



Stable isotopes document inter- and intra-specific variation in feeding ecology of nine large southern Procellariiformes

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ABSTRACT: Investigating the foraging ecology of seabirds is especially challenging given their wide-ranging movements and the practical difficulties of obtaining unbiased information on their feeding behavior. Despite the development of animal-borne tracking devices, several limitations preclude investigations at the scale of a whole community in a given season or year, and, until recently, during the non-breeding period. Here we analyzed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in feathers of chicks and adults to investigate inter- and intra-specific variation in the foraging habitat and trophic position of 9 large procellariiform seabirds from 6 southern breeding localities during the breeding and non-breeding periods. Isotopic ratios of each species were generally consistent among different breeding populations, despite the large geographical scale and potential variation in oceanography in surrounding waters. Both spatial and trophic segregation apparently allowed the co-existence of sympatric species in most breeding localities, except at South Georgia, where both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in chicks showed high overlap among species, probably resulting from the superabundance of alternative food resources during the summer. Low variance in stable isotope ratios among adults in several species indicated high overlap between individuals in feeding habits and trophic levels (i.e. isotopic specialist populations) during the non-breeding period. By contrast, large isotopic variances and the high within- and between-individual components of the trophic niche width suggested that grey-headed and light-mantled sooty albatrosses are generalists. Based on $\delta^{13}\text{C}$, the species that breed in the Southern Ocean can be categorized as residents or subtropical migrants, with the latter including oceanic and neritic subtropical migrants. Albatrosses meet the high energetic challenge of feather synthesis by foraging in different habitats, depending on the length of the non-breeding period. Annual breeders renew their plumage in productive neritic waters in ~4 mo, whereas biennially breeding species moult in less productive oceanic waters over much longer periods (~12 to 16 mo).

KEY WORDS: Albatross · Generalism · Migration · Seabird · Trophic segregation

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INTRODUCTION

Stable isotope analysis is increasingly used to investigate ecology of individuals, populations, species and communities. Among the various applications is the tracking of large-scale movements of terrestrial and marine animals (Hobson & Wassenaar 1997, Rubenstein & Hobson 2004, Phillips et al. 2009, Wiley et al. 2012). Understanding the movements and distributions of organisms allows investigations of fundamental aspects of their ecology and evolutionary history, and is critical for their conservation (Hobson 1999). However, it is especially challenging to obtain information from long-distance migrants, particularly marine species. Large southern-hemisphere procellariiform seabirds forage over thousands of km from the colony during the breeding season (Weimerskirch et al. 1999, Phillips et al. 2005a, 2006), and can move between ocean basins during the non-breeding period (Croxall et al. 2005, Phillips et al. 2005b). Procellariiformes, however, include more threatened species than any other order of birds, with evidence for major, long-term declines particularly of populations in the Southern Ocean (Poncet et al. 2006, Delord et al. 2008, Croxall et al. 2012). Knowledge of the distribution and behavior of breeding birds in relation to the marine environment has increased considerably in recent decades following the development of animal-borne electronic devices (Ropert-Coudert & Wilson 2005). Nevertheless, several limitations (including size and cost) still preclude their use at the scale of a whole community in a given season or year, or, until recently, during the non-breeding period (Croxall et al. 2005, Phillips et al. 2005b, 2006).

The analysis of natural variation in stable isotope ratios in seabird tissues is a powerful method for investigating seabird foraging ecology, especially during the poorly known non-breeding period (Cherel et al. 2000a, 2006, Hedd & Montevecchi 2006, Wiley et al. 2012), and at the community scale (Hobson et al. 1994, Forero et al. 2004, Phillips et al. 2009, 2011). The underlying principle is that the isotopic composition of adult feathers reflects that of their diet during moult, since feather keratin is metabolically inert after synthesis (Hobson & Clark 1992, Bearhop et al. 2002). Moult occurs primarily during the non-breeding period for most petrels and albatrosses in the Southern Ocean (Warham 1990, 1996, Bridge 2006). In contrast, isotope ratios in the feathers of chicks reflect those in prey delivered by their parents during the chick-rearing period. Hence, comparison of adult and chick feathers allows an

assessment of seasonal variation in seabird feeding ecology (Jaeger et al. 2010a). Stable carbon ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$, $\delta^{15}\text{N}$) isotope ratios are used to estimate the consumers' feeding habitat and trophic position, respectively (Newsome et al. 2007). A large-scale sampling program involving the collection of adult and chick feathers from several species during a single field season is relatively straightforward, causes less disturbance and is considerably cheaper than the deployment of tracking devices on a similar number of individuals. At-sea surveys are also useful for investigating at-sea distribution of seabirds (Ainley et al. 2005, Hyrenbach et al. 2007), but provide no information on origin, status or sex of individuals. In contrast, data on stable isotope ratios can be obtained readily from a large number of individuals and species from specific colonies, augmenting and complementing the information obtained from conventional tracking, which usually involves few individuals from a minority of sites. Although several isotopic studies have investigated the feeding ecology and resource partitioning within seabird communities (Hobson et al. 1994, Forero et al. 2004, Phillips et al. 2009) or have compared the same species at different localities (Cherel et al. 2006, Jaquetmet et al. 2008, Polito et al. 2011, Wiley et al. 2012), few have combined multi-species and multi-site comparisons (Roscales et al. 2011, Cherel et al. 2013).

Here we compared stable isotope ratios in feathers of individuals ($n = 436$) of 9 large procellariiform species from 6 different breeding localities in the Southern Ocean in order to (1) compare their foraging ecology during the breeding and non-breeding periods, particularly given the more limited information on the latter; (2) investigate potential spatial variation in feeding ecology among birds from different populations, given their wide breeding distribution on isolated island groups in regions with distinct oceanography; and (3) compare the foraging ecology of annual and biennial breeders during the non-breeding season, given the trade-off between reproduction and feather replacement (Rohwer et al. 2011).

