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Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds

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Abstract To determine whether stable isotope measurements of bird feathers can be used to identify moulting (interbreeding) foraging areas of adult seabirds, we examined the stable-carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic composition of feathers of chicks and adults of black-browed albatrosses (*Diomedea melanophrys*) from Kerguelen Islands, southern Indian Ocean. Albatross chicks are fed primarily fish (75% by mass), the diet being dominated by various species of the family Nototheniidae and Channichthyidae which commonly occur in the shelf waters in the vicinity of the colony. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in chick feathers, which are grown in summer in the breeding area, were lower than values in adult feathers, which are grown in winter ($\delta^{13}\text{C}$: -19.6‰ versus -17.6‰ and $\delta^{15}\text{N}$: 12.4‰ versus 15.7‰ , respectively). No differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were found in adult wing feathers moulted in 1993 and 1994 and in adult feathers formed at the beginning, middle and end of the 1994 moulting period. These data are consistent with adults moulting in the same area and feeding at the same trophic level from one year to the next and with no major changes in foraging ecology within a given moulting season; they suggest that foraging grounds were different in summer and winter and that these differed in their stable-isotope signature. Changes in both feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values indicated feeding south of the Subtropical Front (STF) during chick rearing, which is in agreement with the known foraging ecology at this time and feeding north of the STF during moult. This, together with band recoveries from adult birds, indicates that black-browed albatrosses from Kerguelen Islands win-

tered in subtropical waters off southern Australia. The stable-isotope markers in feathers, therefore, have the potential for locating moulting areas of migratory seabird species moving between isotopically distinct regions and for investigating seabirds' foraging ecology during the poorly known interbreeding period. Such information is needed for studies of year-round ecology of seabirds as well as for their conservation and the long-term monitoring of the pelagic environment.

Key words Albatross · Carbon · *Diomedea melanophrys* · Kerguelen · Nitrogen

Introduction

Seabirds spend most of their time at sea, where they find food and come ashore only for breeding, so that they are accessible for biological investigation for only part of the year. This is particularly relevant for oceanic species like Procellariiformes, for which most of our knowledge of food and feeding ecology is restricted to the breeding period (Prince and Morgan 1987; Cherel and Klages 1998) when birds alternate periods of feeding at sea with periods in the colony for pairing, incubation and the care of young. During the interbreeding period much less dietary and foraging information is available because albatrosses and petrels remain at sea and often move long distances from their nesting sites. This lack of information is of particular concern for two reasons. First, environmental changes during the interbreeding period can affect the survival of individuals or their body condition and thus breeding performance in the subsequent reproductive season (Chastel et al. 1995; Guinet et al. 1998). Second, some populations have shown dramatic declines in recent years because of mortality due to fisheries occurring, at least in part, on their wintering grounds (Robertson and Gales 1998). Essential to both knowledge of life-history tradeoffs and the conservation of albatrosses and petrels is the investigation of their foraging ecology and relationships with human activities outside the breeding period.

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Natural variations in the stable isotopic composition of animal tissues reflect those in the local environment and isotopic analyses have therefore been used to delineate bird feeding habitat (Hobson 1990; Hobson and Sealy 1991), trophic relationships (Hobson and Montevecchi 1991; Hobson et al. 1994; Thompson et al. 1995; Sydeman et al. 1997) and geographic origin (reviewed by Hobson 1999). For birds, the isotopic composition of feathers reflects diet during the moulting period (Mizutani et al. 1990, 1992; Hobson and Clark 1992a; Thompson and Furness 1995), feather keratin being metabolically inert after synthesis.

Moult, reproduction and migration in birds are often events that are essentially exclusive in time. It is generally assumed that periodic moult temporally concentrates energy and nutrient requirements, which therefore do not interfere with other vital functions (Payne 1972). Moult in Procellariiforme seabirds generally conforms to this pattern with no overlap with breeding activity (Warham 1996). In adult albatrosses, all wing, body and tail moult occurs at sea between nesting episodes and the replacement of all wing feathers necessitates two to three successive interbreeding periods, suggesting a resource limitation of time and food (Weimerskirch 1991; Prince et al. 1993; Langston and Rohwer 1996). Sampling of feathers for the determination of their isotopic composition is thus a simple, non-invasive and potentially efficient way to collect information on the feeding ecology of seabirds during the poorly known interbreeding period at sea.

