Vol. 505: 267–280, 2014
doi: 10.3354/meps10795

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published May 28

FREE ACCESS

Seabird year-round and historical feeding ecology: blood and feather $\delta^{13}C$ and $\delta^{15}N$ values document foraging plasticity of small sympatric petrels

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ABSTRACT: The foraging ecology of small seabirds remains poorly understood because of the difficulty of studying them at sea. Here, the extent to which 3 sympatric seabirds (blue petrel, thin-billed prion and common diving petrel) alter their foraging ecology across the annual cycle was investigated using stable isotopes. $\delta^{13}C$ and $\delta^{15}N$ values were used as proxies of the birds' foraging habitat and diet, respectively, and were measured in 3 tissues (plasma, blood cells and feathers) that record trophic information at different time scales. Long-term temporal changes were investigated by measuring feather isotopic values from museum specimens. The study was conducted at the subantarctic Kerguelen Islands and emphasizes 4 main features. (1) The 3 species highlight a strong connection between subantarctic and Antarctic pelagic ecosystems, because they all foraged in Antarctic waters at some stages of the annual cycle. (2) Foraging niches are stage-dependent, with petrels shifting their feeding grounds during reproduction either from oceanic to productive coastal waters (common diving petrel) or from subantarctic to high-Antarctic waters where they fed primarily on crustaceans (blue petrel and thin-billed prion). (3) The common diving petrel segregated from the surface-feeders blue petrel and thin-billed prion by a coastal habitat and lower trophic level prey, while the blue petrel segregated from the thin-billed prion by foraging further south and including more fish in its diet. (4) Feather $\delta^{13}C$ and $\delta^{15}N$ values from historical and recent specimens of thin-billed prion depicted a pronounced temporal shift to higher latitudes in its main moulting ground, where it feeds on higher trophic level prey. The study contributes to growing evidence that seabirds exhibit considerable foraging plasticity and sheds new light on their flexibility at different time scales (from intra-seasonal to decadal).

KEY WORDS: Diet · Museum specimens · Procellariiformes · Resource partitioning · Southern Ocean · Stable isotopes

INTRODUCTION

Seabirds are mid- to high-trophic level consumers whose population dynamics are generally driven by the abundance and availability of their prey (bottom-up control; Frederiksen et al. 2006). In temperate, and especially polar regions, seabirds have to face high spatial and temporal variability in primary and secondary productivities that affects the whole pelagic ecosystem on a seasonal basis. Flexible foraging behaviour is an important mechanism by which seabirds cope with the seasonal progression of environmental events (extrinsic factors) and the unique energetic constraints of each discrete breeding stage and moult (intrinsic factors) (e.g. Weimerskirch et al. 1993, Charrassin et al. 1998). However, despite decades of intensive study, key facets of the foraging ecology of seabirds remain poorly understood because of the dif-

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ficulty of studying them at sea to obtain even simple baseline data, especially outside the breeding period when adult birds are much less accessible.

The Southern Ocean (south of the Subtropical Front) is characterized by both a strong seasonality and the diversity and biomass of its populations of seabirds (~363 million breeding individuals), which are numerically dominated by Procellariiformes (van Franeker et al. 1997). Our main goal was to detail the year-round feeding ecology of 3 abundant species of small sympatric petrels from the Southern Ocean, namely the blue petrel *Halobaena caerulea* (BP), thin-billed prion *Pachyptila belcheri* (TBP) and common diving petrel *Pelecanoides urinatrix* (CDP), for which long-term demographic data have been continuously collected since the breeding season 1986–87 at the Kerguelen Islands (Chastel et al. 1995, Barbraud & Weimerskirch 2005, Nevoux & Barbraud 2006). Traditionnally, feeding ecology is investigated using the conventional method of prey determination (e.g. Bocher et al. 2000a, Cherel et al. 2002a,b) and/or various electronic devices recording foraging behaviour. However, food sampling in seabirds is often restricted to the chick-rearing period, and bio-logging gives no indication on the prey consumed, thus inducing a general lack of dietary information during most of the annual cycle. Hence, we combined food sampling with the use of the isotopic niche as a proxy for the trophic niche (Newsome et al. 2007), focusing on discrete stages of the breeding cycle and on the moulting period. The isotopic method was validated in the southern Indian Ocean (encompassing the petrel feeding areas), with $\delta^{13}C$ values of seabirds indicating their foraging habitats (Cherel & Hobson 2007, Jaeger et al. 2010) and their $\delta^{15}N$ values increasing with trophic level (Cherel et al. 2010). The isotopic niche was determined by using 3 complementary tissues (plasma, blood cells and feathers) that record trophic information at different time scales. Plasma and blood cells are metabolically active tissues that integrate periods of days and weeks before sampling, respectively, whereas feathers reflect the diet at the time they were grown, because keratin is inert after synthesis (Hobson & Clark 1992, 1993, Bearhop et al. 2002). In seabirds, feather isotope values generally represent the feeding habits during the inter-nesting period, because adult birds gradually replace most of their plumage at that time (Cherel et al. 2006, Phillips et al. 2009). Another additional interest of the isotopic method is to provide relevant foraging information quickly and cheaply for large numbers of individuals (Cherel et al. 2013), including species whose small size precludes carrying most electronic devices.

Our aim was 4-fold. Firstly, intra-year variations in feeding ecology were investigated at the species level to depict the various foraging strategies used by a given species. Chick food and feather isotopic values of BP, TBP and CDP were previously determined at the Kerguelen Islands (Bocher et al. 2000a, Cherel et al. 2002a,b, 2006, Connan et al. 2008), but with no detailed isotopic baseline information over the whole annual cycle. Secondly, isotopic values of the 3 species were compared at each main successive breeding stage and during moult to highlight how closely related (BP and TBP) and unrelated (CDP) genera coexist in sympatry. Thirdly, it is generally assumed that adult seabirds consume the same prey for themselves as they provision their chicks. Some dietary and isotopic information has challenged this traditional view (Davoren & Burger 1999, Hodum & Hobson 2000, Cherel 2008), and we hypothesized that, unlike more coastal species (CDP), far-ranging oceanic species (BP and TBP) would present different blood isotopic values in adults and chicks (Cherel et al. 2005). The rationale was that oceanic seabirds feed for themselves on distant foraging grounds and collect food for their chicks on their way back to the colonies. Finally, potential long-term temporal changes in foraging strategies were investigated by comparing the isotopic values of adult feathers between recent and historical specimens. A recent study pointed out a shift in the moulting area of TBP breeding at the Falkland Islands over the last decades (Quillfeldt et al. 2010). Hence, our goal was (1) to verify if a similar pattern occurred in the only other large population of the species, which breeds at the Kerguelen Islands, and (2) to consider whether these findings can be generalized to 2 other subantarctic seabirds (BP and CDP).

MATERIALS AND METHODS

Study site, birds and sampling

Fieldwork was carried out at the Kerguelen Islands (southern Indian Ocean), which is located in the southern part of the Polar Frontal Zone, in the immediate vicinity of the Polar Front (Park & Gambéroni 1997). The study colonies were located at Ile Mayes (49° 28′ S, 69° 57′ E) in the Golfe du Morbihan, where large populations of blue petrels *Halobaena caerulea*, thin-billed prions *Pachyptila belcheri* and common diving petrels *Pelecanoides urinatrix* breed. To avoid potential biases due to inter-annual variations, all sampling took place in 2003 during 2 consecutive

austral summers corresponding to the end and the beginning of the 2002–03 and 2003–04 breeding cycles, respectively. BP and TBP adults were caught either in burrows or by mist-netting, while CDP were caught by mist-netting close to their burrows. Randomly chosen birds (n = 6 to 31) were caught at various stages of the annual cycle, depending on the biology of each species (Table 1). No individual bird was sampled twice. Basically, adult birds were caught on their spring arrival at the colony to breed and during incubation and the chick-rearing period. Well-feathered chicks were handled near fledging. BP adults transiently return to their burrows in fall, with failed breeders and non-breeding birds going back to the colony earlier than successful breeders (Fugler et al. 1987, Marchant & Higgins 1990). Hence, 2 additional groups of BP were caught in April and May (the early and late post-nuptial birds, respectively). At Kerguelen, CDP is one of the rare seabirds present all year round in colonies (Weimerskirch et al. 1989, Bocher et al. 2000b). Thus, 2 groups of birds were sampled during the inter-breeding season, namely the post-nuptial (May) and winter (July) groups. Most of those birds were likely to be 1 yr old individuals rather than adults (Bocher et al. 2000b).