MATERIALS AND METHODS

Fieldwork was carried out at Marion (47° S, 37° E), Amsterdam (37° S, 77° E), Crozet (46° S, 51° E) and Kerguelen (49° S, 70° E) Islands in the southern Indian Ocean, and at South Georgia (54° S, 38° W) and Gough Island (40° S, 9° W) in the southern Atlantic Ocean (Fig. 1). We define the Southern Ocean as the waters between the Subtropical Front (STF) and Antarctica

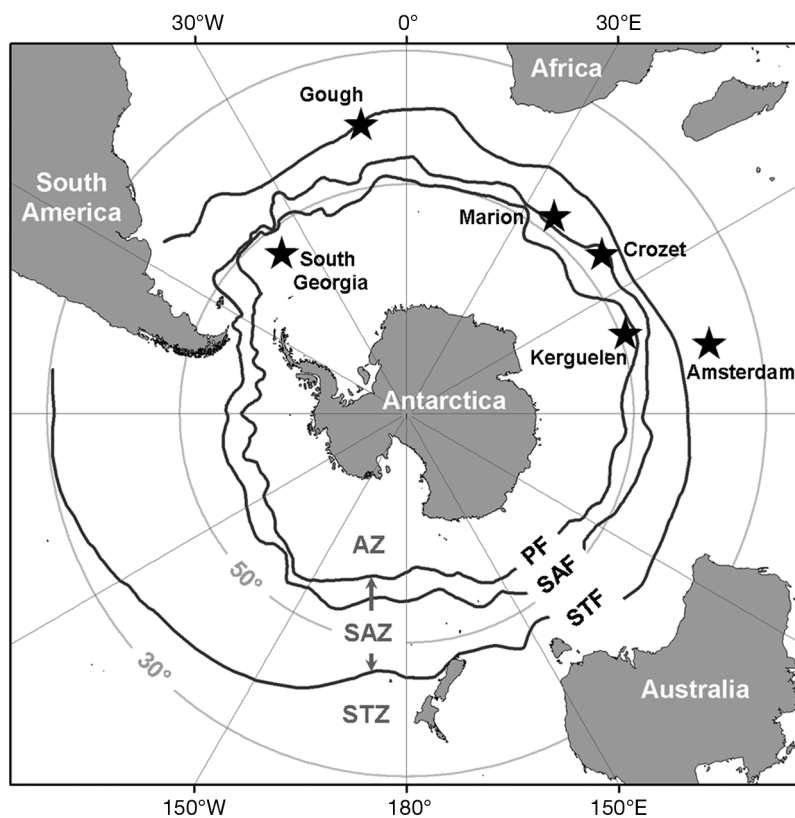


Fig. 1. Sampling sites and main oceanographic fronts and water masses in the Southern Ocean. STF: Subtropical Front; SAF: Subantarctic Front; PF: Polar Front; STZ: Subtropical Zone; SAZ: Subantarctic Zone; AZ: Antarctic Zone

(Orsi et al. 1995), and the subantarctic (SAZ) and Antarctic Zones (AZ), as the zones between the Subtropical Front (STF) and Antarctic Polar Front (PF), and between the PF and continental Antarctica, respectively. The Subtropical Zone (STZ) is the oceanic area north of the STF (Fig. 1). All 6 sampling sites were located either within the Southern Ocean or in warmer fringing waters, including 1 Antarctic (South Georgia), 4 subantarctic (Gough, Marion, Crozet, Kerguelen) and 1 subtropical (Amsterdam) localities.

Feathers were collected from adults and chicks of 1 petrel, the white-chinned petrel (WCP) *Procellaria aequinoctialis* (wingspan ~1.4 m); 5 medium-sized albatrosses (wingspan ~2.0 to 2.5 m): the grey-headed (GHA) *Thalassarche chrysostoma*, Indian yellow-nosed (IYNA) *T. carteri*, Atlantic yellow-nosed (AYNA) *T. chlororhynchos*, black-browed (BBA) *T. melanophris*, and light-mantled sooty (LMSA) *Phoebastria palpebrata*; and of 3 great albatrosses (wingspan ~2.7 to 3.5 m), wandering (WA) *Diomedea exulans*, Amsterdam (AA) *D. amsterdamensis* and Tristan albatross (TA) *D. dabbenena*. The great albatrosses (WA, AA and TA) and 2 of the medium-sized species (GHA and

LMSA) breed biennially, while 4 species (WCP, IYNA, AYNA and BBA) breed annually.

For each study species, a few dorsal body feathers were sampled from randomly chosen chicks and breeding adults (see Table 1). The mean isotopic composition of body feathers is not significantly different from that of wing feathers in breeding albatrosses, and the former therefore represent a safe alternative to flight feathers whose collection impairs flight performance (Jaeger et al. 2009). To avoid potential inter-annual variation in stable isotopic ratios linked to a shift in baseline values (Jaeger & Cherel 2011), as far as possible, all feathers were sampled in the same year. Chick feathers were sampled at the end of the chick-rearing period during the 2005/06 breeding season at Gough and Marion islands, and during the 2004/05 breeding season at the 4 other localities. Adult feathers were all sampled during the 2005/06 breeding season, except those from LMSA at Kerguelen, and some individual AA that were sampled in the 2007/08 season.

