Vol. 295: 295–304, 2005 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published June 23

Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel

Petra Quillfeldt[1, 3,*], Rona A. R. McGill[2], Robert W. Furness[1]

[1]Institute of Biomedical and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK
[2]Scottish Universities Research & Reactor Centre, East Kilbride, Glasgow G75 0QF, UK

[3]*Present address:* Max Planck Institute for Ornithology, Vogelwarte Radolfzell, Schlossallee 2, 78315 Radolfzell, Germany

---

ABSTRACT: Analysis of stable isotope ratios in animal tissues has emerged as a powerful tool for determining the trophic level and composition of prey and foraging location. We summarize here data on the stepwise trophic enrichment in $\delta^{15}N$ and latitudinal gradient in $\delta^{13}C$ in the Southern Ocean, and derive a regression equation to estimate latitudes from $\delta^{13}C$ values. We analysed isotope ratios of feathers of the small, pelagic seabird Wilson's storm-petrel *Oceanites oceanicus*, in different breeding stages, in comparison to isotope ratios of 4 other seabird species breeding in close vicinity on King George Island, South Shetland Islands. $\delta^{15}N$ analysis of feathers and albumen from Wilson's storm-petrels indicated a shift in diet from mainly crustaceans during egg formation to an increased proportion of fish during chick-feeding and moulting. $\delta^{15}N$ values of Wilson's storm-petrels during the chick-rearing season were closer to the mainly piscivorous-carnivorous skuas than to krill-feeding penguins, confirming that fish is an important part of their diet. $\delta^{13}C$ analysis of feathers identified 4 distinct foraging areas: $\delta^{13}C$ values in egg-white suggest that egg-forming females moved south to the sea ice edge. This coincides with the distribution of their main prey, Antarctic krill *Euphausia superba*, during this period. During the breeding season, Wilson's storm-petrels fed in the area around the colony, which is also used by penguins and skuas. $\delta^{13}C$ of the feathers indicate that adults migrated to the Subtropical Front and beyond (north of 44°S) during the inter-breeding period. Feathers were also analysed from 10 Wilson's storm-petrels caught by mistnet and thought to be pre-breeders because they lacked foot markings; 8 of these had moulted in the same area as breeding birds, while 2 birds had moulted in an area further north (north of 30°S). Adélie penguins *Pygoscelis adeliae* and Gentoo penguins *P. papua* had significantly different $\delta^{13}C$, suggesting that the Adélie penguins foraged further south than the Gentoo penguins. The foraging areas of brown skuas *Stercorarius antarctica* and south polar skuas *S. maccormicki* could not be separated by their isotope ratios.

KEY WORDS: Stable isotopes · Diet · Foraging area · *Oceanites oceanicus* · Prey

INTRODUCTION

Understanding trophic relationships in dynamic marine ecosystems requires the analysis of diet of the involved species under different conditions such as different prey availabilities and different breeding contexts. The traditional methods (collection of regurgitates, stomach flushing, etc.) used to sample the diet of seabirds can only be applied to birds in breeding colonies. Monitoring diet over the breeding season requires easy access to the colonies and in many cases repeated handling and invasive sampling methods. Analysis of diet away from the breeding sites, e.g. during adult or juvenile migration, is virtually impossible using conventional methods.

---

*Email: petra.quillfeldt@gmx.de

It is, however, possible to reconstruct certain types of diet from isotope values if the diets consist of isotopically distinct components. Previous studies have shown that isotope ratio variation in bird tissues (e.g. feathers, eggs, toenails, blood serum) is determined by the relative proportions of isotopically distinct dietary components (Hobson 1993, 1995, Bearhop et al. 2002).

Tropho-dynamic research using stable isotopes generally focuses on carbon and nitrogen, since the isotopic ratio of these elements varies in relation to the diet, trophic level and foraging location (Owens 1987, Hobson & Welch 1992). The carbon and nitrogen isotope composition ($\delta^{13}C$ and $\delta^{15}N$) differ between organisms and their diets because of a selective retention of the heavy isotope and excretion of the light isotope (Michener & Shell 1994). As a result, organisms generally become enriched in the heavier isotope, i.e. have a higher δ value than their diet. Because this is a long-term process, stable isotope ratios in tissue reflect the diet over a period of weeks to months (Tieszen et al. 1983, Bearhop et al. 2002). In marine food webs there is generally an enrichment of approximately 3.0 to 5.0‰ in nitrogen and 0.8‰ in carbon per trophic level (Minagawa & Wada 1984, Owens 1987, Michener & Shell 1994). Egg albumen of carnivorous peregrine falcons *Falco peregrinus*, prairie falcons *F. mexicanus* and gyrfalcons *F. rusticolis* was 0.8 to 0.9‰ enriched in carbon and 3.1 to 3.3‰ enriched in nitrogen compared with the diet (Hobson 1995), comparable with rates observed for feathers.

Differences in nitrogen isotope ratios are frequently used to determine trophic level and diet composition (e.g. Dahl et al. 2003, Olive et al. 2003, Morrison & Hobson 2004). In contrast to nitrogen, carbon isotope ratios differ more between terrestrial versus marine, inshore versus offshore and pelagic versus benthic food webs than by trophic level. Carbon can therefore be used to assess foraging location (reviewed in Hobson 1999, Rubenstein & Hobson 2004). In the Antarctic, the carbon isotope ratio of POM also varies with the occurrence of sea ice, and there is a strong latitudinal gradient (Rau et al. 1991a,b). Lower latitude plankton tends to be enriched in $\delta^{13}C$ and $\delta^{15}N$ (Wada et al. 1987).