A 1 ml blood sample was taken from a wing vein of all birds and centrifuged; 70% ethanol was added to blood cells and plasma, which were stored at −20°C until analysis. A few body feathers were collected from the lower back of some adult birds and from chicks. Adults of the 3 petrel species renew their whole plumage on a yearly basis; hence, all collected feathers corresponded to the 2003 moult. In TBP and BP, adult moult occurs after completion of the breeding cycle, mainly in March to May and February to March, respectively, so that BP have fresh plumage at the post-nuptial stage in April to May (Fugler et al. 1987, Marchant & Higgins 1990). In contrast, CDP adults begin to moult during the late chick-rearing period and resume feather synthesis at sea afterwards (Payne & Prince 1979, Marchant & Higgins 1990). Historical feather samples (from 1914 to 1977) were obtained from the lower back of specimens held in the ornithological collection of the Muséum National d'Histoire Naturelle of Paris (France). Age of those specimens was unknown, but they were neither chicks nor fledglings. Body feathers were taken only when complete capture information was present for a particular study specimen (n = 38). Food samples were collected by spontaneous regurgitation of the BP and TBP adults that were blood-sampled during the chick-rearing period. Stomach contents were immediately frozen at −20°C and returned to Chizé, France, for analysis. No food samples were collected from CDP adults, because food sampling requires stomach lavage that is difficult to conduct in diving petrels. Hence, it was assumed that the main CDP prey in 2003 was the hyperiid amphipod *Themisto gaudichaudii* that consistently formed the bulk of the species food during 3 consecutive years in 1995, 1996 and 1997 (Bocher et al. 2000a).

Dietary analysis

In the laboratory, each sample was thawed overnight over a sieve so that the liquid fraction was separated from the solid items. The solid fraction was then placed in a large, flat-bottomed tray, and the accumulated items were discarded (squid beaks, squid and fish lenses, stones, plastic debris). Fresh remains were divided into broad prey classes (crustaceans, cephalopods, fish and others) that were weighed to estimate their proportions by fresh mass in the diet. Then, each prey item was counted and identified to the lowest possible taxon, using published keys and our own reference collection. The abundance of each prey taxon was described by its numerical importance, calculated as the total number of individuals of a given taxon found in all the samples as a percentage of the total number of all prey items ingested in all the food samples.

Sexing

Birds were sexed using a molecular method. DNA was extracted from blood cells and the chromo helicase DNA-binding (CHD) gene was amplified in a polymerase chain reaction procedure as detailed in Weimerskirch et al. (2005).

Stable isotope analysis

Blood cells and plasma samples were freeze-dried and powdered. In contrast to blood cells, the high and variable lipid content of plasma typically necessitates lipid extraction (Cherel et al. 2005). Hence, lipids were removed from plasma with cyclohexane following the method used for seabird muscle and liver (Kojadinovic et al. 2008). One body feather of each individual bird was cleaned of surface lipids and contaminants using a 2:1 chloroform:methanol solution for 2 min, followed by 2 successive methanol

rinses. Feathers were then air dried and homogenised by cutting them into small fragments. Tissue subsamples were weighed (~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). Stable isotope concentrations were expressed in conventional notation ($\delta X = [R_{sample}/R_{standard}) - 1] \times 1000$), where X is ^{13}C or ^{15}N and R is the corresponding ratio ^{13}C:^{12}C or ^{15}N:^{14}N. $R_{standard}$ is Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors <0.15‰ and <0.20‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Table 1. Blood and feather $\delta^{13}C$ and $\delta^{15}N$ values at various stages of the annual cycle of blue petrels *Halobaena caerulea*, thin-billed prions *Pachyptila belcheri* and common diving petrels *Pelecanoides urinatrix* from Mayes Island, Kerguelen Archipelago. Normalized $\delta^{13}C$ values are either corrected plasma $\delta^{13}C$ values according to the C:N mass ratios, which is a proxy of lipid content in animal tissues, or corrected feather $\delta^{13}C$ values according to the increase in atmospheric CO_2 in response to human fossil fuel burning (see 'Data analyses'). Values are means ± SD, with ranges in parentheses. Ind. = Individuals