Prior to isotopic analysis, feathers were cleaned of surface lipids and contaminants by immersion in a solution of 2:1 chloroform:methanol for 2 min in a beaker, followed by 2 successive methanol rinses. Each whole body feather was air dried and cut into small pieces with scissors. Sub-samples were then weighed (~0.4 mg) with a microbalance, packed in tin containers, and nitrogen and carbon isotope ratios were determined by a continuous flow mass spectrometer (Micromass Isoprime) coupled to an elemental analyser (Euro Vector EA 3024). Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors <0.15 and <0.20‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Following Jaeger et al. (2009), variation in feather $\delta^{13}C$ and $\delta^{15}N$ were used to define the degree of specialization in habitat and trophic level, respectively, of adults during the non-breeding period. Isotopic measurements were first made on a single whole body feather per bird to define isotopic specialist

populations (low trophic niche width, TNW) from generalist populations (high TNW), TNW being the variance among single feathers from all individuals of a given population (Bolnick et al. 2003). In a second step and for generalist populations only, isotopic measurements of 3 additional feathers per bird were used to delineate individuals that were specialists (low within-individual component [WIC], high between-individual component [BIC]) from those that were generalists (high WIC, low BIC). For a given group, WIC is the average variance of 4 individual feathers per bird, and BIC the variation among means of the 4 individual feathers. The relative degree of individual specialization was subsequently considered to be the proportion of TNW explained by within-individual variation: WIC/TNW (this ratio varies from 0, or maximum variation among individual, to 1, no variation among individuals; Bolnick et al. 2003).

$\delta^{13}C$ in particulate organic matter (POM) decreases with latitude in pelagic waters in the Southern Ocean (Trull & Armand 2001). Carbon isotope ratios in predators are thus indicative of the water masses in which they forage (Cherel & Hobson 2007, Phillips et al. 2009, Quillfeldt et al. 2010). Due mainly to a slight enrichment of ^{13}C across the food web and to tissue fractionation factors, baseline carbon isotope ratios (isoscapes) of predator foraging areas are better determined using data from predators themselves than from POM, and are specific for each tissue type (Jaeger et al. 2010b). Consequently, to help interpret $\delta^{13}C$ in feathers sampled from our wide-ranging procellariiform seabirds, we compared these to reference values in 3 control species spanning a latitudinal gradient (see Fig. 2): adult northern rockhopper penguins *Eudyptes moseleyi* from Amsterdam Island, adult king penguins *Aptenodytes patagonicus* from Crozet Islands and snow petrel *Pagodroma nivea* chicks from Adélie Land (high-Antarctica, 66° S, 140° E). These species are indicative of foraging within the southern STZ (Tremblay & Cherel 2003), at the PF (Bost et al. 1997) and in the high AZ (Ridoux & Offredo 1989), respectively (authors' unpubl. data; $n = 12, 12$ and 18 , $\delta^{13}C = -17.9 \pm 0.2, -21.2 \pm 0.4$ and $-23.4 \pm 0.2\%$, respectively).

All data were analyzed statistically using R version 2.11.1. Values are means \pm SD. The isotopic ratios measured in the feathers of the adult albatrosses appear in a previous publication (Cherel et al. 2013), but are presented again in a different context, which is a comparison of foraging ecology, including TNW, between the breeding and non-breeding periods.

RESULTS

Breeding and non-breeding isotopic ratios

$\delta^{13}C$ and $\delta^{15}N$ in feathers of chicks and adults of the 19 populations are shown in Tables 1 & 2, respectively. The pattern of seasonal variation in $\delta^{13}C$ and $\delta^{15}N$ differed considerably between species (Fig. 2). Isotopic ratios in feathers from adults and chicks of the different populations of LMSA and GHA were not significantly different (t -test, all $p \geq 0.056$), except those of LMSA ($p = 0.001$ for $\delta^{13}C$) and GHA ($p < 0.0001$ for $\delta^{15}N$) from South Georgia, whereas they differed greatly for all the other populations of the 7 remaining species (all $p < 0.001$).

Hierarchical cluster analyses (Ward's method) performed on carbon and nitrogen isotopic ratios of chick feathers identified 7 distinct clusters, considered here to represent different spatial or trophic niches (Fig. 2a; MANOVA, $p < 0.0001$). $\delta^{13}C$ of Cluster 1 (AA and TA) and Cluster 4 (IYNA and AYNA) did not differ significantly (Tukey's multiple comparison tests, all $p = 0.615$). All other clusters had statistically different carbon isotopic ratios (Fig. 3, Tukey's multiple comparison tests, all $p \leq 0.0001$). In terms of $\delta^{15}N$, 4 groups of clusters were distinct (Tukey's multiple comparison tests, all $p \leq 0.0001$): first group Cluster 1 (AA and TA), second Clusters 2 and 4 (all WA, IYNA and AYNA populations), third Cluster 5 (WCP from Kerguelen and LMSA from South Georgia), and fourth Clusters 3, 6 and 7 (all the remaining populations).

Hierarchical cluster analyses (Ward's method) performed on isotopic ratios in adult feathers again identified 7 distinct spatial or trophic niches during the non-breeding period (Fig. 2b; MANOVA, $p < 0.0001$). Three groups of clusters had statistically different $\delta^{13}C$ (Fig. 4, Tukey's multiple comparison tests, all $p \leq 0.0001$): first group Clusters 6 and 7 (GHA and LMSA populations), second Cluster 2 (BBA from Kerguelen, IYNA and all WA populations) and third Clusters 3, 4 and 5 (all other populations except AA and TA). There were 3 distinct groups in terms of $\delta^{15}N$ (Tukey's multiple comparison tests, all $p \leq 0.011$): first group Clusters 6 and 7 (GHA and LMSA populations), second Cluster 3 (WCP from South Georgia) and third Clusters 2, 4 and 5 (all other populations except AA and TA). Finally, Cluster 1 (AA and TA) exhibited carbon isotopic ratios intermediate between those of Clusters 3, 4 and 5 and those of Cluster 2 (Fig. 4, Tukey's multiple comparison tests, $p \geq 0.244$ and $p = 0.062$, respectively), and nitrogen isotopic values intermediate between those of Cluster 3 and those of Clusters 4 and 5 ($p = 0.096$ and $p \geq 0.093$, respectively).