The objective of this study was to evaluate the use of the stable isotope technique to examine whether the diet of a Procellariiforme species differs between the breeding and non-breeding seasons and thus to delineate its wintering (i.e. moulting) areas. We chose the black-browed albatross *Diomedea melanophrys* from Kerguelen Islands for several practical and ecological reasons:

1. In summer, we know that adult birds forage over the peri-insular shelf and upper slope catching fish and cephalopods to feed their chicks (Weimerskirch et al. 1988, 1997; Cherel and Weimerskirch 1995). This allows comparison between the stable isotope ratios of carbon and nitrogen of feathers from chicks and those of their food to estimate isotope enrichment factors of albatross feathers.
2. Preliminary results from a few ring recoveries suggest that adult birds winter and thus probably moult in coastal waters off Southern Australia (Weimerskirch et al. 1985). Since lower-latitude plankton food bases tend to be enriched in both ^{13}C and ^{15}N relative to higher-latitude waters in the Southern Ocean (Wada et al. 1987) and the geographic range between Kerguelen and Australia spans natural gradients in both carbon and nitrogen isotopes in marine surface waters (François et al. 1993; Altabet and François 1994), it is expected that stable isotope patterns at the base of the food chain should also be reflected in organisms at higher trophic levels. We therefore hypothesized that

stable-carbon and nitrogen isotope ratios should accordingly vary in feathers obtained from adults and chicks.

3. The moult pattern of adult black-browed albatrosses is now well known (Prince et al. 1993). The renewal of all wing feathers necessitates two successive winters, while tail moult is complete over one single season: tail feathers moulted from the outside to the middle, probably commencing and ending before and after primary moult, respectively (Prince et al. 1993). This pattern allowed the collection on each adult black-browed albatross of wing feathers formed in two different years and of tail and wing feathers formed at different times of a given moulting period, to test for interannual and intraseasonal changes in foraging ecology during moult.

Materials and methods

Study site, birds, field collection of samples and food analysis

The study was conducted at the southern colony of Canyon des Sourcils Noirs (49°41'S, 70°14'E), Jeanne d'Arc Peninsula, southern Kerguelen Islands, where 1,000–1,200 pairs of black-browed albatrosses breed annually (Weimerskirch et al. 1989). Ringing there began in the late 1960s and a sub-colony of banded individuals was established in 1979, allowing the estimation of demographic parameters in subsequent years (Weimerskirch and Jouventin 1998). All fledglings and newly recruited non-ringed breeding adults are systematically banded in the area. In this study, we took into account both old ring recoveries (Barré et al. 1976; Weimerskirch et al. 1985) and new recoveries from 1982 up to the present.

Feathers and food were sampled in birds from the same colony as the demographic sub-colony during the 1994–1995 breeding period. Feather samples were collected from 10 adult birds on 6 January 1995, during the brooding period and from 11 fledglings on 29 March 1995. Breeding black-browed albatrosses moult their rectrices (i.e. tail feathers) annually and their primaries biennially during the non-breeding period (Prince et al. 1993), which lasts from late April to early September (Weimerskirch et al. 1989). In adult birds, we consequently collected the top 4 cm of two primaries (P6 and P9, located in the middle of the primaries formed in two successive years; Prince et al. 1993): one new feather (un-abraded and black) and one 1-year-old feather (more abraded and more brownish), that were moulted in the winters of 1994 and 1993, respectively. We also cut the top few centimeters of two tail feathers, one of the two outer rectrices and one of the two inner (central) rectrices, to collect information corresponding to the beginning and the end of the moulting period in winter 1994, respectively. In each fledgling, we cut the tips of two primaries (P9) that were formed during the previous weeks at the breeding colony.