Period (2003)	Tissue type	Ind. (n)	$\delta^{13}C$ (‰)	Normalized $\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N mass ratios
Blue petrel						
Chick-rearing (Jan)	Blood cells	31	−24.1 ± 0.8 (−25.4 to −22.5)		8.1 ± 0.4 (7.3–9.0)	3.42 ± 0.18
	Plasma	31	−25.0 ± 0.7 (−26.2 to −23.6)	−24.0 ± 0.7 (−25.2 to −22.6)	8.5 ± 0.5 (7.6–9.6)	4.40 ± 0.18
Chicks (Feb)	Blood cells	13	−23.2 ± 0.4 (−24.2 to −22.6)		9.2 ± 0.4 (8.5–9.6)	3.36 ± 0.19
	Plasma	13	−24.3 ± 0.7 (−25.0 to −23.1)	−23.0 ± 0.6 (−23.9 to −21.9)	9.4 ± 0.5 (8.5–10.1)	4.71 ± 0.34
	Body feathers	13	−21.8 ± 0.5 (−22.5 to −20.9)	−21.4 ± 0.5 (−22.2 to −20.6)	9.8 ± 0.5 (8.7–10.4)	3.19 ± 0.01
Early post-nuptial	Blood cells	13	−26.0 ± 0.3 (−26.7 to −25.5)		7.0 ± 0.2 (6.7–7.3)	3.35 ± 0.15
(Apr)	Plasma	13	−26.4 ± 0.7 (−27.7 to −25.3)	−25.4 ± 0.7 (−26.7 to −24.1)	8.1 ± 0.7 (7.1–9.5)	4.39 ± 0.23
	Body feathers	13	−24.5 ± 0.7 (−25.5 to −23.4)	−24.4 ± 0.7 (−25.5 to −23.4)	7.8 ± 0.3 (7.1–8.3)	3.17 ± 0.01
Late post-nuptial	Blood cells	12	−25.4 ± 0.6 (−26.3 to −24.4)		7.6 ± 0.6 (6.5–8.8)	3.30 ± 0.09
(May)	Plasma	12	−26.0 ± 0.9 (−27.5 to −24.5)	−25.1 ± 0.9 (−26.5 to −23.6)	8.3 ± 0.6 (7.7–9.6)	4.26 ± 0.16
	Body feathers	12	−24.6 ± 1.0 (−26.6 to −23.2)	−24.5 ± 1.0 (−26.5 to −23.1)	8.1 ± 0.8 (7.0–9.6)	3.17 ± 0.01
Spring arrival (Sep)	Blood cells	22	−23.1 ± 1.6 (−25.3 to −20.2)		9.5 ± 1.1 (7.7–11.5)	3.30 ± 0.03
	Plasma	22	−23.9 ± 1.4 (−25.9 to −21.3)	−23.2 ± 1.3 (−25.2 to −20.7)	10.3 ± 0.9 (9.2–11.7)	4.14 ± 0.28
Laying (Nov)	Blood cells	13	−24.1 ± 0.9 (−25.4 to −22.8)		8.9 ± 0.4 (8.4–9.8)	3.31 ± 0.10
	Plasma	13	−25.2 ± 0.6 (−26.2 to −24.0)	−24.4 ± 0.6 (−25.6 to −23.1)	10.1 ± 0.4 (9.4–10.6)	4.11 ± 0.11
Hatching (Dec)	Blood cells	15	−23.9 ± 1.2 (−25.2 to −21.6)		8.6 ± 0.4 (8.1–9.3)	3.31 ± 0.06
	Plasma	15	−24.5 ± 1.5 (−25.8 to −21.7)	−23.9 ± 1.4 (−25.2 to −21.2)	9.4 ± 0.4 (8.7–10.2)	4.00 ± 0.10
Moult	Body feathers	25	−24.5 ± 0.9 (−26.6 to −23.2)	−24.4 ± 0.9 (−26.5 to −23.1)	7.9 ± 0.6 (7.0–9.6)	3.17 ± 0.01
Moult (1914–1977)	Body feathers	15	−24.1 ± 1.5 (−25.8 to −21.4)	−24.0 ± 1.5 (−25.8 to −21.3)	8.7 ± 1.0 (6.9–11.0)	3.23 ± 0.08
Thin-billed prion						
Chick-rearing (Feb)	Blood cells	6	−23.7 ± 0.5 (−24.2 to −23.1)		7.8 ± 0.2 (7.6–8.2)	3.32 ± 0.07
	Plasma	6	−25.1 ± 0.4 (−25.4 to −24.5)	−24.2 ± 0.3 (−24.6 to −23.7)	8.0 ± 0.4 (7.3–8.3)	4.20 ± 0.21
Chicks (Feb)	Blood cells	9	−23.1 ± 0.8 (−24.2 to −22.1)		8.4 ± 0.4 (7.7–9.0)	3.33 ± 0.15
	Plasma	9	−24.4 ± 0.7 (−25.4 to −23.4)	−23.3 ± 0.8 (−24.1 to −21.9)	8.8 ± 0.5 (7.7–9.4)	4.51 ± 0.30
	Body feathers	9	−21.5 ± 0.5 (−22.2 to −20.8)	−21.2 ± 0.5 (−21.8 to −20.4)	9.1 ± 0.4 (8.6–9.7)	3.19 ± 0.01
Spring arrival (Oct)	Blood cells	21	−21.5 ± 1.4 (−24.7 to −19.8)		8.6 ± 0.7 (7.6–10.3)	3.32 ± 0.12
	Plasma	21	−22.5 ± 1.1 (−24.4 to −20.2)	−22.0 ± 1.2 (−23.9 to −19.6)	9.9 ± 0.5 (9.0–10.9)	3.86 ± 0.15
Incubation (Dec)	Blood cells	13	−22.3 ± 1.1 (−23.8 to −20.5)		8.5 ± 0.1 (8.3–8.7)	3.33 ± 0.14
	Plasma	13	−22.6 ± 1.0 (−24.3 to −21.1)	−22.1 ± 1.0 (−23.6 to −20.7)	9.1 ± 0.2 (8.8–9.5)	3.82 ± 0.18
Moult	Body feathers	20	−23.6 ± 1.6 (−26.7 to −18.6)	−23.5 ± 1.6 (−26.7 to −18.3)	8.0 ± 0.5 (7.4–9.3)	3.18 ± 0.01
Moult (1923–1971)	Body feathers	10	−21.4 ± 0.8 (−23.4 to −20.1)	−21.3 ± 0.9 (−23.3 to −20.0)	9.0 ± 0.4 (8.5–9.7)	3.25 ± 0.05
Common diving petrel						
Chick-rearing (Feb)	Blood cells	13	−18.5 ± 0.9 (−20.2 to −17.4)		11.0 ± 0.7 (9.3–11.9)	3.18 ± 0.04
	Plasma	13	−18.2 ± 0.5 (−18.9 to −17.3)	−17.4 ± 0.4 (−18.0 to −16.8)	11.8 ± 0.3 (11.3–12.3)	4.15 ± 0.26
Chicks (Mar)	Blood cells	17	−17.8 ± 0.3 (−18.4 to −17.4)		11.1 ± 0.3 (10.6–11.5)	3.17 ± 0.05
	Plasma	17	−19.3 ± 0.7 (−20.7 to −18.0)	−17.9 ± 0.4 (−18.9 to −17.0)	11.8 ± 0.6 (10.6–12.8)	4.74 ± 0.35
	Body feathers	17	−17.0 ± 0.5 (−17.8 to −16.4)	−16.7 ± 0.5 (−17.5 to −16.1)	12.1 ± 0.4 (11.5–12.7)	3.24 ± 0.02
Post-nuptial (May)	Blood cells	12	−18.7 ± 2.1 (−21.5 to −16.4)		9.3 ± 1.7 (7.0–11.2)	3.16 ± 0.01
	Plasma	12	−17.5 ± 0.5 (−18.8 to −16.9)	−16.9 ± 0.4 (−17.7 to −16.4)	11.9 ± 0.4 (11.3–12.5)	3.98 ± 0.19
Winter (Jul)	Blood cells	12	−16.8 ± 0.4 (−17.8 to −16.5)		11.7 ± 0.3 (11.0–12.0)	3.17 ± 0.01
	Plasma	12	−17.8 ± 0.4 (−18.7 to −17.2)	−17.1 ± 0.4 (−18.0 to −16.7)	12.5 ± 0.3 (11.9–13.1)	4.07 ± 0.15
Spring arrival (Sep)	Blood cells	12	−22.6 ± 0.8 (−23.1 to −20.3)		7.5 ± 0.8 (6.2–8.8)	3.14 ± 0.06
	Plasma	12	−22.0 ± 1.5 (−22.9 to −17.6)	−21.5 ± 1.5 (−22.4 to −16.9)	9.2 ± 1.1 (7.7–12.3)	3.86 ± 0.15
Incubation (Dec)	Blood cells	17	−19.2 ± 1.9 (−22.4 to −17.0)		9.8 ± 1.1 (8.2–11.8)	3.21 ± 0.05
	Plasma	16	−20.6 ± 2.3 (−23.2 to −17.6)	−19.9 ± 2.4 (−22.7 to −16.9)	10.1 ± 1.4 (8.5–12.1)	4.07 ± 0.15
Moult	Body feathers	29	−21.7 ± 2.5 (−23.8 to −15.5)	−21.4 ± 2.6 (−23.7 to −15.1)	8.5 ± 2.0 (6.2–13.4)	3.25 ± 0.02
Moult (1914–1970)	Body feathers	13	−20.2 ± 2.7 (−23.9 to −15.1)	−20.1 ± 2.7 (−23.9 to −15.0)	9.8 ± 2.1 (7.3–13.5)	3.25 ± 0.04

Data analyses

Data were statistically analysed using SYSTAT 12. Values are means ± SD. In most cases, isotopic comparisons were made on the same tissue type, because it is the most straightforward approach and avoids biases due to tissue-specific metabolic routing and, thus, to tissue-specific isotopic discrimination factors. For example, enrichment in ^{13}C generally increases in the order blood cells < plasma < feathers (Nakashita et al. 2013, Cherel et al. 2014). However, comparisons were also made between tissues with different metabolic rates that reflect dietary records over various periods to collect dietary information at different time scales. The constantly low C:N mass ratios of feathers and blood cells verified their low lipid content (Table 1). In contrast, most C:N mass ratios of lipid-extracted plasmas were >4.0, thus indicating incomplete lipid removal. Lipid-associated biases on $\delta^{13}C$ values were reduced by mathematically normalizing plasma $\delta^{13}C$ using the following equation for aquatic animals: $\delta^{13}C_{normalized} = \delta^{13}C - 3.32 + (0.99 \times C{:}N)$ (Post et al. 2007).

The Southern Ocean is marked by a well-defined latitudinal baseline $\delta^{13}C$ gradient that is reflected in the tissue of consumers (Cherel & Hobson 2007, Jaeger et al. 2010, Quillfeldt et al. 2010). The isotopic consumer data allowed estimation of the carbon position of the main oceanic fronts within the southern Indian Ocean, and thus delineation of robust isoscapes of the main foraging zones for top predators, depending on the targeted tissues. Based on blood (feather) $\delta^{13}C$ isoscapes, values less than −22.9‰ (−21.2‰) and −22.9 to −20.1‰ (−21.2 to −18.3‰) and greater than −20.1‰ (−18.3‰) were considered to correspond to the Antarctic, Subantarctic and Subtropical Zones, respectively (Jaeger et al. 2010).