Procellariiformes (petrels, shearwaters, albatrosses, etc.) are oceanic seabirds. They spend most of their time foraging at sea, and come ashore only for breeding. Procellariiformes are thus accessible for biological investigation for only part of the year, and most of our knowledge of food and feeding ecology is restricted to the breeding period.

In the reproductive period, the birds alternate periods of feeding at sea with periods in the colony for pairing, incubation and care of young. In this part of the year, diet studies are usually carried out by stomach contents sampling obtained as regurgitates or by stomach flushing. Stomach contents obtained with these methods are often biased towards less-digestible material, while soft parts are usually underrepresented. While the stable isotope approach may not provide the kind of taxonomic detail given by these approaches, it is noninvasive, not biased towards less digestible material and allows the analysis of diet outside of the breeding season. It has proved useful to combine both stable isotope analysis and conventional dietary assessments to understand trophic relationships in dynamic marine ecosystems (e.g. Sydeman et al. 1997).

Feathers of seabirds can be sampled nondestructively for isotopic analysis, and because different feathers are grown at different times of year, they can potentially give access to dietary information spanning a number of temporal scales. Isotope ratios of eggs can additionally be used to determine diet in early breeding season.

In the present study, we measure isotope signatures of Wilson's storm-petrels breeding on King George Island (South Shetlands) in the maritime Antarctic. Dietary data obtained by conventional methods suggest variability in diet composition (fish versus krill and amphipods) within and between breeding seasons, as well as between birds of different breeding status (Quillfeldt 2002). We predict that stable isotope analysis of feathers should reflect these changes. The analysis of feathers of other birds with known diet compositions breeding at the same site serves as a calibration. Furthermore, we aim to obtain information on the foraging areas during the breeding and inter-breeding period, and compare seasons with good and poor food availability (Quillfeldt 2001, Büßer et al. 2004). Wilson's storm-petrels from the South Shetlands migrate north and spend the austral winter on the open sea, and feathers grown during migration are analyzed to obtain the first data on diet during the inter-breeding period.

MATERIALS AND METHODS

Study site and study species. Wilson's storm-petrels, brown and Antarctic skuas, as well as Gentoo and Adelie penguins sampled in this study breed on King George Island. All bird species were sampled on Potter Peninsula, with a maximum distance of 5 km between breeding sites.

Wilson's storm-petrels were the main focal species in this study, while samples of chick feathers the other species were included for comparative purposes. Wilson's storm-petrels are the smallest endotherm animals breeding in the Antarctic. The life cycle and basic biology of Wilson's storm-petrels have been described by Roberts (1940) and Beck & Brown (1972). The birds spend the austral winter and spring (May to October) at sea, with many crossing the equator and reaching the northern hemisphere. The species breeds in natural cavities, mainly in rock slopes. Wilson's storm-petrels lay single-egg clutches, and have a monogamous mating system (Quillfeldt et al. 2001) with intensive biparental care during incubation and chick-feeding. The first eggs are laid from mid-December, and in January most of the breeding birds are incubating. The peak of chick hatching is in the first half of February, but there is considerable variation in hatching date within the colony (e.g. 49 d time span in 1996; Quillfeldt & Peter 2000). Chicks are left unattended in the burrow during the day when only a few days old, and they are fed by their parents until fledging, without a desertion period. Fledging starts in the colony in the second half of March.

Long-term studies of this species at King George Island have shown that breeding success is highly variable (Büßer et al. 2004). Wilson's storm-petrels feed predominantly on Antarctic krill *Euphausia superba* (reviewed in Quillfeldt 2002). Although the area around the South Shetland Islands does not seem to have a standing stock of krill (Siegel 1986, Priddle et al. 1988), krill may be abundant there in summer (Siegel 1986) depending on krill stock dynamics and oceanographic conditions (Quillfeldt 2001, Büßer et al. 2004). The breeding success from 1996 to 2000 mainly depended on food availability (Quillfeldt 2001), but in other years entombment by snow may be the main cause of chick mortality (Büßer et al. 2004). In the observed period, food availability varied between the years (Büßer et al. 2004). The best food availability was registered in 1996, followed by 2000, while poor prey abundance was evident in the early part of 1998 and especially throughout 1999 (Büßer et al. 2004). These data, initially obtained from feeding rates to chicks, were supported by data on krill abundance in the region (Büßer et al. 2004).

The diets of penguins, skuas and storm-petrels in this area have been determined using conventional methods (Volkmann et al. 1980, Trivelpiece et al. 1987, Reinhardt 1997, Quillfeldt 2002). The methods used were stomach samples of penguins, regurgitates of Wilson's storm-petrels and analysis of pellets of skuas. The diets of seabirds in this area are dominated by 2 prey species that occur at disparate trophic levels: Antarctic krill *Euphausia superba* and Antarctic silverfish *Pleuragramma antarcticum*. In addition, brown skuas are known to take penguins (Reinhardt 1997), and Wilson's storm-petrels have been found to feed on amphipods when krill is scarce (Quillfeldt 2001, 2002).