A total of 69 dietary samples were collected from albatross chicks after a returning parent had completed feeding them during February–March 1995. All stomach contents were returned deep-frozen (-20°C) to the laboratory in France for analysis. Each sample was thawed, drained and accumulated cephalopod beaks subsequently sorted. Beaks can persist in predator stomachs for weeks and even months, thus overemphasizing their importance in seabird diets; accumulated beaks were consequently not taken into account in the present study. Fresh remains were divided into broad prey classes (fish, cephalopods, crustaceans, penguins and others), which were weighed to calculate their proportion by mass in the diet. Identification of prey relied almost totally on the examination of otoliths and bones for fish and keratinized beaks for cephalopods, because the digested condition of the samples prevented the use of any external diagnostic features. Prey items were

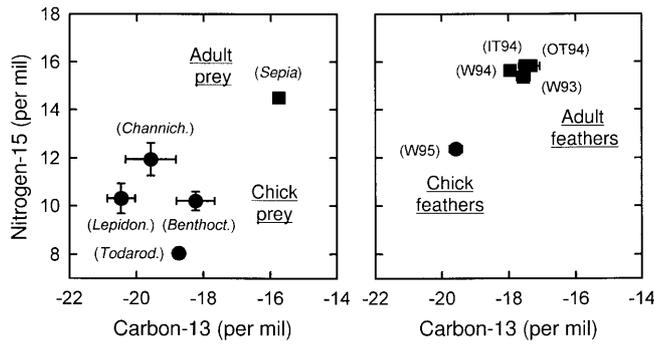


Fig. 1. Stable carbon and nitrogen isotope values for **a** prey and **b** feathers of black-browed albatrosses. Prey were either caught in Kerguelen waters in summer (chick prey) or in Australian waters in winter (adult prey) (*Benthoc.*, *Benthocotopus thielei*, *Channich.*, *Channichthys rhinocerosus*, *Lepidon.*, *Lepidonotothen squamifrons*, *Todarod.*, *Todarodes angolensis*, *Sepia*, *Sepia apama*, IT94 adult inner tail feathers moulted in winter 1994, OT94 adult outer tail feathers moulted in winter 1994, W93 adult wing feathers moulted in winter 1993, W94 adult wing feathers moulted in winter 1994, W95 chick wing feathers moulted in summer 1995). Values are means \pm SD (not drawn when 2 SD were less than height of symbols)

therefore identified by reference to the available literature (Clarke 1986; Williams and McEldowney 1990) and by comparison with material held in our own reference collection.

Specimens of some of the main prey of albatross chicks at Kerguelen were collected early in 1995 either as bycatch of the Patagonian toothfish (*Dissostichus eleginoides*) trawl fishery (the fishes *Channichthys rhinocerosus* and *Lepidonotothen squamifrons* and the octopus *Benthocotopus thielei*), or as intact prey in the stomach of Patagonian toothfish (the squid *Todarodes angolensis*). Little is known of the dietary habits of albatrosses outside the chick-rearing period (see review in Cherel and Klages 1998). One of the best documented observations of albatrosses in winter is the regular occurrence of large numbers of albatrosses, including black-browed, feeding on floating moribund cuttlefishes *Sepia apama* off Australia (Wood 1992; Nicholls et al. 1995). Some adult cuttlefishes were therefore collected off Wollongong, southeastern Australia, during the austral winter 1996.

Tissue preparation and isotopic analysis

Whole specimens of fish and cephalopods were stored frozen at Kerguelen Islands and were returned frozen to the laboratory at Chizé, France, while buccal masses of *Sepia apama* from Australia were preserved in 70% ethanol. Preservation in ethanol or by freezing does not result in changes to stable-carbon and nitrogen

isotope ratios of samples (Hobson et al. 1997). Prior to isotopic analysis, samples were freeze dried or dried in an oven at +60°C and ground to a fine powder in an analytical mill. Lipids were then removed using a Soxhlet apparatus with chloroform solvent for 4–6 h. Feathers were cleaned of surface contaminants using a 2:1 chloroform:ether rinse, air dried and then cut with stainless steel scissors into small fragments.

