{,}000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The R_{standard} values were based on the PeeDee Belemnite (VPDB) for ^{13}C and atmospheric N_2 for ^{15}N.

Statistical and isotopic mixing model analysis

We compared blood stable isotope ratios between sex and sites, and between females, males, and chicks in Antarctica using separate ANOVA along with Tukey multiple comparisons and normality tests using Kolmogorov–Smirnov test. We used similar ANOVA procedures to test for differences in body feather isotopic ratios between sex and breeding site and across common southern giant petrel prey species. We used the SIAR Bayesian multi-source isotopic mixing model in the R environment (R Development Core Team 2007) to quantify the breeding season diet composition of females, males, and chicks sampled at Antarctic colonies. The SIAR model estimates probability distributions of multiple source contributions to a mixture while accounting for the observed variability in source and mixture isotopic signatures, dietary isotopic fractionation, and elemental concentration (Parnell et al. 2010). Using petrel blood $\delta^{13}C$ and $\delta^{15}N$ signatures, we used the SIAR model to predict the contribution of krill, squid, fish, penguin, and seal prey sources to the diets of adults and chicks. For SIAR models, we incorporated diet to whole blood discrimination factors derived from captive studies of four piscivorous birds (see review by Cherel et al. 2005; $\delta^{15}N$: $+2.7 \pm 0.4$; $\delta^{13}C$: $+0.0 \pm 0.7$) and ran 1 million iterations, thinned by 15, with an initial discard of the first 40,000 resulting in 64,000 posterior draws.

For comparative purposes, we plotted our petrel isotopic data against literature values from adult southern giant petrel blood and feather samples from South Georgia (Anderson et al. 2009) and adult blood samples from northern Patagonia (Forero et al. 2004) along with approximate isotopic boundaries of major oceanographic zones in the Southern Ocean and South Atlantic as identified by Phillips et al. (2009). However, previous studies suggest that although variability is similar between these two tissues, whole blood is predictably enriched in ^{15}N and ^{13}C compared with feathers grown on the same diet (Quillfeldt et al. 2008). To visually facilitate these inter-tissue and thus inter-seasonal comparisons, we adjusted all blood stable isotope values using the mean difference between feathers and whole blood derived from captive studies of four piscivorous birds (Cherel et al. 2005; $\delta^{15}N$: +1.3 ‰; $\delta^{13}C$: +0.6 ‰) prior to plotting these data. Statistical analysis was carried out using Minitab 14. Significance was assumed at $p < 0.05$, and means are given with SD.

Results

We found significant differences in blood isotopic signatures of blood between males and females but not between sites for the two Antarctic colonies in both $\delta^{15}N$ (two-way ANOVA—sex: $F_{1,14} = 17.38$, $p < 0.01$; site: $F_{1,14} = 0.6$, $p = 0.45$; sex × site: $F_{1,14} = 0.04$, $p = 0.85$) and $\delta^{13}C$ (sex: $F_{1,14} = 4.52$, $p = 0.05$; site: $F_{1,14} = 0.12$, $p = 0.73$; sex × site: $F_{1,14} = 1.1$, $p = 0.31$). Females presented higher isotopic values than males (Table 1). When combining all Antarctic colonies males, females, and chicks, blood nitrogen and carbon isotope values differed significantly (ANOVA: $\delta^{15}N$: $F_{2,23} = 116.5$, $p < 0.01$; $\delta^{13}C$: $F_{2,23} = 14$, $p < 0.01$; and all comparisons were significant at $p < 0.05$). Nitrogen and carbon values were higher in females than in males, while chicks presented the lowest values (Table 1; Fig. 2).