Table 1. $\delta^{13}\text{C}$ (‰) in body feathers of 9 large Procellariiformes from 6 southern hemisphere breeding localities. Values are mean \pm SD (sample size) and those in the same rows not sharing a common superscript letter are significantly different ($p < 0.05$). Second row of values for adults indicate the species trophic niche width (TNW). Albatrosses — WA: wandering *Diomedea exulans*; AA: Amsterdam *D. amsterdamensis*; TA: Tristan *D. dabbernea*; GHA: grey-headed *Thalassarche chrysostoma*; IYNA: Indian yellow-nosed *T. carteri*; AYNA: Atlantic yellow-nosed *T. chlororhynchos*; BBA: black-browed *T. melanophris*; LMSA: light-mantled sooty *Phoebastria palpebrata*; and WCP: white-chinned petrel *Procellaria aequinoctialis*

Species	Status	South Georgia	Kerguelen	Crozet	Marion	Gough	Amsterdam
WA	Chicks	-19.5 ± 0.2 (10) ^{a,b}	-19.3 ± 0.4 (15) ^a	-19.4 ± 0.4 (21) ^a	-19.9 ± 0.6 (12) ^b		
	Adults	-17.4 ± 1.1 (10) ^a	-16.8 ± 0.6 (12) ^a	-17.1 ± 0.7 (12) ^a	-17.5 ± 1.0 (12) ^a		
		1.1	0.3	0.5	0.9		
AA	Chicks						-17.7 ± 0.3 (16)
	Adults						-16.2 ± 0.4 (18)
							0.2
TA	Chicks					-17.2 ± 0.4 (12)	
	Adults					-16.4 ± 0.5 (12)	
						0.2	
GHA	Chicks	-20.0 ± 0.6 (10) ^a			-20.6 ± 0.4 (12) ^b		
	Adults	-19.2 ± 1.8 (10) ^a			-19.5 ± 1.9 (11) ^a		
		2.7			3.1		
BBA	Chicks	-20.1 ± 0.8 (10) ^a	-18.5 ± 0.8 (18) ^b				
	Adults	-14.8 ± 1.1 (10) ^a	-17.2 ± 1.1 (13) ^b				
		0.9	1.0				
AYNA	Chicks					-17.7 ± 0.3 (14) ^a	
	Adults					-15.6 ± 0.4 (12) ^b	
						0.1	
IYNA	Chicks						-17.8 ± 0.4 (12) ^a
	Adults						-16.9 ± 0.6 (10) ^a
							0.3
LMSA	Chicks	-22.9 ± 0.3 (10) ^a	-21.0 ± 0.4 (15) ^b	-21.3 ± 0.5 (10) ^b	-21.3 ± 0.5 (7) ^b		
	Adults	-20.6 ± 2.3 (11) ^a	-20.6 ± 2.7 (10) ^a	-20.5 ± 2.1 (10) ^a	-19.9 ± 2.5 (7) ^a		
		4.1	9.9	3.9	6.9		
WCP	Chicks	-19.8 ± 0.8 (3) ^a	-22.2 ± 0.7 (14) ^b	-21.2 ± 0.8 (10) ^c			
	Adults	-15.3 ± 0.8 (10) ^a	-15.5 ± 0.7 (14) ^a	-14.2 ± 0.2 (10) ^b			
		0.5	0.5	0.1			

Trophic niche width in the non-breeding period

Variances in adult feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were used as proxies of the species TNW during the non-breeding period. Two important features were apparent regarding the TNW of the albatrosses and the white-chinned petrel (Tables 1 & 2). First, TNW was generally low (0.1–1.1 and 0.2–0.9‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) regardless of species or population. Second, two exceptions were the large TNW of LMSA and GHA from all breeding localities (2.7–9.9 and 1.5–5.2‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively). Following our 2-step protocol (Jaeger et al. 2009), isotope ratios in 3 additional body feathers (for a total of 4 feathers per individual) were measured in each adult GHA to determine the WIC and BIC (Table 3). Individual specialization of LMSA has already been studied at Crozet (Jaeger et al. 2010a) and the results are included in Table 3. The WIC/TNW ratios of LMSA and GHA were moderate, indicating both significant intra- and inter-individual variation.

DISCUSSION

Breeding-season foraging ecology

Comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in feathers of chicks helped to define different foraging habitats and trophic levels for 9 procellariiform species from the Southern Ocean. The first segregating mechanism is spatial. Cluster and other statistical analyses identified 6 groups in terms of chick $\delta^{13}\text{C}$ (Fig. 3). Based on latitudinal variation in $\delta^{13}\text{C}$ of marine organisms in the Southern Hemisphere (e.g. Jaeger et al. 2010b), those 6 groups correspond to 4 main feeding habitats: subtropical oceanic (Clusters 1 and 4), subantarctic (Clusters 2, 6 and 7) and Antarctic waters (Cluster 5), and neritic waters (Cluster 3). Cluster 1 included the species that breed on islands in the subtropics (IYNA and AA) and feed their chicks with prey caught in subtropical oceanic waters, which is in agreement with tracking studies (Pinaud & Weimerskirch 2007). Interestingly, the $\delta^{13}\text{C}$ of TA and