Stable-carbon and nitrogen isotope assays were performed on 1-mg subsamples of homogenized materials by loading into tin cups and combusting at 1800°C in a Robo-Prep elemental analyzer. Resultant CO₂ and N₂ gases were then analyzed using an interfaced Europa 20:20 continuous-flow isotope ratio mass spectrometer (CFIRMS) with every five unknowns separated by two laboratory standards. Stable isotope abundances were expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000,$$

where X is ¹³C or ¹⁵N and R is the corresponding ratio ¹³C/¹²C or ¹⁵N/¹⁴N. The R_{standard} values were based on the PeeDee Belemnite (PDB) for ¹³C and atmospheric N₂ (AIR) for ¹⁵N. Replicate measurements of internal laboratory standards (albumen) indicate measurement errors of $\pm 0.1\%$ and $\pm 0.3\%$ for stable-carbon and nitrogen isotope measurements, respectively.

Data were statistically analysed using SYSTAT 7.0 for Windows (Wilkinson 1997). Values are means \pm SD.

Results

Stable isotope analysis

Albatross feathers were segregated by their stable isotope values (MANOVA, Wilk's λ , $F_{8,90}=22.61$, $P<0.0001$) (Fig. 1). Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were identical in the four groups of adult feathers, and were not significantly different between wing feathers moulted in 1993 and those moulted in 1994, or between feathers formed at the beginning (outer tail feathers), middle (wing feathers 1994) and end (inner tail feathers) of the moulting period (Table 1). However, both carbon and nitrogen stable-isotope values of chick feathers were significantly lower than those of adult feathers (post hoc Tukey HSD multiple comparison tests, all $P<0.0001$; Table 1).

Feather stable isotope values differed among individual adult birds (MANOVA, Wilk's λ , $F_{18,58}=2.45$, $P=0.0052$). However, because there was no variation in $\delta^{13}\text{C}$ values (ANOVA, $F_{9,30}=1.69$, $P=0.1350$), this was driven by differences in $\delta^{15}\text{N}$ values (ANOVA, $F_{9,30}=3.77$, $P=0.0029$). One bird had a mean $\delta^{15}\text{N}$ value

Table 1 Stable-carbon and nitrogen isotope values (mean \pm SD‰) in feathers of breeding adults and chicks of black-browed albatrosses at Kerguelen Islands and results of one-way ANOVA for differences among feathers for each isotope. Values in the same column not sharing a common superscript letter are significantly different (post hoc Tukey HSD multiple comparison test, $P<0.05$)

Sampling group	Season and year of moult	Location of moult	<i>n</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
ADULTS					
Wing feathers	Winter 1993	Unknown	10	-17.6 \pm 0.6 ^a	15.4 \pm 0.3 ^a
Wing feathers	Winter 1994	Unknown	10	-18.0 \pm 0.5 ^a	15.6 \pm 0.7 ^a
Outer tail feathers	Winter 1994	Unknown	10	-17.3 \pm 0.8 ^a	15.8 \pm 0.5 ^a
Inner tail feathers	Winter 1994	Unknown	10	-17.5 \pm 0.6 ^a	15.8 \pm 0.3 ^a
CHICKS					
Wing feathers	Summer 1995	Kerguelen	11	-19.6 \pm 0.6 ^b	12.4 \pm 0.7 ^b
ANOVA				$F_{4,46}=22.08$ $P<0.0001$	$F_{4,46}=80.17$ $P<0.0001$

Table 2 Stable-carbon and nitrogen isotope values (mean \pm SD‰) in fish and cephalopod prey of black-browed albatrosses and results of one-way ANOVA for differences among species for each isotope. Values in the same column not sharing a common superscript letter are significantly different (post hoc Tukey HSD multiple comparison test, $P<0.05$)