Sampling of feathers and egg white. In Wilson's storm-petrels, undertail covert feathers were sampled from live fledglings in their burrows, while a rectrix was sampled from breeding adults and mistnet-captured adults. Only 1 feather of each bird was included in the analysis. In the 1996 breeding season, early sampling of rectrices was followed by later sampling of the regrown feathers, giving dietary information for the inter-breeding and breeding seasons. One feather each was sampled from a total of 52 individuals. These comprised feathers from 5 to 6 chicks each in 1999 and 2000; feathers from adults grown during the inter-breeding period (6 each, sampled in 1996, 1997, 1999 and 2000, plus 3 feathers in 2003); 6 feathers from adults grown during the breeding season 1996 and 10 feathers of adults caught by mistnet in 2003. In Wilson's storm-petrels, black spots form with increasing age in the yellow areas of the foot web, thus giving a method of estimating the percentage of prospecting birds in a sample (Quillfeldt et al. 2000). In February 2003, rectrix was sampled from 10 Wilson's storm-petrels captured by mistnet (see Quillfeldt et al. 2000), none of which had black spots in the yellow areas of the foot web of both feet, and 3 of which had one foot only with foot markings. Thus, all 10 birds are relatively young, most probably prebreeders that are prospecting colonies. Egg-white was also sampled for Wilson's storm-petrels, from failed eggs (from 3 eggs in 1998 and 2 eggs in 1999). Egg white was sampled in preference to egg yolk because it has a much lower lipid content.

Body feathers of penguins were collected from chicks killed by brown skuas. In skuas, 2 to 3 chick body feathers were taken by clipping during nest controls from live chicks (1 chick per nest). Sample sizes for feathers of other top predators were: 5 Adelie penguin chicks, 5 Gentoo penguin chicks, 2 chicks of brown skuas, and 8 chicks of south polar skuas.

Before isotopic analysis, egg whites were freeze dried. Feathers and egg whites were ground to a homogeneous fine powder at liquid nitrogen temperature in an analytical mill.

Analysis of isotope ratios. Carbon and nitrogen isotope ratios were measured by continuous-flow isotope ratio mass spectrometry (CF-IRMS) using a Carlo Erba C/N/S analyser linked to a Finnigan Tracer Mat. Approximately 0.7 mg of each sample was combusted in a tin cup for the simultaneous determination of carbon and nitrogen isotope ratios. Two laboratory standards were analysed for every 8 unknown samples in each analytical sequence, allowing instrument drift to be corrected if required. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) deviation from the international standards V-Pee dee belemnite (carbon) and AIR (nitrogen), according to the following equation:

Table 1. Stable isotope ratios of carbon and nitrogen in the Southern Ocean determined in pelagic prey types

Sample	Location	δ^{13}C (‰)	δ^{15}N (‰)	Source
Phytoplankton				
Phytoplankton	63 to 67°S, 64 to 74°W	–27.7	2.2	Frazer (1996)
Zooplankton				
Larval *Euphausia superba*	63 to 67°S, 64 to 74°W	–24.7	3.3	Frazer (1996)
Adult *E. superba*	65°S, 118°E	–29.3	2.7	Wada et al. (1987)
Adult *E. superba*	65°S, 64°W	–29.8	3.6	Dunton (2001)
Adult *E. superba*	62°S, 58°W	–27.2		Corbisier et al. (2004)
Euphausids	59°S, 43°W	–25.7	4.2	Wada et al. (1987)
E. vallentini	47°S, 38°W	–22.0	4.5	Kaehler et al. (2000)
Amphipods	65°S, 64°W	–23.1	5.6	Dunton (2001)
Parathemisto gaudichaudi	60°S, 116°E	–27.1	1.8	Wada et al. (1987)
Crustaceans (Euphausids/copepods) from broad-billed prions	44°S, 176°W	–20.1	6.5	Thompson & Furness (1995)
Crustaceans (mainly *Themisto gaudichaudi*) from thin-billed prions	49°S, 70°E	–25.5	4.5	Cherel et al. (2002a)
Crustaceans (mainly *E. vallentini*) from Antarctic prions	49°S, 70°E	–22.9	3.6	Cherel et al. (2002a)
Mysids	77°S, 166°E	–28.1		Mizutani & Wada (1988)
Cephalopods				
Todarodes angolensis	49°S, 70°E	–18.7	8.1	Cherel et al. (2000)
Benthoctopus thielei	49°S, 70°E	–18.2	10.2	Cherel et al. (2000)
Fish				
Lepidonotothen squamifrons	49°S, 70°E	–20.5	10.3	Cherel et al. (2000)
L. larseni	47°S, 38°W	–21.0	8.0	Kaehler et al. (2000)
Myctophids (97 %) from King Penguins	51°S, 58°W	–21.8	8.4	Cherel et al. (2002b)
Pleuragramma antarcticum	77°S, 166°E	–28.3	10.9	Burns et al. (1998)
Electrona antarctica	61°S, 150°E	–27.1	7.5	Wada et al. (1987)

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

where X is ^{15}N or ^{13}C and R is the corresponding ratio ^{15}N/^{14}N or ^{13}C/^{12}C. Measurement precision of both δ^{15}N and δ^{13}C was estimated to be ≤0.3‰.