Table 2. $\delta^{15}\text{N}$ (‰) in body feathers of 9 large Procellariiformes from 6 southern hemisphere breeding localities. See Table 1 for details

Species	Status	South Georgia	Kerguelen	Crozet	Marion	Gough	Amsterdam
WA	Chicks	15.0 ± 0.3 (10) ^a	14.2 ± 0.4 (15) ^b	13.9 ± 0.3 (21) ^b	14.1 ± 0.4 (12) ^b		
	Adults	15.4 ± 0.6 (10) ^a 0.3	15.8 ± 0.8 (12) ^a 0.5	15.7 ± 0.7 (12) ^a 0.5	15.4 ± 0.7 (12) ^a 0.5		
AA	Chicks						15.7 ± 0.3 (16)
	Adults						16.7 ± 0.6 (18) 0.3
TA	Chicks					16.0 ± 0.4 (12)	
	Adults					16.5 ± 0.7 (12) 0.5	
GHA	Chicks	12.1 ± 0.4 (10) ^a			11.8 ± 0.5 (12) ^a		
	Adults	10.7 ± 0.8 (10) ^a 1.5			11.7 ± 1.5 (11) ^a 2		
BBA	Chicks	12.6 ± 0.7 (10) ^a	12.9 ± 0.5 (18) ^a				
	Adults	15.9 ± 0.8 (10) ^a 0.6	15.7 ± 0.6 (13) ^a 0.3				
AYNA	Chicks					14.2 ± 0.3 (14) ^a	
	Adults					15.8 ± 0.5 (12) ^a 0.3	
IYNA	Chicks						14.1 ± 0.4 (12) ^a
	Adults						15.4 ± 0.9 (10) ^a 0.7
LMSA	Chicks	11.3 ± 0.6 (10) ^a	12.6 ± 0.4 (15) ^b	12.4 ± 0.4 (10) ^b	12.7 ± 0.7 (7) ^b		
	Adults	11.8 ± 2.0 (11) ^a 3.1	12.5 ± 1.9 (10) ^a 5.2	11.9 ± 2.1 (10) ^a 3.6	12.1 ± 2.0 (7) ^a 3.9		
WCP	Chicks	12.9 ± 1.0 (3) ^a	11.3 ± 0.7 (14) ^b	12.2 ± 0.7 (10) ^a			
	Adults	17.8 ± 1.0 (10) ^a 0.9	16.1 ± 0.7 (14) ^b 0.4	16.7 ± 0.5 (10) ^b 0.2			

AYNA that breed on Gough Island, which is close to the northern margin of the subantarctic zone, indicates that both species foraged mainly in subtropical oceanic waters, and not in subantarctic waters, which is corroborated by tracking data from TA (Cuthbert et al. 2005). Cluster 3 included BBA from Kerguelen, which was the only near-exclusive neritic feeder, with the high $\delta^{13}\text{C}$ typical of the Kerguelen shelf (Cherel et al. 2000a,b).

Based on $\delta^{13}\text{C}$, chicks of all the other populations and species are mainly fed on prey taken in subantarctic and northern Antarctic waters, with an apparent latitudinal gradient from north to south as follows: all WA populations, WCP and BBA from South Georgia, the 2 populations of GHA, WCP from Crozet and Kerguelen, and all the LMSA populations. Since adults are known to forage over large areas during chick-rearing, $\delta^{13}\text{C}$ of chick feathers integrate the food collected by both parents, potentially in different water masses. Hence, the relatively high $\delta^{13}\text{C}$ of WA reflect foraging by adults in waters from the STZ to the AZ, with most prey caught in subantarctic waters (Weimerskirch et al. 1993, 1997, Nel et al. 2002). In contrast, the consistently low $\delta^{13}\text{C}$

of LMSA, GHA and WCP (from the Indian Ocean) indicate that adults forage both in the subantarctic and Antarctic zones, in general accordance with tracking studies (Catard et al. 2000, Nel et al. 2001, Péron et al. 2010). For example, the very low $\delta^{13}\text{C}$ in LMSA chicks from South Georgia exemplifies the southerly location of the island, and that adults favour feeding areas even further to the south during chick-rearing (Phillips et al. 2005a). Results from BBA and WCP from South Georgia are more complex, because their chicks have an apparent subantarctic $\delta^{13}\text{C}$ signature, whereas adults mainly forage in northern Antarctic waters during chick-rearing (Phillips et al. 2004, 2006). The most likely explanation of that discrepancy is that each species forages in both oceanic and neritic waters, and the higher baseline isotope signature of the latter increases the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in these consumers; hence their mean values suggest the use of intermediate (i.e. subantarctic) waters (e.g. Cherel & Hobson 2007, Phillips et al. 2009).