Body feather isotopic values did not differ significantly between males and females or between the two Antarctic colonies for both $\delta^{15}N$ (two-way ANOVA—sex: $F_{1,15} = 2.01$, $p = 0.17$; site: $F_{1,15} = 0.54$, $p = 0.47$; sex × site: $F_{1,15} = 0.21$, $p = 0.65$) and $\delta^{13}C$ (sex: $F_{1,15} = 4.24$, $p = 0.06$; site: $F_{1,15} = 0.17$, $p = 0.68$; sex × site: $F_{1,15} = 0.3$, $p = 0.88$). Independent of sex, carbon and nitrogen feathers' isotopic values differed between sites when including the Patagonian colony ($\delta^{15}N$: $F_{2,31} = 99.6$, $p < 0.01$; $\delta^{13}C$: $F_{2,31} = 46.85$, $p < 0.01$). Post hoc multiple comparisons showed that individuals from Observatorio Island in southern Patagonia had significantly higher feather $\delta^{15}N$ and $\delta^{13}C$ values than individuals at the two Antarctic colonies that had similar isotopic signatures (Table 1).

We found differences in the $\delta^{15}N$ and $\delta^{13}C$ values of species in our library of common southern giant petrel prey items that, in combination, effectively separated krill, squid, fish penguins, and seals functional prey groups (Table 2; Fig. 2; $\delta^{15}N$: $F_{6,91} = 301.58$, $p < 0.01$; $\delta^{13}C$: $F_{6,91} = 25.47$, $p < 0.01$). Our mixing model analysis predicted that female southern giant petrels breeding at our Antarctic colonies predominantly consume fish and smaller amounts of prey such as krill, squid, penguins, and seals (Table 3). Model predictions also suggest that males consume a large proportion of fish prey, but they consume a slightly higher amount of penguin, and seal prey relative to

Table 1 The carbon- to-nitrogen ratio (C/N) and stable isotope signatures (δ^{13}C and δ^{15}N) of whole blood and feathers from southern giant petrel adults and chicks from two breeding locations in Antarctica (Cape Geddes and Potter Peninsula) and a single location in southern Patagonia (Observatorio Island)

Tissue, breeding site	Group	*n*	C/N	δ^{13}C (‰)	δ^{15}N (‰)
Whole blood					
Potter Peninsula	Adult female	4	3.5 ± 0.1	−23.2 ± 0.8	13.1 ± 0.3
	Adult male	4	3.5 ± 0.1	−23.6 ± 0.5	12.3 ± 0.2
	Chicks[a]	8	3.5 ± 0.1	−24.6 ± 0.4	10.5 ± 0.4
Cape Geddes	Adult female	5	3.5 ± 0.1	−23.0 ± 0.6	12.9 ± 0.4
	Adult male	5	3.5 ± 0.1	−24.0 ± 0.7	12.3 ± 0.3
Body feathers					
Potter Peninsula	Adult female	4	3.5 ± 0.1	−19.9 ± 1.0	14.1 ± 0.5
	Adult male	4	3.2 ± 0.1	−21.4 ± 0.7	13.2 ± 1.1
Cape Geddes	Adult female	6	3.2 ± 0.1	−20.1 ± 2.5	13.5 ± 1.2
	Adult male	5	3.1 ± 0.1	−21.8 ± 1.4	13.0 ± 1.2
Observatorio Island	Adult[a]	15	3.1 ± 0.1	−16.2 ± 0.4	18.2 ± 0.8