When long time series of historical and recent samples of $\delta^{13}C$ are analysed, the raw $\delta^{13}C$ values have to be adjusted according to the increase in atmospheric CO_2 in response to human fossil fuel burning (Hilton et al. 2006). Firstly, the resulting rise in aqueous CO_2 increases, in turn, the phytoplankton fractionation, thus reducing its $\delta^{13}C$ isotopic values (Rau et al. 1992). However, the magnitude of the change is rather low (Jaeger & Cherel 2011), and it was not considered here. Secondly, fossil carbon introduced into the atmosphere has a lower $\delta^{13}C$ value than background carbon, thus inducing an accelerating decrease in $\delta^{13}C$ in the biosphere (the Suess effect; Keeling 1979). Since the Suess effect decreases with increasing latitudes (Hilton et al. 2006), the raw $\delta^{13}C$ values were corrected according to the moulting grounds indicated by the feather $\delta^{13}C$ values themselves, namely Antarctic or subantarctic waters. It should be noted that the isotopic change due to the Suess effect is small compared to the large range of feather $\delta^{13}C$ values observed here, with a maximal correction factor of 0.34‰.

RESULTS

Blue petrel *Halobaena caerulea*

The mass of the solid fraction of food samples averaged 14.9 ± 6.5 g (n = 31). In agreement with other sampled years (Cherel et al. 2002b, Connan et al. 2008), chick food in 2003 was dominated by crustaceans (61.7% by fresh mass), with fish ranking second (33.3%) and cephalopods third (4.0%). Owing to their small size and mass, crustaceans accounted for most of the prey by number (98.3%), with the main item being the hyperiid amphipod *Themisto gaudichaudii* (73.4%). Other significant crustaceans were the hyperiids *Cyllopus magellanicus* (9.1%) and *Vibilia antarctica* (6.7%), together with the euphausiids *Euphausia vallentini* (3.5%) and *E. superba* (2.4%). Diet in 2003 was marked by the near lack of *Thysanoessa macrura/vicina*, which was a major crustacean item in other years. Fish diet mainly included several species of myctophid fishes (n = 22 specimens) and the gempylid *Paradiplospinus gracilis* (n = 8).

Isotopic data from both sexes were pooled for statistical analyses, because no significant isotopic differences were found between BP females and males, whatever the tissue type and breeding stage (Mann-Whitney *U*-tests, all $p \geq 0.057$). In the same way, $\delta^{13}C$ and $\delta^{15}N$ values from early and late post-nuptial birds were pooled, because they showed limited differences, with no or small biological meaning. Blood cells from chicks and adults at various stages of the annual cycle were segregated by their stable isotope values (MANOVA, Wilks' Lambda, $F_{10,224} = 19.39$, $p < 0.0001$) (Fig. 1), with both $\delta^{13}C$ and $\delta^{15}N$ values showing significant variations across the breeding cycle (ANOVA, $F_{5,113} = 20.41$ and 35.45, respectively, both $p < 0.0001$). Three features were notable: (1) adult $\delta^{15}N$ values decreased continuously throughout the annual cycle, from 9.5 ± 1.1‰ on arrival in the colony in September to 7.3 ± 0.5‰ at the post-nuptial stage in April to May. (2) $\delta^{13}C$ and $\delta^{15}N$ values were lower in post-nuptial birds than in all the other groups (post hoc Tukey's honestly significant difference multiple comparison tests, all $p < 0.0001$). (3) $\delta^{15}N$ values were higher in chicks than in adults dur-

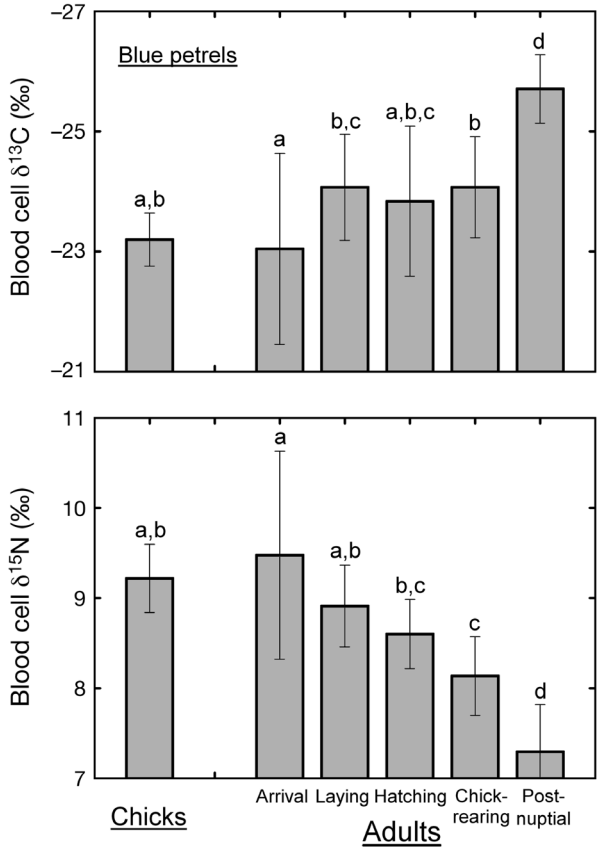

Fig. 1. Blood cell $\delta^{13}C$ (upper panel) and $\delta^{15}N$ (lower panel) values of chicks and adults of blue petrels *Halobaena caerulea* at various stages of the annual cycle. Values not sharing the same superscripted letter are significantly different. Values are means ± SD

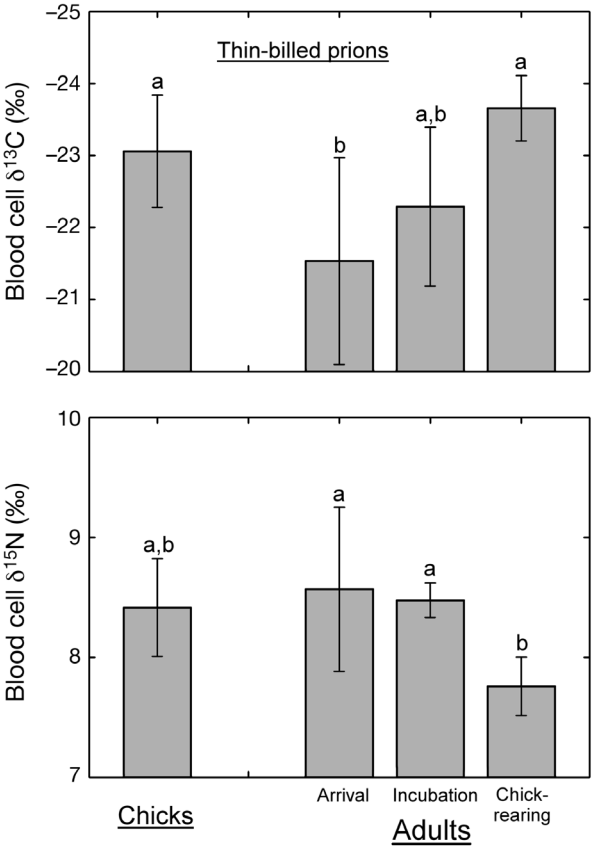

Fig. 2. Blood cell $\delta^{13}C$ (upper panel) and $\delta^{15}N$ (lower panel) values of chicks and adults of thin-billed prions *Pachyptila belcheri* at various stages of the annual cycle. Values not sharing the same superscripted letter are significantly different. Values are means ± SD

ing the chick-rearing period ($p < 0.0001$). Normalized plasma $\delta^{13}C$ and $\delta^{15}N$ values followed a similar pattern (statistics not shown).

Feathers from chicks, adults and historical specimens were segregated by their stable isotope values (Wilks' Lambda, $F_{4,98} = 18.31$, $p < 0.0001$) (Table 1). Both normalized $\delta^{13}C$ and $\delta^{15}N$ values were generally different ($F_{2,50} = 38.76$ and 28.36, respectively, both $p < 0.0001$). Feather $\delta^{13}C$ and $\delta^{15}N$ values were higher in chicks than in adults and historical specimens (all $p < 0.0001$). Normalized $\delta^{13}C$ values for adults and historical samples were not significantly different ($p = 0.425$), but historical samples had higher $\delta^{15}N$ values than adults sampled in 2003 ($p = 0.010$).

Thin-billed prion *Pachyptila belcheri*

The mass of the solid fraction of food samples averaged 16.0 ± 4.7 g (n = 6). In agreement with other sampled years (Cherel et al. 2002a), chick food in 2003 was dominated by crustaceans (98.4 and 99.9% by fresh mass and number, respectively), with the main prey items being the hyperiid amphipod *Themisto gaudichaudii* (79.3% by number) together with cypris larvae of *Lepas australis* (17.4%). Like BP food, TBP diet in 2003 was marked by the absence of *Thysanoessa macrura/vicina*, which was a major crustacean item in other years.