Data analysis. The δ^{15}N and δ^{13}C values were compared among birds of different species, age and year using 1-way ANOVA techniques. Because some groups had small sample sizes, we used nonparametric ANOVAs throughout. Significance was assumed at $p < 0.05$.

RESULTS

Carbon and nitrogen isotope ratios of these primary prey species taken from a literature survey (summarised in Table 1) show marked variation in δ^{15}N due to trophic separation, whereas δ^{13}C appears to be influenced by latitude (Table 1, Fig. 1). Stable isotope ratios of carbon and nitrogen of seabirds in the Southern Ocean are summarized in Table 2. Samples derived from low latitudes had high δ^{13}C values (Fig. 1, linear regression for all trophic groups: $\delta^{13}C = -8.52 - 0.26 \times$ latitude, R = –0.77, df = 34, $p < 0.001$); linear regression for seabird chicks only: $\delta^{13}C = -10.24 - 0.21 \times$ latitude, R = –0.82, df = 13, $p < 0.001$). The different trophic levels are well separated in their δ^{15}N values (Tables 1 & 2, Fig. 1).

In our data set of 5 species, we found significant differences in δ^{13}C values and δ^{15}N values between the 5 species (Fig. 2, Table 3; feathers only included; ANOVA for δ^{13}C ratio: $F_{4,74} = 11.6$, p = 0.020; ANOVA for δ^{15}N ratio: $F_{4,74} = 30.4$, $p < 0.001$).

The stable isotope ratios determined for different samples of Wilson's storm-petrels are shown in Table 3. There were differences between groups of Wilson's storm-petrels in δ^{13}C (Fig. 3, Table 3; ANOVA for δ^{13}C: $F_{9,49} = 121.9$, $p < 0.001$; ANOVA for δ^{15}N: $F_{9,49} = 44.9$, $p < 0.001$), and the feather samples can be assigned to 3 groups (Fig. 3).

There was a statistically significant difference between chicks of the 2 yr, 1999 and 2000, in carbon but not in nitrogen isotopes (Fig. 3, Table 3; *t*-test for δ^{13}C: $t = 2.6$, df = 9, p = 0.027, *t*-test for δ^{15}N: $t = 1.6$, df = 9, p = 0.134).

There were no differences between the isotope ratios of adult in different years if only naturally (winter) moulting birds were included (Fig. 3, Table 3; ANOVA for δ^{13}C: $F_{4,27} = 3.7$, p = 0.449; ANOVA for δ^{15}N: $F_{4,27} = 1.9$, p = 0.141). However, the feathers grown during the breeding season 1996 were different in isotope signa-

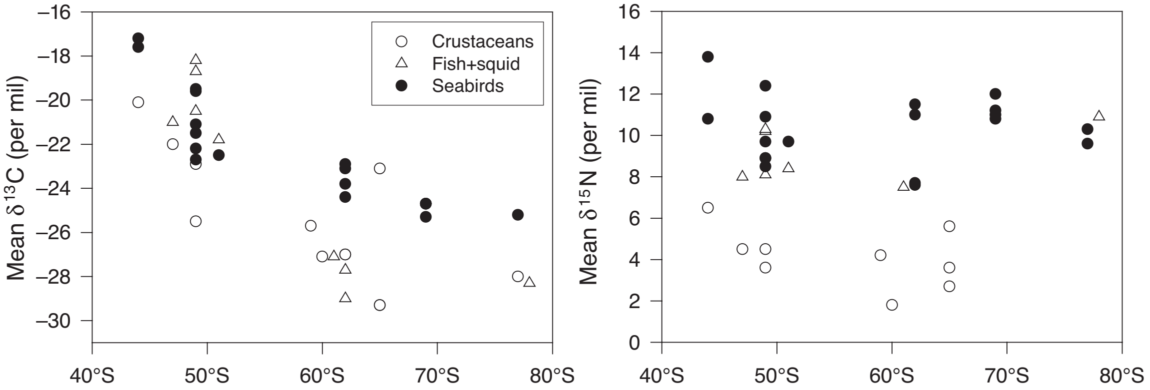

Fig. 1. Variation in the stable isotope ratios of carbon in seabirds and pelagic prey types in the Southern Ocean (for data and sources see Tables 1 & 2)

Table 2. Stable isotope ratios of carbon and nitrogen in the Southern Ocean determined in seabirds in previous studies. Feathers of adult birds marked with * were sampled in the breeding colonies, but were grown elsewhere during moult