Values are presented as mean ± SD

[a] Birds of unknown sex

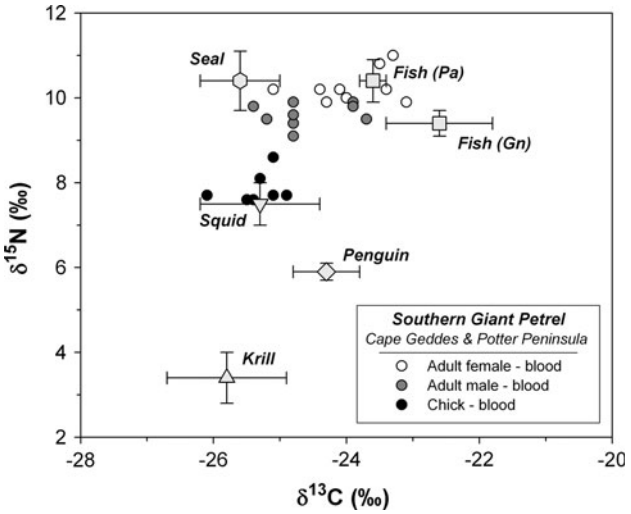

Fig. 2 Whole blood stable isotope signatures (δ^{13}C and δ^{15}N) of individual southern giant petrels (adult females, males, and chicks) from two Antarctic breeding colonies (Cape Geddes and Potter Peninsula) in relation to six common prey species. Petrel blood isotope values are presented after correction for dietary isotopic discrimination (Cherel et al. 2005). Prey values are presented mean ± SD and include krill (*E. superba*), squid (*P. glacialis*), fish: Ea (Pa: *P. antarcticum*; Gn: *G. nicholsi*), penguin (*P. antarctica*), and seal (*A. gazella*) species

females. Chick diets contain the highest predicted combined proportions of krill, penguin and seal prey and a lower proportion of fish relative to adult's males.

Comparing our data to the approximate isotopic boundaries of major oceanographic zones suggests that individuals from the Antarctic colonies appeared to be feeding in Antarctic waters during the breeding season (whole blood isotope value) and in both Antarctic and subantarctic waters when examining the whole year (feather isotope values; Fig. 3). Southern giant petrels breeding at South Georgia show a similar trend, with relatively more variable feather stable isotope than whole blood stable isotope values, suggesting the movement of some individuals towards more subantarctic waters outside of the breeding season (Anderson et al. 2009). Adult feathers from individuals at Observatorio Island in southern Patagonia indicate that adults breeding at this colony feed year-round over subtropical and continental shelf waters (Fig. 3). Furthermore, the isotopic signatures of whole blood samples from individuals breeding in Chubut Province, northern Patagonia, suggest a similar subtropical and continental shelf foraging habitat during the breeding season (Forero et al. 2005).

Discussion

We found evidence of dietary sexual segregation in southern giant petrels during the breeding season at our two locations in Antarctica. Our results suggest that the relatively high δ^{15}N values of female whole blood relative to males in Antarctica are likely due to their greater reliance on marine prey such as fish relative to carrion sources, such as penguins and seals during the breeding season. This is because fish species can often have higher δ^{15}N and δ^{13}C values than penguins and seals in Antarctica due to high levels of consumption of low trophic level krill found in these two taxa relative to fish (Quillfeldt et al. 2005, this study). Similar sex-related differences in giant petrel diets (Hunter 1983; Hunter and de Brooke 1992) and foraging

Table 2 The carbon- to-nitrogen ratio (C/N) and stable isotope signatures (δ^{13}C and δ^{15}N) of tissue from six common southern giant petrel prey species collected from around the South Shetlands and South Orkney Islands, Antarctica, in 2006–2009

Prey group, species	Tissue	*n*	C/N	δ^{13}C (‰)	δ^{15}N (‰)
Krill, *E. superba*	Whole body	20	3.8 ± 0.3	−25.8 ± 0.9	3.4 ± 0.6
Squid, *P. glacialis*	Whole body	12	3.3 ± 0.1	−25.3 ± 0.6	7.5 ± 0.5
Fish, *P. antarcticum*	Whole body	8	3.0 ± 0.1	−23.6 ± 0.2	10.4 ± 0.5
Fish, *G. nicholsi*	Whole body	6	3.4 ± 0.1	−22.6 ± 0.8	9.4 ± 0.3
Penguin, *P. antarctica*	Chick down (muscle)[a]	16	3.1 ± 0.1	−24.4 ± 0.5 (−24.3 ± 0.5)	7.5 ± 0.2 (5.9 ± 0.2)
Seal, *A. gazella*	Milk (muscle)[a]	31	3.6 ± 0.4	−25.2 ± 0.6 (−25.6 ± 0.6)	9.1 ± 0.7 (10.4 ± 0.7)

Values are presented as mean ± SD

[a] Penguin chick down and seal milk values were adjusted to reflect avian and pinniped muscle tissue (Hobson and Clark 1992; Hobson et al. 1997) prior to incorporation in dietary mixing models