Taxa	Location of capture	n	Standard length or mantle length (mm)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
FISH					
<i>Channichthys rhinoceratus</i>	Kerguelen	4	246 \pm 17	-19.6 \pm 1.5 ^{a,b}	11.9 \pm 1.4 ^a
<i>Lepidonotothen squamifrons</i>	Kerguelen	5	255 \pm 23	-20.5 \pm 0.9 ^b	10.3 \pm 1.4 ^{a,b}
CEPHALOPODS					
<i>Todarodes angolensis</i>	Kerguelen	2	204–208	-18.7 \pm 0.1 ^{a,b}	8.1 \pm 0.2 ^b
<i>Benthoctopus thielei</i>	Kerguelen	5	80 \pm 12	-18.2 \pm 1.3 ^a	10.2 \pm 0.9 ^{a,b}
<i>Sepia apama</i>	Australia	5	377 \pm 39	-15.7 \pm 0.3 ^c	14.5 \pm 0.4 ^c
ANOVA				$F_{4,16}=14.58$	$F_{4,16}=19.64$
				$P<0.0001$	$P<0.0001$

lower than those from three other adult albatrosses (post hoc Tukey HSD multiple comparison tests, $P=0.0034$, 0.0214 and 0.0270).

Albatross prey were segregated by their stable isotope values (MANOVA, Wilk's λ , $F_{8,30}=15.72$, $P<0.0001$; Fig. 1) with both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values being significantly different (Table 2). The cuttlefish *Sepia apama* had $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values different from those of all other prey species (post hoc Tukey HSD multiple comparison tests, all P s at least <0.05). Among prey caught in Kerguelen waters, the fish *Lepidonotothen squamifrons* had an average $\delta^{13}\text{C}$ value that was lower than that of the octopus *Benthoctopus thielei* ($P=0.0267$) and the fish *Channichthys rhinoceratus* had a mean $\delta^{15}\text{N}$ value higher than the value from the squid *Todarodes angolensis* ($P=0.0041$).

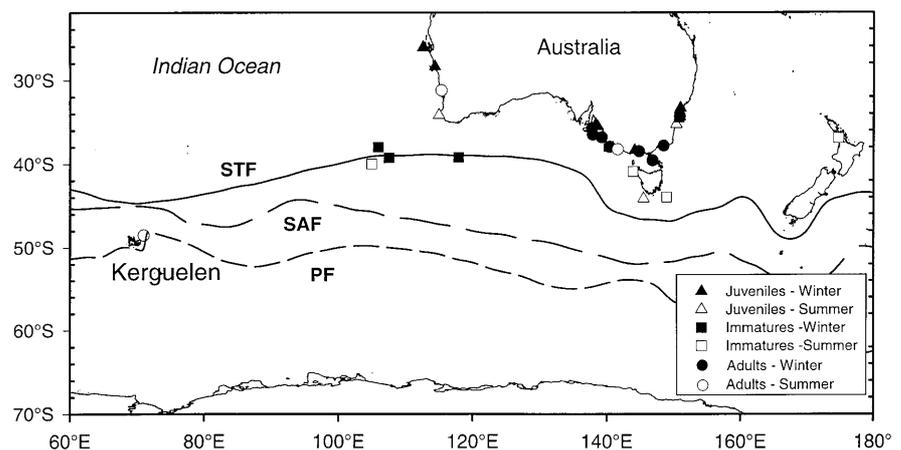
Food analysis

Overall (i.e. all the 69 samples pooled), chick food of black-browed albatrosses at Kerguelen Islands in February–March 1995 was dominated by fish, which accounted for 75.2% of diet by mass. Other significant food sources were penguins (13.1% by mass) and cephalopods (8.9%), while crustaceans and various other organisms were only minor items (0.1% and 2.7%, respectively). In terms of individual food samples, fish prevailed

by mass in 72.5% ($n=50$) of the stomachs and penguin flesh in 13.0% ($n=9$), cephalopods in 10.1% ($n=7$) and carrion of undetermined origin in 4.4% ($n=3$) of the remaining samples.