Seabird species	Breeding location	δ^{13}C (‰)	δ^{15}N (‰)	Source
Sphenisciformes				
Adélie penguins*	65°S, 64°W	−23.1	5.6	Dunton (2001)
Adélie penguin chicks	77°S, 166°E	−24.5	9.6	Ainley et al. (2003)
Adélie penguin chicks	77°S, 166°E	−25.2	10.3	Mizutani & Wada (1988)
Chinstrap penguin*	65°S, 64°W	−27.0	6.9	Dunton (2001)
King penguins (blood cells)	51°S, 58°W	−22.5	9.7	Cherel et al. (2002b)
Procellariiformes				
Antarctic fulmar				
Chicks	69°S, 79°E	−24.7	11.2	Hodum & Hobson (2000)
Adults*		−24.3	10.5	
Antarctic petrel				
Chicks	69°S, 79°E	−25.3	10.8	Hodum & Hobson (2000)
Adults*		−24.8	9.5	
Cape petrel				
Chicks	69°S, 79°E	−24.7	11.0	Hodum & Hobson (2000)
Adults*		−24.6	9.9	
Snow petrel				
Chicks	69°S, 79°E	−24.7	12.0	Hodum & Hobson (2000)
Adults*		−24.5	9.9	
South Georgian diving petrel				
Chicks	49°S, 70°E	−21.1	8.9	Bocher et al. (2000)
Adults*		−21.5	9.3	Bocher et al. (2000)
Common diving petrel				
Chicks	49°S, 70°E	−19.5	10.9	Bocher et al. (2000)
Adults*		−21.5	9.4	Bocher et al. (2000)
Broad-billed prion chicks	44°S, 176°W	−17.6	10.8	Thompson & Furness (1995)
Thin-billed prion				
Chicks	49°S, 70°E	−22.7	8.9	Cherel et al. (2002a)
Adults*		−24.3	8.5	Cherel et al. (2002a)
Antarctic prion				
Chicks	49°S, 70°E	−21.5	8.5	Cherel et al. (2002a)
Adults*		−17.0	10.5	Cherel et al. (2002a)
Blue petrel				
Chicks	49°S, 70°E	−22.2	9.7	Cherel et al. (2002c)
Adults*		−24.2	9.1	Cherel et al. (2002c)
Black-browed albatross				
Chicks	49°S, 70°E	−19.6	12.4	Cherel et al. (2000)
Adults*	30 to 40°S, 100 to 150°E	−17.6	15.7	Cherel et al. (2000)
Northern giant petrel adults (blood cells)	54°S, 38°W	−21.0	14.4	González-Solís & Croxall (2005)
Southern Giant petrel adults (blood cells)	54°S, 38°W	−22.6	13.1	González-Solís & Croxall (2005)
Lariiformes				
Subantarctic skuas	44°S, 176°W	−17.2	13.8	Thompson & Furness (1995)

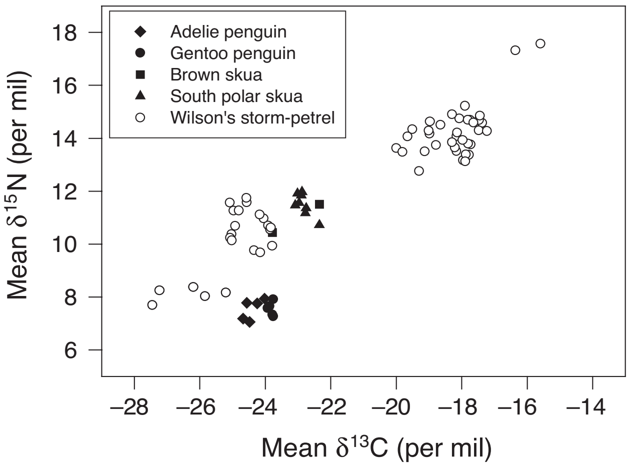

Fig. 2. Variation in the stable isotope ratios of carbon and nitrogen in feathers of 5 species of seabirds breeding at King George Island, South Shetlands (see Table 3 for data)

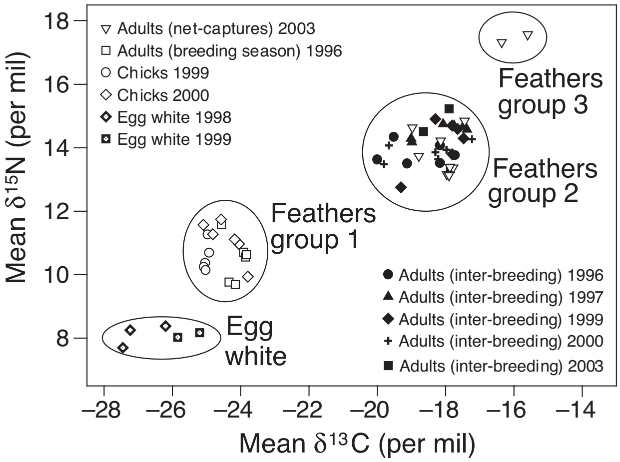

Fig. 3. *Oceanites oceanicus.* Variation in the stable-isotope ratios of carbon and nitrogen in the sample groups of Wilson's storm-petrels (feathers and egg albumen) at King George Island, South Shetlands (see Table 3 for data)

ture to all naturally (winter) moulted feathers of adults (Fig. 3, Table 3; *t*-test for δ^{13}C: $t = 17.2$, df = 31, $p < 0.001$; *t*-test for δ^{15}N: $t = 13.7$, df = 31, $p < 0.001$).

We also observed differences between the 2 penguin species. Adelie and Gentoo penguins had significantly different carbon isotope ratios (Table 3; *t*-test: $t = 4.71$, df = 8, p = 0.002), while the nitrogen isotope ratios were similar (Table 3; *t*-test: $t = 0.020$, df = 8, p = 0.985).