The second segregating mechanism leading to resource partitioning during breeding operates through selection of prey at differing trophic levels,

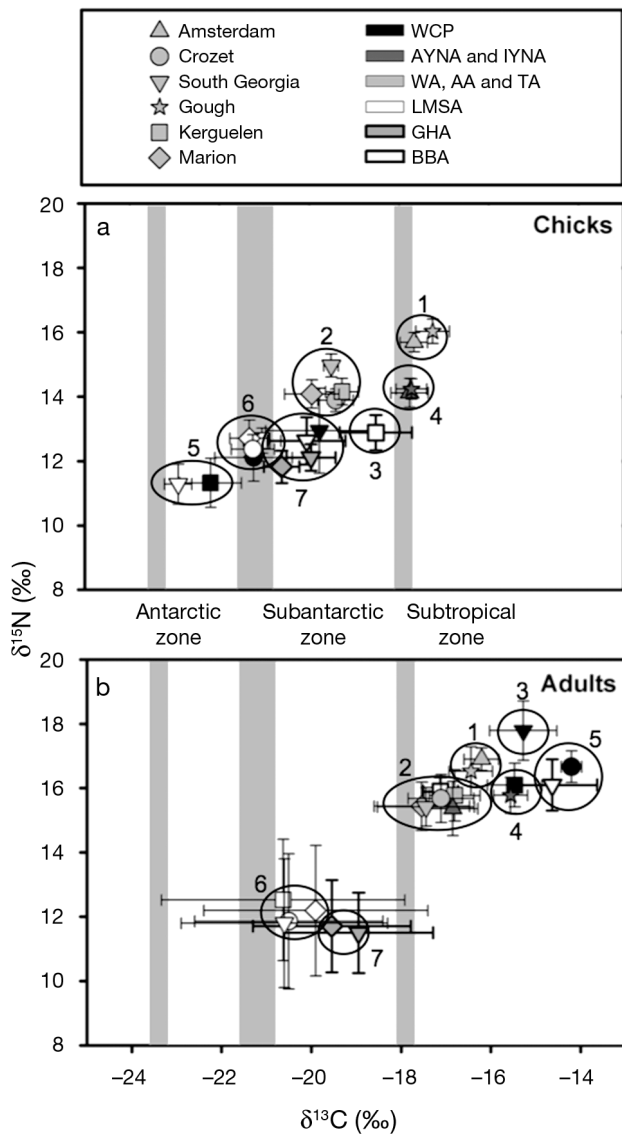


Fig. 2. Mean \pm SD $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in feathers of (a) chicks and (b) adults of 9 large procellariiform seabirds from 6 southern hemisphere breeding localities. Circles and associated numbers: clusters resulting from hierarchical cluster analyses performed on chick and adult feather isotopic ratios (see text for details). Grey areas: range (mean \pm SD) of $\delta^{13}\text{C}$ in feathers of snow petrels, king penguins and northern rockhopper penguins (in this order on the diagrams) that are known to forage in the high-Antarctic Zone, at the Polar Front and in the Subtropical Zone, respectively (see 'Materials and methods'). See Table 1 for bird abbreviations

with the 3 *Diomedea* albatrosses feeding consistently at a higher trophic level than the other species (Fig. 2a). WA chicks are mainly fed with large squid and fish (Cherel & Klages 1998), which are likely to be also the main prey of TA and AA, whose diets are poorly-known. By contrast, the food of the other albatrosses and white-chinned petrel is mostly composed

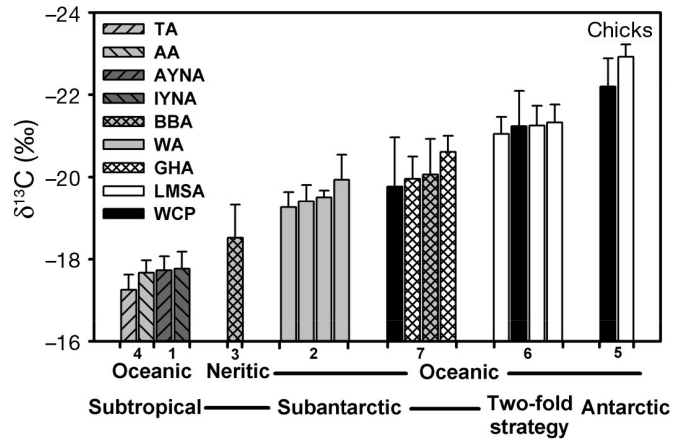


Fig. 3. Histogram of $\delta^{13}\text{C}$ in feathers (mean \pm SD) of chicks of 9 large procellariiform seabirds from 6 southern hemisphere breeding localities (each bar a different population) grouped according to feeding habitats/strategies of their parents. Numbers along x-axis: cluster numbers from Fig. 2a. Two-fold strategy indicates foraging in both Antarctic and subantarctic zones. See Table 1 for bird abbreviations

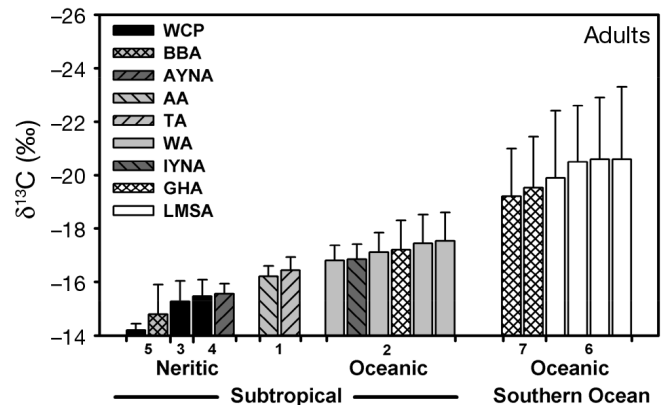


Fig. 4. Histogram of $\delta^{13}\text{C}$ in feathers (mean \pm SD) of adults of 9 large procellariiform seabirds from 6 southern hemisphere breeding localities (each bar a different population) grouped according to their feeding habitat during the non-breeding periods. Numbers along x-axis: cluster numbers from Fig. 2b. See Table 1 for bird abbreviations

of smaller squid, fish and Antarctic krill *Euphausia superba* (Cherel & Klages 1998) that have lower nitrogen signatures (Cherel et al. 2008, Anderson et al. 2009). Finally, the higher $\delta^{15}\text{N}$ of TA, AA, IYNA and AYNA when compared to WA, the other *Thalasarche* species and LMSA, respectively, are likely to result from higher $\delta^{15}\text{N}$ baseline levels (that propagate up the food web) in subtropical than subantarctic waters (Quillfeldt et al. 2005, Jaeger et al. 2010b).