Table 3 The predicted diet composition of southern giant petrel females, males, and chicks from two Antarctic colonies (Cape Geddes and Potter Peninsula) during the breeding season

Prey group, species	Giant petrel breeding season diet (% composition)		
	Adult female	Adult males	Chicks
Krill, *E. superba*	1.7 (0.1–4.7)	3.1 (0.3–7.8)	17.8 (5.8–28.7)
Squid, *P. glacialis*	3.1 (0.2–9.0)	6.9 (0.6–16.8)	17.0 (2.7–31.8)
Fish, *P. antarcticum*	55.2 (26.3–79.9)	36.1 (14.1–58.7)	16.4 (2.7–30.6)
Fish, *G. nicholsi*	28.3 (6.1–52.5)	31.3 (13.1–48.8)	15.4 (3.4–27.1)
Penguin, *P. antarctica*	2.1 (0.1–6.2)	4.1 (0.4–10.1)	18.4 (4.4–32.1)
Seal, *A. gazella*	9.6 (0.7–27.5)	18.5 (4.8–32.8)	15.0 (3.9–25.7)

Diet compositions were estimated based on whole blood δ^{13}C and δ^{15}N values using the multi-source Bayesian isotopic mixing model SIAR (Parnell et al. 2010) and are presented as mean estimates with 95 % CIs (in parentheses)

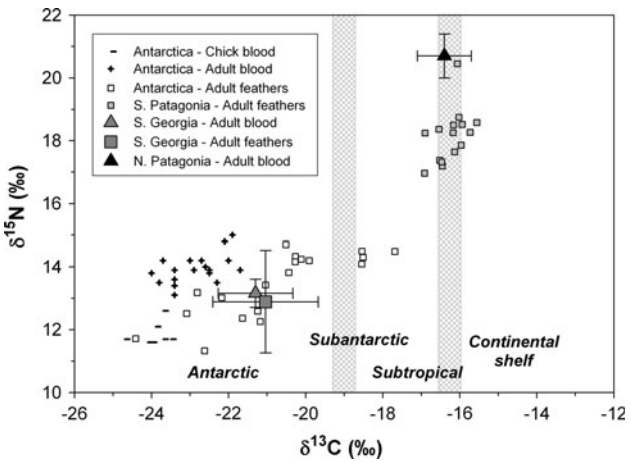

Fig. 3 Whole blood (adult and chicks) and feather (adult only) stable isotope signatures (δ^{13}C and δ^{15}N) of individual southern giant petrels from Antarctica and southern Patagonia in relation to the approximate isotopic boundaries of major oceanographic zones in the Southern Ocean and South Atlantic as identified by Phillips et al. (2009). The δ^{13}C and δ^{15}N values of southern giant petrels breeding at South Georgia (Anderson et al. 2009; whole blood: $n = 16$; feather: $n = 16$) and northern Patagonia (Forero et al. 2004; whole blood: $n = 50$) are plotted as mean ± SD. Whole blood values were adjusted prior to plotting using the mean difference between feathers and whole blood derived from captive studies to better facilitate inter-tissue comparisons (Cherel et al. 2005)

areas (González-Solís et al. 2000; Copello et al. 2011) have been found at breeding locations outside of Antarctica using the conventional methods as well as stable isotope analysis (Forero et al. 2005; though see Phillips et al. 2011). While the two Antarctic colonies examined in this study are located approximately 760 km apart, we found no differences in whole blood isotope signatures. Thus, segregation was stronger between sexes than sites. This result is not surprising given the trend found between southern and northern giant petrels (*Macronectes halli*) breeding sympatrically at South Georgia where sex differences were stronger than species differences (González-Solís et al. 2000). Our whole blood isotope values from Antarctica are also similar to those found at South Georgia, indicating that at these three localities giant petrels occupy a similar trophic level (Forero et al. 2005; Anderson et al. 2009). In contrast, while individuals at northern Patagonia colonies likely forage at a similar functional trophic level, whole blood isotope values from previous studies exhibit relatively higher nitrogen and carbon values, which are indicative of feeding in the continental shelf and subtropical waters that have more complex food webs (Fig. 3; Forero et al. 2004, 2005; Copello et al. 2008).