Using the linear regression for carbon isotope ratios as a function of latitude (Fig. 1), we can estimate the latitude at which Wilson's storm-petrels were foraging in different stages of the breeding cycle. According to this, during egg production Wilson's storm-petrels foraged between 62 and 69° S, during the breeding season between 60 and 62° S, and during winter between 35 and 44° S. Finally, 2 of the mistnet-captured Wil-

Table 3. Stable-isotope ratios of carbon and nitrogen in feathers and albumen of seabirds sampled at King George Island, South Shetlands. Mean and standard errors are given. All summer feathers were grown at 62° S, 58° W (plus foraging range for breeding adults), while the locality of winter moult is unknown

Sampling group	Season of moult or egg	N	δ^{13}C (‰)	δ^{15}N (‰)	Diet	Foraging range (km)	Source (diet and range)
Adélie penguin chicks	Summer 2001	5	−24.4 ± 0.1	7.7 ± 0.2	99% *Euphausia superba*		Volkman et al. (1980)
Gentoo penguin chicks	Summer 2001	5	−23.8 ± 0.1	7.6 ± 0.1	85% *E. superba*	16	Trivelpiece et al. (1987), Wilson et al. (1998)
South Polar skua chicks	Summer 2001	8	−22.9 ± 0.1	11.5 ± 0.2	83% fish, 5% krill		Reinhardt (1997)
Brown skua chicks	Summer 2001	2	−23.1 ± 0.1	11.0 ± 0.5	63% penguins, 17% krill	5	Reinhardt (1997)
Wilson's storm-petrels							
Adults 1996	Winter 1995	6	−18.9 ±0.4	13.8 ± 0.1			
Adults 1997	Winter 1996	6	−18.1 ± 0.3	14.5 ± 0.1			
Adults 1999	Winter 1998	6	−17.9 ± 0.3	14.7 ± 0.3			
Adults 2000	Winter 1999	6	−18.5 ± 0.4	13.9 ± 0.1			
Adults 2003	Winter 2002	3	−18.5 ±0.4	13.9 ± 0.5			
Adults 1996	Summer 1996	3	−24.1 ± 0.1	10.5 ± 0.3		250	Croxall & Prince (1980)
Adults (mistnet) 2003	Winter 2002	10	−17.7 ± 0.3	14.5 ± 0.5			
Chicks 1999	Summer 1999	6	−25.0 ± 0.03	10.5 ± 0.2	79% krill, 20% fish, 30% amphipods		Quillfeldt (2002)
Chicks 2000	Summer 2000	6	−24.4 ± 0.2	11.1 ± 0.3	83% krill, 36% fish, 6% amphipods		Quillfeldt (2002)
Egg white 1998	Summer 1998	3	−27.0 ± 0.1	8.1 ± 0.2			
Egg white 1999	Summer 1999	2	−25.5 ± 0.1	8.1 ± 0.1			

son's storm-petrels had isotope ratios indicating they foraged between 31 and 29° S (outside of the Southern Ocean).

DISCUSSION

In the present study, we summarize previously published data on the stepwise trophic enrichment in δ^{15}N and latitudinal gradient in δ^{13}C in the Southern Ocean, and derive a regression equation to estimate latitudes from δ^{13}C values. This is in line with previous findings for plankton in the Antarctic, where lower latitude plankton tends to be enriched in δ^{13}C (Wada et al. 1987). Natural variations in the stable isotopic composition of animal tissues such as bird feathers reflect those in the local environment.

We applied the results in the interpretation of stable isotope data of feathers and egg-white of a small pelagic seabird, the Wilson's storm-petrel *Oceanites oceanicus*. We found a very wide range of carbon and nitrogen isotope ratios in feathers and egg-white of Wilson's storm-petrels (Fig. 2). Similarly, in a sample of 12 seabird species captured in the Weddell Sea, Wilson's storm-petrels exhibited the largest range of δ^{13}C and δ^{15}N values (Rau et al. 1992), suggesting that the diet composition as well as the feeding areas are more variable than in other sampled seabirds. We found pronounced differences in ^{13}C and ^{15}N isotope ratios between different sample groups of Wilson's storm-petrels, suggesting that they differ in foraging grounds and food composition.

Foraging locations of Wilson's storm-petrels

Wilson's storm-petrels forage in sea ice, along the ice edge and in open water (Ainley et al. 1994). The birds have been observed in association with the sea ice mainly in spring (Ainley et al. 1994). Our data are consistent with this pattern, as they suggest southern foraging locations during egg laying.

About 10 d before egg laying, female Wilson's storm-petrels depart from the colony to feed intensely while the large egg (11 g, or 28% of adult body weight) is formed, and adults can potentially cover considerable distances in this time. The egg data was too scarce for statistical analysis, but in 1998 all 3 eggs had lower δ^{13}C values than the eggs in 1999 (Fig. 3), corresponding to a foraging area of 69 to 65° S in 1998 and 65 to 62° S in 1999. This is consistent with other data that suggested that there was a scarcity of food during the early part of the breeding season 1998 around the South Shetland Islands (Quillfeldt 2001, Büßer et al. 2004). For example, in the 1998 breeding season, low breeding activity of Wilson's storm-petrels and late hatching dates, as well as low hatching success were observed. The proposed environmental conditions responsible for the scarcity are an extensive ice cover in spring, which can cause a delay in the release of krill into the open water and subsequent absence of westerly winds, which are necessary for the transport of krill and other prey types from the Bellingshausen Sea to the South Shetlands (Quillfeldt 2001, Büßer et al. 2004).