Most TBP adults were males, thus precluding investigating sex-related differences. However, females had higher blood cell $\delta^{13}C$ values than males on their arrival at the colony to breed (−20.9 ± 0.9 and −22.4 ± 1.5‰, n = 12 and 9, respectively, $U = 89.0$, $p = 0.013$). Blood cells from chicks and adults at various stages of the annual cycle were segregated by their stable isotope values (Wilks's Lambda, $F_{6,88} = 5.52$, $p < 0.0001$) (Fig. 2). Blood cell $\delta^{13}C$ and $\delta^{15}N$ values showed significant variations across the breeding cycle ($F_{3,45} = 6.98$ and 4.23,

p = 0.001 and 0.010, respectively), with normalized plasma $\delta^{13}C$ and $\delta^{15}N$ values following the same pattern (statistics not shown). Two features were notable: (1) adult $\delta^{13}C$ and $\delta^{15}N$ values decreased throughout the annual cycle, from arrival in the colony in October to the chick-rearing period in February, and (2) $\delta^{15}N$ values were higher in chicks than in adults during the chick-rearing period (p = 0.072 and 0.004 for blood cells and plasma, respectively).

One adult outlier with a high feather $\delta^{13}C$ value was excluded from statistical analyses, because it falls far outside recent and historical values (Fig. 3). Feathers from chicks, adults and historical specimens were segregated by their stable isotope values (Wilks' Lambda, $F_{4,68}$ = 20.01, p < 0.0001). Both normalized $\delta^{13}C$ and $\delta^{15}N$ values were generally different ($F_{2,35}$ = 32.17 and 42.27, respectively, both p < 0.0001). Normalized feather $\delta^{13}C$ and $\delta^{15}N$ values were not statistically different in chicks or historical specimens, thus contrasting with the lower values of adult birds that moulted in 2003 (all p < 0.0001).

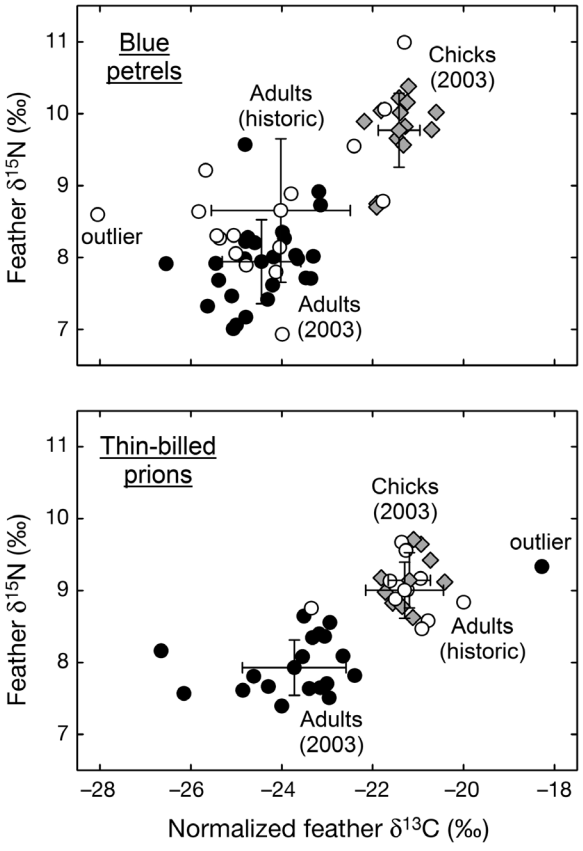

Fig. 3. Feather $\delta^{15}N$ versus normalized $\delta^{13}C$ values of chicks (◇), adults (●) and historical specimens (○) of blue petrels *Halobaena caerulea* (upper panel) and thin-billed prions *Pachyptila belcheri* (lower panel). Values are individual isotopic signatures and means ± SD

Common diving petrel *Pelecanoides urinatrix*

Isotopic data of blood cells and feathers from both sexes were pooled for statistical analyses, because only one significant isotopic difference was found between CDP females and males, namely in blood cells during incubation (U = 6.0 and 2.0, p = 0.005 and 0.001 for $\delta^{13}C$ and $\delta^{15}N$, respectively). Blood cells from chicks and adults at various stages of the annual cycle were segregated by their stable isotope values (Wilks's Lambda, $F_{10,152}$ = 23.31, p < 0.0001), with both $\delta^{13}C$ and $\delta^{15}N$ values showing significant variations across the breeding cycle ($F_{5,77}$ = 29.46 and 35.13, respectively, both p < 0.0001). Three features were notable: (1) blood cell $\delta^{13}C$ and $\delta^{15}N$ values were lower in spring birds arriving at the colony to breed than they were in all the other groups (all p < 0.0001). (2) Adult $\delta^{13}C$ and $\delta^{15}N$ values increased throughout the breeding cycle, from arrival in the colony in September to the chick-rearing period in February. (3) Chicks and adult birds during the chick-rearing period had similar blood cell $\delta^{13}C$ and $\delta^{15}N$ values. Normalized plasma values followed the same pattern for the most part (Fig. 4). However, plasma $\delta^{13}C$ and $\delta^{15}N$ values were similar for chick-rearing, post-nuptial and winter birds (all p ≥ 0.213), with some birds showing contrasting plasma and blood cell isotopic values. For example, 4 post-nuptial birds had much higher $\delta^{13}C$ and $\delta^{15}N$ values in plasma than in blood cells –-17.3 ± 0.2 versus −21.3 ± 0.3‰ and 11.7 ± 0.2 versus 7.3 ± 0.4‰, respectively), thus minimizing plasma variance in that group (Table 1). Overall, plasma $\delta^{13}C$ values (Fig. 5) and the related $\delta^{15}N$ values (not shown) of CDP adults showed a bimodal pattern, with 2 well-segregated groups of values.

Isotopic data from adult feathers also showed 2 isotopic groups, including a few high $\delta^{13}C$ (Fig. 5) and $\delta^{15}N$ (not shown) values. Feathers from chicks, adults and historical specimens were segregated by their stable isotope values (Wilks's Lambda, $F_{4,110}$ = 11.18, p < 0.0001) (Table 1). Both normalized $\delta^{13}C$ and $\delta^{15}N$ values were generally different ($F_{2,56}$ = 24.16 and 23.25, respectively, both p < 0.0001). Feather $\delta^{13}C$ and $\delta^{15}N$ values were higher in chicks than in adults and historical specimens (all p ≤ 0.002), with the 2

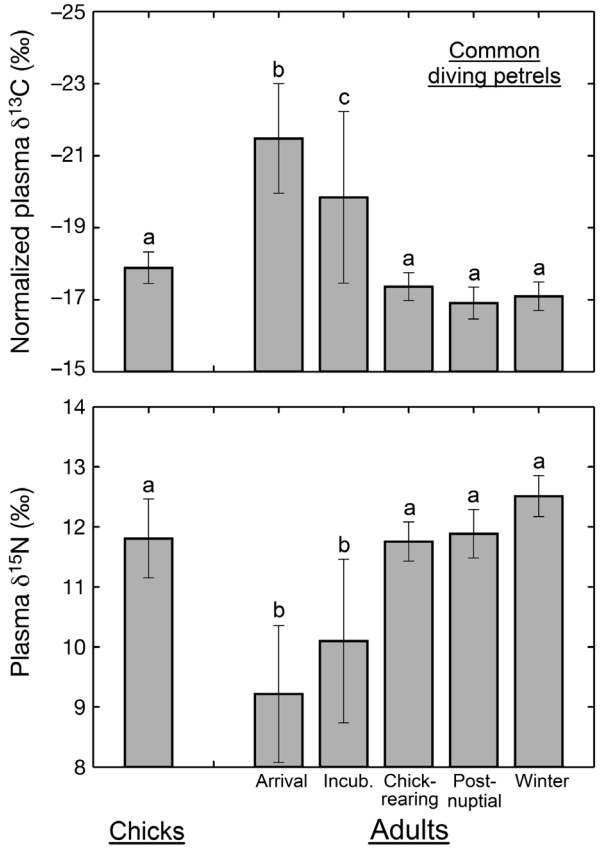

Fig. 4. Normalized plasma $\delta^{13}C$ (upper panel) and $\delta^{15}N$ (lower panel) values of chicks and adults of common diving petrels *Pelecanoides urinatrix* at various stages of the annual cycle. Values not sharing the same superscripted letter are significantly different. Values are means ± SD