A total of 612 fresh prey items was recovered from the 69 dietary samples, including 349 crustaceans, 156 fishes and 55 cephalopods. Most of the crustaceans were apparently fish and penguin prey secondarily ingested by albatrosses. The two commonest crustacean species were the hyperiid amphipod *Themisto gaudichaudii* ($n=210$) and the euphausiid shrimp *Euphausia vallentini* ($n=69$), which are known to be major prey for neritic fish and penguins in Kerguelen waters (Duhamel and Hureau 1985; Bost 1991; Y. Cherel, unpublished work). The fish diet was dominated by the channichthyid *Channichthys rhinoceratus* ($n=37$ individuals) which occurred in 44.9% of the samples, followed by the two nototheniids *Notothenia cyanobrancha* ($n=18$ individuals, 23.2% of the samples) and *Lepidonotothen squamifrons* ($n=17$, 23.2%) and by the only other species of channichthyid occurring in the area, the icefish *Champsocephalus gunnari* ($n=16$, 13.0%). Two cephalopods were important prey of black-browed albatrosses in summer: the ommastrephid squid *Todarodes* sp. ($n=33$, 23.2%), probably *Todarodes angolensis* (Cherel and Weimerskirch 1995) and the benthic octopus *Benthoctopus thielei* ($n=16$, 18.8%).

Fig. 2 Distribution of recoveries of black-browed albatrosses banded at Canyon des Sourcils Noirs, Kerguelen Islands (STF Subtropical Front, SAF Subantarctic Front, PF Polar Front). Positions of fronts follow Belkin and Gordon (1996) and Park and Gamberoni (1997)



Ring recoveries

A total of 41 black-browed albatrosses of known age were recovered in the Southern Ocean. They included 14 fledglings (i.e. less than 1 year old), 10 immatures (between 1 and 6 years old) and 17 adults (more than 6 years old; Weimerskirch and Jouventin 1998). All fledglings were found in southern Australia (including Tasmania), except one bird recovered in New Zealand (Fig. 2). Eight immatures were also found in southern Australia, but one occurred in New Zealand and the last in South Africa, at 34°11'S, 22°08'E.

Nine adult albatrosses were recovered in winter (April–September) and the eight remaining birds in summer (October–March). All the winter birds and two summer birds were found on the southern Australian coast, the remaining albatrosses ($n=6$) having been caught in summer on Soviet trawlers operating on the Kerguelen shelf (Fig. 2). Overall (i.e. three age classes pooled), 22 of the 23 black-browed albatrosses recovered in winter were located in southern Australia (Fig. 2), the only exception being an immature recorded from the South African coast.

Discussion

A major finding of the present study is the highly significant difference in stable isotope ratios of feathers between adults and chicks of black-browed albatrosses. Chicks grew feathers in the colony at Kerguelen Islands during summer, during which they were fed neritic prey captured by adults in the vicinity of the colony. The large changes in stable isotope ratios of feathers therefore suggest that foraging grounds and prey species were different during the chick-rearing and adult moulting periods.

A plausible explanation of the higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in adult feathers could be a latitudinal change in foraging grounds occurring in winter, because lower-latitude plankton food bases tend to be enriched in both ^{13}C and ^{15}N relative to higher-latitude waters in the Southern Ocean (Wada et al. 1987). In the Indian Ocean, variations with latitudes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of particulate organic matter (POM) show major changes between 40°S and 45°S, in the vicinity of the Subtropical Front (STF). Briefly, POM values enriched in ^{13}C and ^{15}N occur north of 40°S and depleted values south of 45°S, with an abrupt decrease from north to south at the STF, differences in phytoplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between north and south of the STF averaging 4.5‰ and 3.5‰, respectively (François et al. 1993; Altabet and François 1994). Best and Schell (1996) made use of this isotopic difference to interpret periodic fluctuations in the baleen of southern right whales (*Eubalaena australis*) that move across this oceanic front seasonally. Similarly, we suggest that such a difference in POM $\delta^{15}\text{N}$ values across the front can account for the higher $\delta^{15}\text{N}$ value (+3.3‰) in adult feathers than that of chick feathers and can partly explain the higher (i.e. +2.0‰) $\delta^{13}\text{C}$ value in adult

feathers. The enrichment of adult feathers in both ^{13}C and ^{15}N is consistent with adult moult taking place north of the STF, in an area north of the breeding foraging grounds, because the Kerguelen Islands are located south of STF (Belkin and Gordon 1996; Park and Gamberoni 1997).