Several studies of seabird suggest an adaptive benefit for parents to feed chicks from a different prey source than they feed on for themselves (Hodum and Hobson 2000; Forero et al. 2002; Dahdul and Horn 2004). At our Antarctic breeding sites, southern giant petrel chicks had lower whole blood stable carbon and nitrogen isotope values than adult males and females, and mixing model analysis indicated that adults provide their offspring with a relatively higher amount of penguin and seal prey (Table 3). This finding confirms the work of Forero et al. (2005) at South Georgia and northern Patagonia that suggests that southern giant petrel chicks are preferentially fed penguin and seal (often as carrion). The relatively closer isotopic values of chicks and adult males could be indicative of sex-specific provisioning behaviours with males feeding chicks more frequently as carrion is abundant and available close to the colony (Hunter 1983). In addition, the higher-energy content found in penguins and seals relative to krill, fish, and squid species (9.6–20.2 vs. 4.0 to 8.4 mJ kg^{-1}) may contribute to the prevalence of carrion in chick diets (Watanuki 1992; Boyd et al. 1994; Barrera-Oro 2002; Forcada et al. 2009). Our mixing model predictions also suggest that chicks may consume a higher amount of krill relative to adults (Table 3). However, a study of chick regurgitations at our two Antarctic study sites in 1998/1999 suggests that krill, while commonly found in the diet, comprises <1 % by mass of chick diets during the breeding season (N. Coria, unpublished data). It may be that krill are not directly targeted but are secondarily consumed when adults are scavenging on krill predators such as penguins and seals. If so, it is likely that the inclusion krill, with its low δ^{15}N value, in our mixing model may obscure the relative importance of other important prey sources with intermediate δ^{15}N values, such as penguins. Removing krill as a potential prey source from our analyses would increase the importance of carrion sources such as penguins in chick and, to lesser extent, adult male diets and strengthen our findings of sex- and age-specific dietary partitioning.

An alternate hypothesis to explain age-related differences in the stable isotope values of whole blood between adults and chicks are the potential differences in isotopic discrimination associated with the growth and development (Quillfeldt et al. 2008; Harding et al. 2008; Williams et al. 2007; Sears et al. 2009). Bearhop et al. (2000) indicated that differences in nitrogen metabolism in growing chicks can result in higher blood urea concentration and greater nitrogen-use efficacy, which reduces isotopic discrimination and decreases blood δ^{15}N values. In a controlled study, Sears et al. (2009) found no effect of growth on blood δ^{13}C but suggest that the blood δ^{15}N values of chicks may be depleted by as much as 0.5 ‰ due to the growth relative to the blood of adults consuming the same diet. It is possible that growth may have affected the δ^{15}N values of the chicks in our study to a similar degree. However, we sampled petrel chicks at 50–60 days which is after the linear growth phase and when growth has begun to reach an asymptote likely reducing this effect (Conroy 1972, Hunter 1984b). In addition, the large differences we observed between chicks and adult males (~1.8 ‰) and females (~2.5 ‰) suggest that other factors, such as diet, must also significantly influence age-related differences in whole blood δ^{15}N values. Studies examining chick provisioning also reinforce the hypothesis that the age-related differences in stable isotope values found in our study are primarily a reflection of sexual dietary differences with males provisioning chicks more frequently and with higher amounts of carrion than females (Hunter 1983, González-Solís et al. 2000, N. Coria unpublished data).