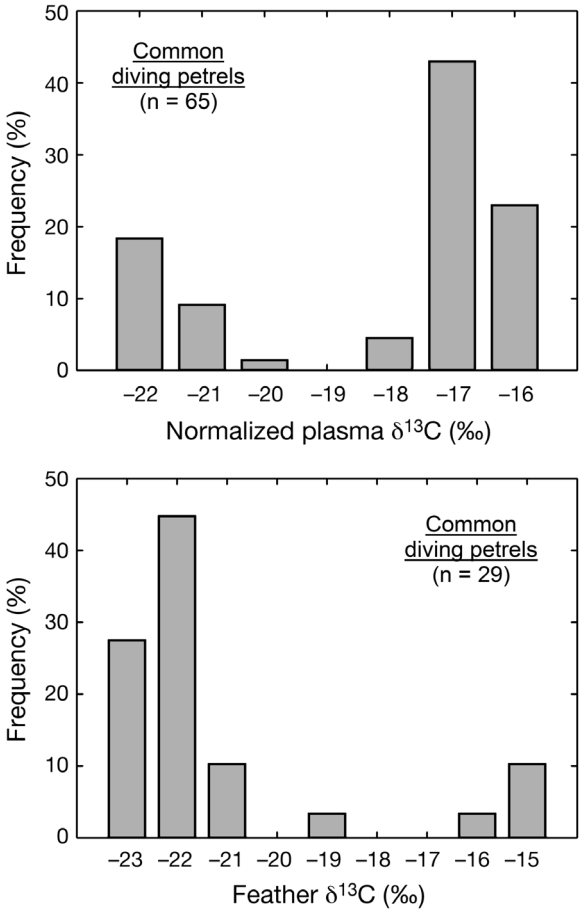

Fig. 5. Frequency distribution of normalized plasma (upper panel) and feather (lower panel) $\delta^{13}C$ values of adult common diving petrels *Pelecanoides urinatrix*

latter groups having similar isotopic signatures (p = 0.223 and 0.065, respectively).

Among-species isotopic comparisons

Blood cells of BP, TBP and CDP were segregated by their stable isotope values at various stages in the breeding cycle, namely, arrival at the colony to breed, incubation, chick-rearing and chicks (Wilks' Lambda, $p < 0.0001$ for each stage) (Fig. 6). In univariate analyses, both $\delta^{13}C$ and $\delta^{15}N$ values were different (all $p \leq 0.002$), with 3 notable features: (1) CDP was always segregated from BP and TBP (post hoc tests, all $p \leq 0.005$), except for $\delta^{13}C$ in spring ($p = 0.656$ between BP and CDP and $p = 0.084$ between CDP and TBP). (2) BP and TBP were segregated by $\delta^{13}C$ and/or $\delta^{15}N$ values, except during the chick-rearing period ($p = 0.471$ and 0.203, respectively). (3) When they differed, BP had lower $\delta^{13}C$ values (arrival, incubation) and higher $\delta^{15}N$ values (arrival, chicks) than TBP.

Feathers of BP, TBP and CDP were segregated by their stable isotope values in adult birds, historical specimens and chicks (Wilks's Lambda, all $p < 0.0001$). In univariate analyses, $\delta^{13}C$ values were always different ($p < 0.0001$), while $\delta^{15}N$ values were different in chicks ($p < 0.0001$), but not in adult birds ($p = 0.265$) nor in historical specimens ($p = 0.100$). In agreement with blood cell data, chick feather $\delta^{13}C$ and $\delta^{15}N$ values showed differences between CDP and the 2 other species (all $p < 0.0001$) and BP had a higher $\delta^{15}N$ value than did TBP ($p < 0.0001$). Feather $\delta^{13}C$ values of BP and CDP were different in both adult birds and historical samples ($p < 0.0001$). In contrast, feather $\delta^{13}C$ values of TBP and BP were identical in adult birds ($p = 0.204$) and different in historical specimens (normalized values, $p = 0.004$), with an opposite pattern for $\delta^{13}C$ values of TBP and CDP ($p = 0.002$ and 0.335, respectively).

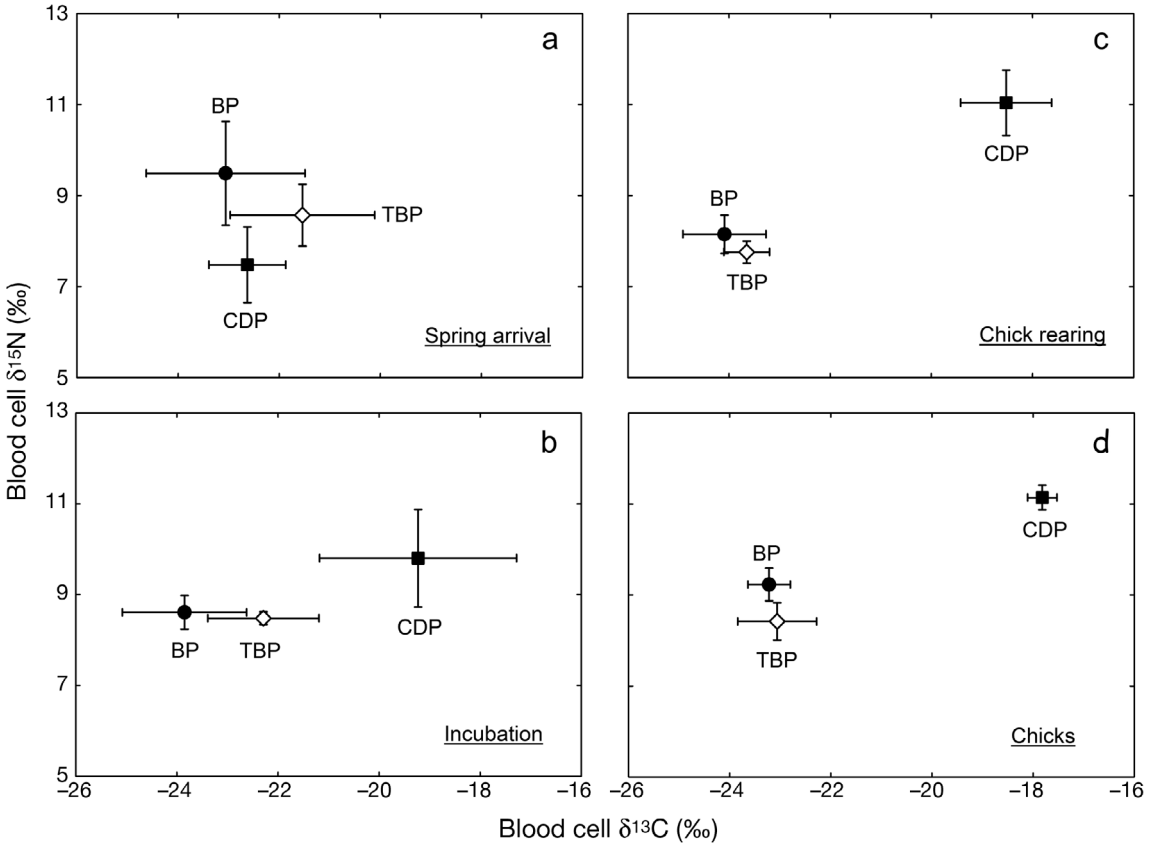

Fig. 6. Blood cell $\delta^{13}C$ and $\delta^{15}N$ values of blue petrels *Halobaena caerulea* (BP), thin-billed prions *Pachyptila belcheri* (TBP) and common diving-petrels *Pelecanoides urinatrix* (CDP) at various stages of the breeding cycle: (a) arrival, (b) incubation, (c) chick-rearing and (d) chicks. Values are means ± SD