Populations of black-browed albatrosses are known to partially segregate in their marine distribution during winter. Band returns show that South Georgian birds mainly winter in South African waters, while the Falkland population congregates off the east coast of South America at this time (Marchant and Higgins 1990; Prince et al. 1998). Sightings of dyed birds and band recoveries from Kerguelen Islands albatrosses indicate that they winter off southern Australia (Weimerskirch et al. 1988; this study). Observations at sea are in agreement with that pattern. Black-browed albatrosses are very rare in oceanic waters of the Southern Ocean in May–August (Marchant and Higgins 1990), a period during which they are more abundant off Southern Australia (Swanson 1973; Wood 1992). This, together with the higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in adult feathers, strongly support the hypothesis that adult black-browed albatrosses from Kerguelen Islands winter and moult in southern Australian waters, which are located north of the STF (Belkin and Gordon 1996).

Little is known of the natural food of wintering albatrosses in southern Australia, except that dead and dying *Sepia apama* provide a predictable and accessible resource in inshore waters at that time (Wood 1992; Nicholls et al. 1995). However, distribution of black-browed albatrosses in Australian marine zones indicate that only 8% of the birds forage in inshore waters while 38%, 35% and 19% have been recorded in more offshore neritic waters, upper slope and lower slope waters, respectively (calculated from Wood 1992). Observations at sea thus suggest that black-browed albatrosses feed mainly upon prey species more oceanic than *S. apama* in winter. Since several previous works on marine trophic webs have shown that offshore/pelagic organisms are more depleted in ^{13}C than inshore/benthic animals (Hobson 1993; Hobson et al. 1994; France 1995), the hypothesis that albatrosses forage further offshore is reinforced by the $\delta^{13}\text{C}$ value of adult feathers which is lower than expected if the main food in winter was *S. apama*. More direct information is clearly needed to determine the feeding habits of albatrosses wintering off southern Australia.

Variations in $\delta^{15}\text{N}$ values in consumers are generally related to dietary differences and changes in trophic levels (Wada et al. 1987; Hobson 1993). In the present study, higher $\delta^{15}\text{N}$ values in adult feathers could indicate that during moult adults fed in the same area but at a higher trophic level than they did during the breeding season. This is unlikely to occur because first, only a few birds occur in the area in winter (Stahl et al., in press) and second, black-browed albatrosses were already feeding on top predators in summer, including the piscivorous fish *Channichthys rhinoceratus* and penguins. Most

of the penguins are moreover migratory and do not occur in the area in winter. Instead, we again find the most likely explanation to be that the different $\delta^{15}\text{N}$ values (together with different $\delta^{13}\text{C}$ values) found in chick and adult feathers occur because adult black-browed albatrosses fed at the same general trophic level but in two different marine areas during summer and winter, south and north of the STF, respectively.

At Kerguelen, the diet of black-browed albatrosses was dominated by fish of the family Nototheniidae and Channichthyidae, which taken together, accounted for 76% of the total number of fish. These fish species are known to occur only on the Kerguelen shelf and upper slope (Duhamel 1997), thus confirming data from satellite tracking showing that breeding albatrosses forage almost exclusively within the 1000 m depth contour in Kerguelen waters (Cherel and Weimerskirch 1995; Weimerskirch et al. 1997).