Given the latitudinal variations in δ^{13}C values of marine organisms in the Southern Ocean (Quillfeldt et al. 2005; Cherel and Hobson 2007), our data indicate region-specific differences in foraging distribution and trophic niche during the breeding season (whole blood) and throughout much of the year (feathers) following correction for tissue-specific isotopic discrimination (Fig. 3). Individuals breeding at Antarctica are likely feeding in Antarctic during the breeding season (blood) and move into Antarctic and subantarctic waters throughout much of the entire year (feathers). It is plausible that post-breeding, southern giant petrels from Antarctica abandon their territories and move northwards as weather conditions worsen and higher-energy prey (penguins and seals) disperse in the winter months. The trophic niche of individuals from Antarctic colonies also appears to widen outside of the breeding season, given the larger variance in feathers carbon and nitrogen isotope values compared with the blood samples (Cherel et al. 2007). The generally broader trophic niche outside of the breeding season also reduces apparent sex-related differences in diet as statistical differences in the isotopic signatures of feathers were absent due to the higher individual variability within sexes; though this result may have also been influenced but our limited sample sizes. Similarly, isotopic and tracking data from South Georgia suggest that male and female southern giant petrels forage in Antarctic and subantarctic waters throughout much of the year, and that trophic niche broadens and sexual differences are reduced near the end and outside of the breeding season (Fig. 3; Forero et al. 2005; González-Solís and Croxall 2005; Anderson et al. 2009; Phillips et al. 2009; Phillips et al. 2011).

In contrast, the δ^{13}C values of adult feathers from Observatorio Island suggest that individuals breeding in southern Patagonia feed predominantly over the continental shelf and subtropical water masses for much of the year (Fig. 3). Unfortunately, whole blood samples at Observatorio Island from the breeding season were not examined in

our study, and we could not assess sex-related trends as our feather samples from this location were from adults of unknown sex. However, previous stable isotope studies of whole blood from northern Patagonian colonies suggest that both sexes feed over the continental shelf and in subtropical water masses during the breeding season (Fig. 3; Forero et al. 2004, 2005). Interestingly, the δ^{15}N and δ^{13}C values of adult feathers from Observatorio Island are also less variable than those collected at our two Antarctic colonies (Table 1; Fig. 3). This suggests that individuals from Observatorio Island may have less seasonally variable trophic niches and/or foraging areas, relative to individuals from Antarctica when examined across the entire year. This trend may be influenced by the contrasting conditions found in these two regions, with individuals from southern Patagonia (Observatorio Island) feeding in a more seasonally stable marine environment and facing less pressure to adjust their trophic niche or foraging range. However, it is also possible that individuals breeding in southern Patagonia disperse northwards outside of the breeding season but remain over isotopically similar water masses feeding at the same trophic niche.

Our results expand on previous studies of the trophic ecology of southern giant petrels and provide new insights into foraging niche segregation between and within breeding colonies in Antarctica and Patagonia. In general, adults breeding in Antarctica preferentially provision their offspring with penguin and seal prey, and sex-specific dietary segregation in adults is apparent during the breeding season (blood samples) but reduced or absent when examined relative to an integrated annual signal (feather samples). Individuals from the Antarctic and South Georgia colonies appear to forage primarily in Antarctic and subantarctic water masses, while those breeding in Patagonian colonies appear to forage in subtropical waters and in continental shelf habitats year-round. These sex and breeding location-specific diet and foraging habitat difference likely act to reduce intra- and inter-specific competition via niche diversification (Forero et al. 2002, 2005; Weimerskirch et al. 2009) and may represent evolutionary adaptation to the highly variable Antarctic and Southern Ocean marine system.

Acknowledgments We would like to thank CONICET and Instituto Antártico Argentino for institutional support. Special thanks to the Argentine Navy for transportation to Staten Island and Dirección Nacional del Antártico for the logistical support to the Antarctic colonies. Thanks to R. Sáenz Samaniego, N. Rosciano, and J. M. Raya Rey for their help in the field. Many thanks to M. Goebel, C. Jones, S. Trivelpiece, W. Trivelpiece, J. Walsh, A. VanCise, and others from the US Antarctic Marine Living Resources (AMLR) program who helped collect the prey samples used in this manuscript. K Durenberger, J Seminoff, and N Spear provided helpful assistance with lipid extractions and stable isotope analysis. Southern giant petrel and penguin samples were collected under approved animal use protocols and Antarctic Conservation Act permits provided by Secretaría de Desarrollo Sustentable y Ambiente and Dirección Nacional del Antártico and the US National Science Foundation.

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