DISCUSSION

To date, few studies based on stable isotopes have examined the extent to which seabirds alter their foraging strategies across discrete stages of the breeding cycle (e.g. Williams et al. 2008, Davies et al. 2009), and none, to our knowledge, has included historical samples from museum specimens in the analysis. Four main features emerge from our detailed isotopic investigation. (1) All 3 petrel species stayed all year long within the Southern Ocean and only a very few TBP and CDP individuals foraged further north (Cherel et al. 2006, present study). The birds' foraging strategies document a strong connection between the subantarctic and Antarctic pelagic ecosystems, with the 3 subantarctic species foraging significantly within the Antarctic Zone. (2) Isotopic niches and hence foraging niches are stage-dependent, with petrels coping with environmental seasonality and energetic constraints throughout the breeding cycle by shifting their feeding grounds either from oceanic to productive coastal waters (CDP) or from subantarctic to high-Antarctic waters where they preyed primarily upon crustaceans (BP and TBP). (3) The diving CDP was segregated from the surface-feeders BP and TBP by both its more coastal habitat and its lower-trophic level prey, while BP was segregated from TBP by foraging further south and including more fish in its diet. (4) In contrast to BP and CDP, TBP has shifted its main moulting grounds to higher latitudes over the last decades. From a methodological point of view, the study highlights the usefulness of measuring the isotopic values of complementary tissues with different temporal integrations to depict trophic variations at both the population and individual levels (Martínez del Rio et al. 2009, Hobson & Bond 2012), and of including historical samples in isotopic investigations to depict potential long-term temporal changes (Thompson et al. 1995, Jaeger & Cherel 2011).

Petrel isotopic values in 2003 were similar to the species' $\delta^{13}C$ and $\delta^{15}N$ values in other recent years (Bocher et al. 2000a, Cherel et al. 2002a,b, unpubl. data), thus indicating that they were representative

of the birds' normal isotopic niche. Adult survival rates of BP, TBP and CDP in 2003 were close to the species means, as was the fledging success of BP (authors' unpubl. data). In contrast, the fledging success of TBP in 2003 was well below the average (authors' unpubl. data), suggesting a possible detrimental effect of the lack of *Thysanoessa macrura/vicina* in food samples for TBP chicks, but not for BP chicks. Other food components in 2003 were consistent with previous dietary information, with BP feeding on fish and with *Themisto gaudichaudii* being a main crustacean item in both BP and TBP food samples (Cherel et al. 2002a,b, Connan et al. 2008).

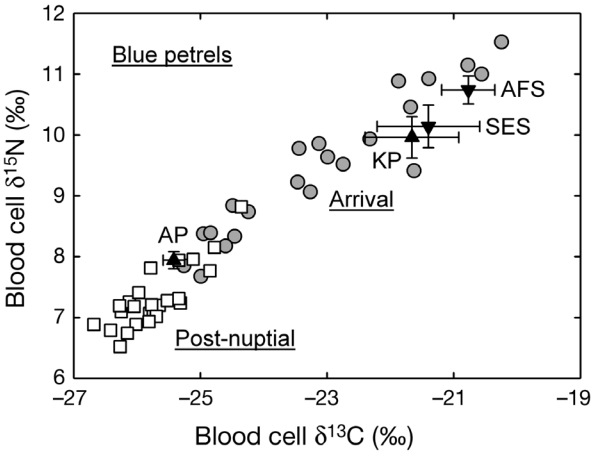

Fig. 7. Blood cell $\delta^{15}N$ versus $\delta^{13}C$ values of individual adult blue petrels *Halobaena caerulea* on arrival at the colony to breed in September (●) and in the post-nuptial stage in April to May (□). Control species: adult Adélie penguins (AP) that feed primarily on krill in high-Antarctic waters, and lactating female Antarctic fur seals (AFS), adult king penguins (KP) and female southern elephant seals (SES) that feed on myctophid fish in warmer waters. Values are means ± SD

Species-level analyses

According to the latitudinal $\delta^{13}C$ gradient in the Southern Ocean (Cherel & Hobson 2007, Jaeger et al. 2010, Quillfeldt et al. 2010), blood cell, plasma and feather $\delta^{13}C$ values of BP show that the species forages primarily within the Antarctic Zone all year long. Feeding in cold waters is in agreement with the $\delta^{13}C$ values of feathers collected in the period from 1995 to 1997 at the Kerguelen Islands and of feathers and blood cells from adults rearing chicks in South Georgia (Cherel et al. 2002a, 2006, Anderson et al. 2009, Navarro et al. 2013). However, the larger variance, together with the continuum of individual blood cell $\delta^{13}C$ values from −25.3 to −20.1‰, indicates that BP fed within a broader latitudinal range, from high-Antarctic to subantarctic waters, in the few weeks preceding breeding in late winter (Fig. 7). The variable $\delta^{13}C$ values were associated with a concomitant large range of $\delta^{15}N$ values, from 7.7 to 11.5‰, which encompasses >1 trophic level. A part of that variation is likely due to a change in the $\delta^{15}N$ baseline with latitude (Jaeger et al. 2010), but the main driving factor of the $\delta^{15}N$ increase is a latitudinal dietary change from lower-trophic level prey (most likely Antarctic krill) in Antarctic waters to higher-trophic level prey (most likely myctophid fish) in subantarctic waters. This dietary plasticity is well exemplified by comparing the blood $\delta^{15}N$ values between BP and species with well-known feeding ecology. Low BP $\delta^{15}N$ values are close to those of the high-Antarctic Adélie penguin, which consumes Antarctic and ice krill (Cherel 2008), while the higher BP $\delta^{15}N$ values are remarkably similar to those of the much larger myctophid-eating king penguin, Antarctic fur seal and southern elephant seal (Cherel et al. 2008) (Fig. 7). The foraging behaviour of some individuals that fed almost exclusively on mesopelagic fish confirms the importance of myctophids in the nutrition of BP that was already pointed out for the period during chick-rearing (Connan et al. 2007, 2008).

Blood cell, plasma and feather $\delta^{13}C$ values of TBP adults show that the species foraged primarily over oceanic waters of the Subantarctic and Antarctic Zones all year long. Feeding in oceanic waters of the Southern Ocean is in agreement with the $\delta^{13}C$ values of feathers collected in the period from 1995 to 1997 at Kerguelen (Cherel et al. 2002b, 2006), but not with some isotopic and tracking data from the Falkland Islands. At the latter locality, most TBP feed in the neritic waters of the Patagonian shelf during the chick-rearing period and in late winter (Quillfeldt et al. 2008, 2013). A main characteristic of the BP and TBP breeding cycles at the Kerguelen Islands was an overall progressive summer decrease in blood cell and plasma $\delta^{13}C$ values, together with a concomitant decrease in $\delta^{15}N$ values (Figs. 1 & 2). The main explanation for the isotopic changes is a progressive spatial and dietary shift to higher latitudes where the birds fed more on Antarctic krill, thus benefiting from the progressive retreat of sea-ice that drives seasonal krill availability. Indeed, BP and TBP of unknown status have been repeatedly observed foraging and feeding in summer in the high-Antarctic waters south of the Kerguelen Islands, where visual obervations of BP have been positively correlated with the abundance of Antarctic krill (Ryan & Cooper 1989, J. C. Stahl et al. unpubl. data). Foraging progressively

further south as summer progresses in order to feed on krill has already been depicted in satellite-tracked white-chinned petrels (Catard & Weimerskirch 1999) and has isotopically been recorded in the vibrissae of some male Antarctic fur seals (Cherel et al. 2009).

Unlike BP and TBP, CDP showed progressive and large increases in its plasma and blood cell $\delta^{13}C$ and $\delta^{15}N$ values throughout the breeding cycle. The 2 well-defined groups of plasma $\delta^{13}C$ values indicate foraging in 2 distinct marine environments (Fig. 5). Visual observations, together with dietary analyses and net sampling, showed that adults rearing chicks feed in coastal waters near the colony within a large enclosed bay (Weimerskirch et al. 1989, Bocher et al. 2000a, 2001, 2002). Coastal waters are generally marked by high $\delta^{13}C$ and $\delta^{15}N$ baselines, thus explaining the group of high isotopic values. In contrast, birds arriving at the colony to breed had much lower plasma and blood cell $\delta^{13}C$ and $\delta^{15}N$ values, indicating that adult birds migrated from low-Antarctic and subantarctic waters, where they fed on crustaceans. Unlike isotopic data of breeding birds in September, the $\delta^{13}C$ and $\delta^{15}N$ values in July showed that winter birds foraged in coastal waters near the colony. The resident behaviour of winter birds contrasts with the migrating pattern of breeding diving petrels, thus confirming that the few CDP present in the colony in winter will not breed the following spring (Bocher et al. 2000b). Shifting between the 2 habitats at the individual level is exemplified clearly by the contrasting isotopic values in the plasma and blood cells of a few post-nuptial birds, with higher (blood cells) and lower (plasma) integration periods indicating foraging in oceanic and coastal waters, respectively. Feather isotopic values were also clustered into 2 groups, with most breeding CDP moulting in Antarctic oceanic waters and a few birds moulting near the colony (Fig. 5). In South Georgia, colonies were located near the open sea, and, accordingly, isotopic data and the tracking of birds in summer indicate that the species forages in offshore waters (Anderson et al. 2009, Navarro et al. 2013).