Stable-carbon and nitrogen isotope ratios varied little among prey of black-browed albatross chicks (Table 2). The higher $\delta^{13}\text{C}$ value of the octopus *Benthoctopus thielei* compared with that of the fish *Lepidonotothen squamifrons* is probably related to its benthic mode of life, benthic organisms often showing more enriched $\delta^{13}\text{C}$ values than pelagic animals (McConnaughey and McRoy 1979; Hobson 1993; France 1995). Since $\delta^{15}\text{N}$ generally provides trophic information (Wada et al. 1987; Hobson 1993), the lower $\delta^{15}\text{N}$ value for medium-sized juveniles of the squid *Todarodes angolensis* can be linked to its diet of pelagic crustaceans and small fish (Y. Cherel, unpublished work), corresponding to a lower trophic level than the fish *C. rhinoceros*, which is exclusively piscivorous (Duhamel and Hureau 1985).

Taking into account both food composition by mass and isotopic values of prey, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of albatross chick diet were estimated to be -19.8% and 11.1% , respectively. Albatross chick feathers thus show a derived enrichment relative to food amounting 0.2% and 1.3% for ^{13}C and ^{15}N , respectively. These values are amongst the lowest enrichment factors, but within the range of values (-0.4 to 4.4% for $\delta^{13}\text{C}$ and 1.1 – 5.6% for $\delta^{15}\text{N}$), obtained from feathers of various species of birds (Mizutani et al. 1990, 1992; Hobson and Clark 1992a, 1992b; Thompson and Furness 1995).

Chicks may differ from adults in their metabolism such that stable isotope fractionation during feather synthesis is not consistent between adults and chicks. However, no changes or changes resulting from dietary shifts were found in the stable isotope ratios between adult and young of various animal species (Minagawa and Wada 1984; Sutoh et al. 1987; Tieszen et al. 1989; Hobson and Welch 1995; Hobson and Sease 1998). The most parsimonious explanation for relative differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in albatross chick and adult feathers is therefore that it reflects different stable isotope values in foods of chicks and adults, rather than a systematic age-related difference in isotopic fractionation (Hobson 1993; see also Schwarcz and Schoeninger 1991).

Stable-carbon and nitrogen isotope ratios were identical in all groups of feathers from adult black-browed albatrosses, and this has important implications for moult itself and the food and feeding ecology during the interbreeding period. Assuming that foodweb isotopic signatures remained constant spatially and seasonally, the lack of isotopic differences between years suggests that birds had similar foraging ecology in both winter 1993 and 1994 and that albatrosses moult in the same area and feed at the same trophic level from one year to the next. In addition, identical stable isotope ratios in feathers formed at the beginning, middle and end of the moulting period indicates no major changes in foraging ecology at this time. Lastly, only a little variation in $\delta^{15}\text{N}$ values and no change in $\delta^{13}\text{C}$ values was observed among individual adult albatrosses, suggesting that most of the population had similar feeding habits and wintering grounds.

The picture emerging from this study is thus that adult black-browed albatrosses from Kerguelen Islands spend most of the wintertime north of the STF, most probably in southern Australian waters, where they feed on natural prey that remain largely unknown.

In conclusion, this study shows that the stable isotope composition of feathers appears particularly suitable for providing information on the location of moulting areas of seabirds and investigating trophic relationships at this time. Due to temporal and spatial segregation between breeding and moulting areas in most seabirds, our knowledge of their food and feeding ecology is mainly restricted to the breeding season when they are accessible in colonies, while little is known when they spend weeks and months at sea between two breeding events. Since feathers are metabolically inert, they conserve and integrate over space and time the isotope signature of the prey ingested during keratin synthesis. They are thus an easy and safe way to gain a new insight on the foraging ecology during the winter months. Such information is needed not only for investigating foraging strategies and for monitoring marine pelagic ecosystems, but also for conservation of seabirds. The stable-isotope analysis of feathers appears particularly suitable for endangered populations for which the small number of individuals precludes an efficient use of the conventional method of ring recovery, and for small species difficult to identify at sea and for which size precludes the use of the more recent method of satellite tracking.

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