During the breeding season, Wilson's storm-petrels had δ^{13}C values comparable to the near-shore foragers breeding at King George Island (Gentoo and Adelie penguins), suggesting that they foraged relatively close to the colony. This is in line with estimates of the foraging radius during the breeding season (212 km according to Pennycuick et al. 1984; 250 km according to Croxall & Prince 1980). In the poor season 1999, when 49% of the chicks died from starvation (Quillfeldt 2001, Büßer et al. 2004), chicks had slightly lower carbon ratios than in 2000, indicating more southern origin of their diet. In that season, the chicks were not fed for up to 4 d (P. Quillfeldt unpubl. data), and adults might thus have undertaken foraging trips of longer distance than in 2000.

In the inter-breeding period, the δ^{13}C values of Wilson's storm-petrels were similar to those reported for adult black-browed albatrosses *Diomedea melanophrys* from Iles Kerguelen, which are known to moult in subtropical waters (Table 2; Cherel et al. 2000), and adult Antarctic prions (Table 2; Cherel et al. 2002a). Our calculation of latitude for wintering adults (35 and 44° S) is in agreement with the latitudes used by wintering black-browed albatrosses, suggesting that Wilson's storm-petrels migrate to the area north of 40 to 45° S, known as the Subtropical Front, marked by a strong gradient of δ^{13}C as well as δ^{15}N values of primary production in marine surface waters (François et al. 1993, Altabet & François 1994). Higher δ^{15}N values in adult feathers than in chick feathers of Wilson's storm-petrels are also probably a consequence of this increase in δ^{15}N of POM, rather than different trophic levels of adult birds between the chick-rearing and moulting periods. The enrichment of adult feathers in both δ^{13}C and δ^{15}N is thus consistent with adult foraging in different water masses during breeding and wintering, i.e. south and north of 40 to 45° S, respectively.

We also analysed feathers from a group of 10 Wilson's storm-petrels caught by mistnet and thought to be prebreeders. Of these 10, 8 appeared to have moulted in the same area as the breeding birds, while 2 birds had moulted significantly further north, as suggested by their high δ^{13}C values. Wilson's storm-petrels are often observed in the northern hemisphere, and our data suggest that these may be mainly prebreeders, while adult breeding birds seem to use the South Atlantic at the Subtropical Front.

Foraging locations of penguins and skuas

The 2 penguin species had slight but statistically significant differences in their $\delta^{13}C$ values (Table 3). Because Gentoo penguins are known for their restricted foraging ranges, the data suggest that Adelie penguins foraged slightly further south of the breeding colonies than Gentoo penguins.

In comparison with the penguins, all chicks of South polar skuas and 1 chick of brown skuas were fed prey from an area slightly further north, as suggested by increased $\delta^{13}C$ values. One brown skua chick had a $\delta^{13}C$ value similar to that of penguins, suggesting that this chick was mainly fed a penguin diet on Potter Peninsula.

Diet composition of Wilson's storm-petrels

The diet composition of Wilson's storm-petrels varies between 50 and 100% pelagic crustaceans, the remainder being mainly pelagic fish (see summary in Quillfeldt 2002). While open-water krill filter-feeds on phytoplankton and often has variable amounts of undigested phytoplankton in the intestines, some amphipods are largely carnivorous (e.g. *Themisto gaudichaudii*; Pakhomov & Perisonotto 1996). Thus, the $\delta^{15}N$ values of crustaceans are not homogenous, but vary according to their diet and recent feeding history (see also the large spread of $\delta^{15}N$ values of crustaceans in Table 1 and Fig. 1). Wilson's storm-petrels may take a variety of crustacean prey. It is therefore not possible to calculate exact proportions of crustaceans and fish in the diet from the present data. However, the present data suggest that a shift in diet took place between egg-producing and chick-provisioning adults (Fig. 3). Quillfeldt (2002) found a shift from krill-dominated diet to a mixed diet. This is supported by the present data. In the egg white of Wilson's storm-petrels, we found $\delta^{15}N$ values similar to those of krill-feeding penguins. In contrast, feathers of Wilson's storm-petrels grown during the chick-rearing seasons had $\delta^{15}N$ values similar to skuas (which take a mixed diet with fish as a major component). Eggs in Wilson's storm-petrels are formed during the 'honeymoon' period, in which females do not attend the colony, but feed intensely. Therefore, and because of the large size of the egg, it is unlikely that Wilson's storm-petrels use endogenous reserves, and we are therefore confident that the isotope data from eggs mirror the diet taken during egg-formation (see also Klaassen et al. 2001, Morrison & Hobson 2004).

In contrast to our hypothesis, the nitrogen isotope ratios did not differ between chicks that had received diets differing in the fish versus crustacean ratio. This may be explained by the relatively small difference in the percentage of fish (in 1999, 20% of diet samples contained fish versus 36% in 2000; Quillfeldt 2002), or by the occurrence of a proportion of carnivorous amphipods in 1999.

SUMMARY AND CONCLUSIONS

While the present nitrogen isotope data support a change in diet between incubation and chick-provisioning, smaller dietary changes present between breeding seasons were not distinguishable. The carbon isotope ratios seem to be a useful indicator of foraging areas in terms of latitude, and may be used to study differences between breeding seasons both during egg-formation and chick-provisioning.