Spatial and trophic segregation among species

Species comparisons were made at 5 stages of the breeding cycle, namely spring arrival, incubation, chick-rearing, chick and moult. The most obvious difference was the isotopic segregation between the diving CDP and the surface-seizing BP and TBP during most of the breeding cycle. The much higher plasma and blood cell $\delta^{13}C$ values of CDP indicate feeding in coastal waters, while BP and TBP are oceanic consumers. Inshore feeding of breeding CDP can be linked to central-place foraging, together with the high energetic cost of flying of diving petrels relative to blue petrels and prions (Roby & Ricklefs 1986, Taylor et al. 1997, Weimerskirch et al. 2003a). However, these constraints do not preclude foraging in nearby offshore waters, as the sympatric South Georgian diving petrel does (Bocher et al. 2000a). Hence, CDP favors coastal waters, and it is the most inshore procellariiform seabird at the Kerguelen Islands and probably elsewhere within the Southern Ocean (J. C. Stahl et al. unpubl. data). However, CDP also foraged in offshore waters in some non-breeding stages of the annual cycle, with most moulting adults and all spring birds feeding in Antarctic and subantarctic waters in the vicinity of the Polar Front. There, spring birds caught lower trophic level prey than did TBP and BP (Fig. 6), most likely herbivorous copepods and omnivorous euphausiids rather than carnivorous hyperiid amphipods.

Isotopic segregation between BP and TBP was less pronounced, and it changed over breeding stages. On arrival at the colony, adults of the 2 species foraged in different habitats and fed on different prey; during incubation, only the habitats were different; and there was no obvious segregation during chick-rearing or the subsequent moult. One limitation of the isotopic method is that $\delta^{13}C$ values of seabirds indicate their latitudinal, but not their longitudinal feeding grounds (Cherel & Hobson 2007, Jaeger et al. 2010). Hence, more information is needed using miniaturized geolocator sensors to precisely define the respective foraging grounds of BP and TBP all year long (Quillfeldt et al. 2013). When statistically different, however, $\delta^{13}C$ and $\delta^{15}N$ values indicate that BP adults foraged further south and fed on higher-trophic level prey than did TBP adults. Dietary segregation is exemplified by the higher $\delta^{15}N$ value of BP chicks, which is explained by both the larger proportion of fish in the chick food of BP than that of TBP (Cherel et al. 2002a,b, present study) and the higher trophic positions of mesopelagic fish compared to pelagic swarming crustaceans (Cherel et al. 2008, 2010).

Self-feeding versus chick provisioning

The assumption that oceanic, but not coastal species, would present different blood isotopic values in adults and chicks was partially verified. As expected, plasma and blood cell $\delta^{13}C$ and $\delta^{15}N$ values of adults and chicks were not significantly different in the

coastal CDP, indicating that adult birds foraged for themselves and for their chicks in the same habitat and on the same prey, most likely the hyperiid amphipod *Themisto gaudichaudii* and the large copepod *Paraeuchaeta antarctica* (Bocher et al. 2000a, 2001, 2002). As expected also, BP adults showed lower $\delta^{13}C$ and $\delta^{15}N$ values than their chicks, thus indicating that parent birds foraged for themselves in colder waters, where they fed primarily on crustaceans, and that they caught more fish at lower latitudes for their chicks. Catching some fish for their offspring is also the likely explanation for the higher $\delta^{15}N$ values of TBP chicks than of adults (Cherel et al. 2002a). Such partial trophic segregation between adults and chicks was previously found in Antarctic procellariiforms and penguins, with adults provisioning offspring with higher quality food to facilitate their growth (Hodum & Hobson 2000, Cherel 2008). Indeed, mesopelagic fish are protein- and lipid-rich organisms (Donnelly et al. 1990, Cherel & Ridoux 1992), and fatty fish are known to be the best-quality nutritional food promoting growth in seabird chicks (Heath & Randall 1985). Unlike the initial assumption, however, $\delta^{13}C$ values were almost identical for TBP adults and chicks, suggesting that they all fed on a mixture of Antarctic and subantarctic prey, with slightly more Antarctic food in adult birds.

Historical ecology during adult moult

CDP feather $\delta^{13}C$ and $\delta^{15}N$ values were not significantly different in recent and historical specimens. The high isotopic variance implies that historical specimens also moulted in the 2 contrasting marine environments described for the 2003 birds, with most CDP foraging in the Subantarctic Zone and a few of them in coastal waters near the colony. Unlike BP isotopic data, TBP feather $\delta^{13}C$ and $\delta^{15}N$ values were significantly different in recent and historical specimens, with almost no overlap between the 2 groups (Fig. 3) and with similarly low $\delta^{13}C$ values in recent feathers collected in 2003 (present study) and those collected from 1995 to 1997 (Cherel et al. 2002a). Two non-exclusive explanations may account for the difference in $\delta^{13}C$ values, namely ecosystemic and species-specific changes. First, since the baseline $\delta^{13}C$ value is positively linked to phytoplankton growth (Laws et al. 1995), a decrease in primary productivity induces a lower $\delta^{13}C$ baseline that is reflected in organisms at higher trophic levels (Schell 2000, Jaeger & Cherel 2011). The lack of parallel change in historical feather $\delta^{13}C$ values of both TBP and BP, however, suggests that no substantial decrease of primary productivity has taken place in the area over the last decades. Moreover, the shift in TBP $\delta^{13}C$ values was very large, almost certainly too large to have been caused by a changing $\delta^{13}C$ baseline level. Secondly, the most likely explanation is that birds' foraging behaviour has changed over the last decades, with TBP adults shifting their moulting areas to higher latitudes, where they feed on higher trophic level prey. Historical and more recent samples indicate lower latitude foraging grounds during most of the 20th century (1923 to 1971), with a shift to high-Antarctic waters occurring before 1995 to 1997 and no change thereafter. Why moulting TBP altered their foraging behaviour remains to be investigated, but it is notable that an atmospheric temperature-defined regime shift occurred in the 1970s in the southern Indian Ocean (Weimerskirch et al. 2003b). Interestingly, TBP from the Falkland Islands in the southern Atlantic Ocean showed a similar historical trend in their $\delta^{13}C$ values (Quillfeldt et al. 2010), thus suggesting either that a second factor may have induced the distributional shift in the South Atlantic population independently or, more probably, that an identical phenotypically or genetically operating mechanism occurred at the species level. To our knowledge, no similar change in movement patterns has been described in any other seabird species. The TBP isotopic data thus highlight the foraging plasticity of seabirds, including their ability to change long-term feeding strategies during the inter-nesting period. Such foraging flexibility is a beneficial attribute for seabird populations attempting to cope with changing environmental conditions and energetic constraints at different time scales (from intra-seasonal to decadal).

Acknowledgements. The authors thank the fieldworkers who helped collect samples at the Kerguelen Islands, S. Dano for seabird molecular sexing, G. Guillou for stable isotope analysis and C. Barbraud for looking at demographic data. We are indebted to E. Pasquet and J. Cuisin for permission to collect feathers from historical specimens at the Muséum National d'Histoire Naturelle of Paris. The present work was supported financially and logistically by the Institut Polaire Français Paul Emile Victor (Programme No. 109, H. Weimerskirch) and the Terres Australes et Antarctiques Françaises.

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Editorial responsibility: Christine Paetzold, Oldendorf/Luhe, Germany

Submitted: December 6, 2013; Accepted: March 21, 2014
Proofs received from author(s): May 15, 2014