During the breeding season, the WCP and most of the albatross species exhibited low variance in their isotopic ratios between the different breeding populations. Why do birds foraging in different ocean

Table 3. *Phoebastria palpebrata* and *Thalassarche chrysostoma*. Trophic niche width (TNW) and its within-individual component (WIC) and between individual component (BIC) calculated from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in feathers of adult albatrosses from generalist populations (see 'Materials and methods')

Species	N	TNW (‰) ($\delta^{13}\text{C}/\delta^{15}\text{N}$)	WIC (‰) ($\delta^{13}\text{C}/\delta^{15}\text{N}$)	BIC (‰) ($\delta^{13}\text{C}/\delta^{15}\text{N}$)	WIC/TNW ($\delta^{13}\text{C}/\delta^{15}\text{N}$)
Light-mantled sooty albatross					
Crozet	10	3.9/3.6	2.6/2.1	1.3/1.5	0.7/0.6
Grey-headed albatross					
South Georgia	10	2.7/1.5	1.4/1.3	1.3/0.2	0.5/0.8
Marion	11	3.1/2.0	1.5/1.3	1.6/0.7	0.5/0.6

basins retain the same $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures? The stratified structure of the main oceanographic features (fronts and water masses) encircling Antarctica (Fig. 1) shapes the Southern Ocean isoscape, thus inducing a well-defined latitudinal—but no obvious longitudinal— $\delta^{13}\text{C}$ gradient. Hence, consumers breeding at different island groups that forage at the same latitudes have broadly similar $\delta^{13}\text{C}$ (Cherel & Hobson 2007, Jaeger et al. 2010b). The low inter-population variation in $\delta^{15}\text{N}$ further indicates that each species forages at a very similar trophic position whatever the region (Table 2). However, chick $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ generally differed between species at each location, indicating that sympatric breeding species forage in different spatial or trophic niches. A notable exception occurred at South Georgia; GHA, BBA and WCP, which all feed at least partly on krill (Croxall et al. 1997) showed large overlaps in their isotopic ratios (Fig. 2a). This may be explained by reduced competition due to the superabundance of Antarctic krill in the western South Atlantic (Atkinson et al. 2004). The location of South Georgia thus contrasts with that of Marion, Crozet and Kerguelen Islands, where no Antarctic krill occur and where seabirds consequently show greater segregation in terms of foraging strategy (Weimerskirch et al. 1986, Ridoux 1994).

Non-breeding season foraging ecology, TNW and seasonal variations

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in feathers of adults indicated that the albatrosses fed in a variety of foraging habitats and at different trophic levels during the non-breeding period (Cherel et al. 2013). According to $\delta^{13}\text{C}$ there were 3 main feeding habitats: subtropical neritic waters, subtropical oceanic waters, and oceanic waters of the Southern Ocean (Fig. 4). Most of the albatross species sampled in our study leave the Southern Ocean for subtropical neritic (BBA, AYNA,

IYNA) or oceanic (WA, AA, TA) waters, and only 2 species (LMSA, GHA) remain in low latitudes (Cherel et al. 2013). Feather $\delta^{15}\text{N}$ are more difficult to elucidate because of the considerable variation in baseline $\delta^{15}\text{N}$ in different ecosystems (Post 2002), but 2 important features arose concerning the nitrogen isotopic ratios of adult feathers. First, as feathers of adult LMSA and GHA had similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to those of their chicks, they probably fed on the same

diet (a mixture of fish, squid and crustaceans) year-round. Second, adult WA had similar isotopic values to AA and TA chicks, indicating they fed on high trophic level prey, most likely targeting large squid and fish in subtropical waters, during the non-breeding period.

All WCP populations exhibited high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, suggesting foraging in productive neritic waters marked by high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baselines during the non-breeding period. Band recoveries and tracking studies of WCP from Crozet (Weimerskirch et al. 1985) show that they visit the Benguela upwelling system in winter, and their carbon signatures were identical to that of Cape gannets *Morus capensis* that forage over the South African shelf all year long (Jaquemet & McQuaid 2008). WCP from Kerguelen had $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ close to those of BBA from South Georgia, indicating foraging in the Benguela upwelling system that is confirmed by a recent study using geolocators (Péron et al. 2010, ACAP 2011). By contrast, WCP from South Georgia, which are known to winter on the Patagonian shelf or in the Humboldt Current off Chile (Phillips et al. 2006), had distinct isotopic values.

Considering TNWs, most species exhibited low values, indicating that they were isotopic specialists, with negligible WIC during the non-breeding period. These populations moult therefore in areas that may be very large but have similar carbon and nitrogen isotopic ratios. By contrast, all LMSA and GHA populations showed large variances in their isotope ratios, which indicate considerable intra-specific differences in foraging habitat. Indeed, the isotopic measurement of several body feathers per individual indicated that LMSA from Crozet are generalists (large TNW and WIC and WIC/TNW ≥ 0.5), reflecting the use of 2 distinct diets and moulting regions: Antarctic krill in the Antarctic zone, and higher trophic level prey in subantarctic waters (Jaeger et al. 2010a). The large variance in isotope ratios of

LMSA from other populations suggests the situation is similar at South Georgia, Kerguelen and Marion islands. Data from non-breeding GHA from both populations similarly showed large TNW and WIC, and $WIC/TNW \geq 0.5$ (Table 3), indicating that GHA are also generalists. Their feather isotopic signatures indicate that moulting GHA remained mainly in the subantarctic zone (60% of the feathers analyzed), although other body feathers were synthesized in the Antarctic zone (14%) or the subtropics (26%).

As in the breeding season, isotopic values in feathers of adults suggest a strong isotopic/trophic segregation between species during the non-breeding period. However, similar $\delta^{13}C$ and $\delta^{15}N$ indicate only that birds forage broadly in the same latitudes, but not necessarily in the same geographical area (region). Comparison of chick and adult $\delta^{13}C$ within each species confirms 3 annual strategies for procellariiform seabirds breeding in the Southern Ocean (Jaeger et al. 2010a). A few species are 'Southern Ocean residents' (e.g. LMSA and GHA), which forage predominantly all year long within the limits of the Southern Ocean. In contrast, most other species migrate north of the STF, with 'oceanic migrants' (WA) foraging predominantly in subtropical oceanic waters and occasionally visiting coastal waters, and 'neritic migrants' (WCP, BBA and AYNA) primarily wintering over productive shelf waters. Adult AA and TA exhibited carbon and nitrogen isotopic ratios intermediate between subtropical oceanic and neritic migrants. Due to a lack of a suitable isoscape for lower latitude waters, it is difficult to draw conclusions about their non-breeding diet or foraging habitat. It is possible that they share characteristics with the congeneric WA, which showed low seasonal variation in trophic level, feed at a high trophic level during the non-breeding period and visit subtropical oceanic and neritic waters.

Breeding frequency and biological productivity of moulting grounds

Two constraints shape the pattern of moult in birds. First, the scaling of primary growth rate with body mass explains why feather replacement requires disproportionately more time in large birds (Rohwer et al. 2009), i.e. ~3 non-breeding periods for a complete renewal in albatrosses (Prince et al. 1997). Second, moult is a costly process in terms of energy and nutrients, which in most seabirds means it is not undertaken at the same time as reproduction, which is also particularly demanding (Bridge 2006), although there

are some exceptions (Hunter 1984, Spear & Ainley 1998). Hence, albatrosses replace their feathers at sea during the non-breeding period, which varies in length from ~4 to 16 mo depending on the breeding frequency and duration of the nesting period for each species. The non-breeding period spans one winter (~4 mo) in most *Thalassarche* albatrosses that breed annually, a full year (~12 mo) in great albatrosses *Diomedea* spp. in which the breeding season is unusually prolonged, and a full year plus the following winter (~16 mo) in *Phoebastria* albatrosses and the minority of *Thalassarche* species (GHA) that breed biennially. As retention of old, worn feathers may ultimately require albatrosses to skip an extra breeding season (Rohwer et al. 2011), we hypothesise that species with shorter non-breeding periods, and therefore less time available to acquire the energy and nutrients for moult, are more likely to target areas of high resource abundance.

Our isotope results, together with banding and tracking data, indicate that the annual breeders (BBA, AYNA, IYNA and WCP) that are more temporally constrained do indeed moult in productive neritic areas during their short non-breeding season (~4 mo). Noticeably, BBA from South Georgia, AYNA from Gough and WCP from Crozet and Kerguelen renew their feathers in the Benguela current, and WCP from South Georgia in the Patagonian Shelf, all of which are amongst the most productive marine ecosystems worldwide, with high resource predictability all year round (Perissinotto & Walker 1998). Large *Diomedea* albatrosses are biennial breeders, because the length of the breeding period (~12 mo) together with the need to moult precludes breeding every year. They are less constrained than annual breeders in the choice of moulting grounds because they must inevitably wait ~12 mo before they can breed again. The last group of albatrosses includes the 2 medium-sized, biennial species, LMSA and GHA, which both spend their long non-breeding period (~16 mo) over less productive oceanic waters.

Another crucial activity during the non-breeding period is the recovery of body condition following breeding, which is energetically highly demanding. We could hypothesize that the higher the productivity in the non-breeding region, the faster would be the restoration of body condition. Concurrent with feather replacement, species migrating to highly productive areas should therefore restore their body condition in a shorter time, making annual breeding more likely. The ultimate explanation for adoption of a biennial rather than an annual breeding strategy in albatrosses is likely to be the longer duration of the

chick-rearing period in some species, reflecting the large size of the chick in the great *Diomedea* albatrosses, and provisioning rate limitations given the distance to feeding grounds (Jouventin & Dobson 2002). Here we provide evidence that the time available for moult may also have direct implications for habitat selection during the non-breeding period.

Several additional arguments support our hypothesis. Firstly, the biennial breeder and oceanic forager (GHA) replaces fewer feathers during the non-breeding period than the annual breeder and neritic forager (BBA) (Prince et al. 1997). Secondly, albatrosses renew fewer primaries in years marked by a decrease in marine productivity (Cobley & Prince 1998). Finally, the breeding frequency, moulting pattern and foraging areas of the 4 Pacific albatrosses of the genus *Phoebastria* illustrate well the moult–breeding trade-offs in relation to marine productivity. Like their southern counterparts, waved and short-tailed albatrosses (*P. irrorata* and *P. albatrus*, respectively), which are annual breeders, forage over neritic waters during their short moulting period (Gales 1993, Suryan et al. 2007, ACAP 2011). By contrast, the Laysan and black-footed albatrosses (*P. immutabilis* and *P. nigripes*, respectively) favoured more oceanic waters at that time (Gales 1993, Fisher et al. 2009, ACAP 2011), and they consequently show unusual moulting and breeding patterns by alternating large (long) and small (short) primary moults that determine their breeding frequency, with individuals showing both annual and biennial breeding patterns (Edwards 2008).

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