Acknowledgements. We are grateful to S. Hahn, M. Ritz and A. Gladbach for contributing feather samples and to NERC for funding the isotope facility. P.Q. received logistical support from the Alfred Wegener Institute for Marine and Polar Research (Bremerhaven, Germany), the National Antarctic Institute of Argentina and Hapag Lloyd Seetouristik GmbH. This study was partly funded by grants provided by the German Academic Exchange Service DAAD and the Deutsche Forschungsgemeinschaft, Germany (Qu 148/1). The study was carried out with permission of the Environmental Agency (Umwelt-Bundesamt) of Germany. The manuscript benefited from the comments of Jacob Gonzáles-Solís and 3 anonymous referees.

LITERATURE CITED

Ainley DG, Ribic CA, Fraser WR (1994) Ecological structure among migrant and resident seabirds of the Scotia-Weddell confluence region. J Anim Ecol 63:347–364

Ainley DG, Ballard G, Barton KJ, Karl BJ, Rau GH, Ribic CA, Wilson PR (2003) Spatial and temporal variation of diet within a presumed metapopulation of Adélie penguins. Condor 105:95–106

Altabet MA, François R (1994) Sedimentory nitrogen isotopic ratio as a recorder for surface ocean nitrate utilization. Global Biogeochem Cycles 8:103–106

Bearhop S, Waldron S, Votier SC, Furness RW (2002) Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. Physiol Biochem Zool 75:451–458

Beck JR, Brown DW (1972) The biology of Wilson's Storm petrel, *Oceanites oceanicus* (Kuhl), at Signy Island, South Orkney Islands. Br Antarct Surv Sci Rep 69:1–54

Bocher P, Cherel Y, Hobson KA (2000) Complete trophic segregation between South Georgian and common diving petrels during breeding at Iles Kerguelen. Mar Ecol Prog Ser 208:249–264

Burns JM, Trumble SJ, Castellini MA, Testa JW (1998) The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. Polar Biol 19:272–282

Büßer C, Kahles A, Quillfeldt P (2004) Breeding success and chick provisioning in Wilson's storm-petrels *Oceanites oceanicus* over seven years — frequent failures due to food shortage and entombment. Polar Biol 27:613–622

Cherel Y, Hobson KA, Weimerskirch H (2000) Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. Oecologia 122:155–162

Cherel Y, Bocher P, De Broyer C, Hobson KA (2002a) Food and feeding ecology of the sympatric thin-billed *Pachyptila belcheri* and Antarctic *P. desolata* prions at Iles Kerguelen, Southern Indian Ocean. Mar Ecol Prog Ser 228: 263–281

Cherel Y, Pütz K, Hobson KA (2002b) Summer diet of king penguins (*Aptenodytes patagonicus*) at the Falkland Islands, southern Atlantic Ocean. Polar Biol 25:898–906

Cherel Y, Bocher P, Trouvé C, Weimerskirch H (2002c) Diet and feeding ecology of blue petrels *Halobaena caerulea* at Iles Kerguelen, Southern Indian Ocean. Mar Ecol Prog Ser 228:283–299

Corbisier TN, Petti MAV, Skowronski RSP, Brito TAS (2004) Trophic relationships in the nearshore zone of Martel Inlet (King George Island, Antarctica): delta C-13 stable-isotope analysis. Polar Biol 27:75–82

Croxall JP, Prince PA (1980) Food, feeding ecology and ecological segregation of seabirds at South Georgia. Biol J Linn Soc 14:103–131

Dahl TM, Falk-Petersen S, Gabrielsen GW, Sargent JR, Hop H, Millar RM (2003) Lipids and stable isotopes in common eider, black-legged kittiwake and northern fulmar: a trophic study from an Arctic fjord. Mar Ecol Prog Ser 256: 257–269

Dunton KH (2001) Delta N-15 and delta C-13 measurements of Antarctic peninsula fauna: Trophic relationships and assimilation of benthic seaweeds. Am Zool 41:99–112

François R, Altabet MA, Goericke R (1993) Changes in the δ13 C of surface water particulate organic matter across the subtropical convergence in the SW Indian Ocean. Global Biogeochem Cycles 7:627–644

Frazer TK (1996) Stable isotope composition (delta 13C and delta 15N) of larval krill, Euphausia superba, and two of its potential food sources in winter. J Plankton Res 18: 1413–1426

González-Solís J, Croxall JP (2005). Differences in foraging behaviour and feeding ecology in giant petrels. In: Ruckstuhl KE, Neuhaus P (eds) Sexual segregation in vertebrates. Cambridge University Press, Cambridge

Hobson KA (1993) Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Mar Ecol Prog Ser 95:7–18

Hobson KA (1995) Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: Patterns of isotopic fractionation and turnover. Condor 97: 752–762

Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120:314–326

Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using d-13C and d-15N analysis. Mar Ecol Prog Ser 84:9–18

Hodum PJ, Hobson KA (2000) Trophic relationships among Antarctic fulmarine petrels: insights into dietary overlap and chick provisioning strategies inferred from stable-isotope (δ^{15}N and δ^{13}C) analyses. Mar Ecol Prog Ser 198: 273–281

Kaehler S, Pakhomov EA, McQuaid CD (2000) Trophic structure of the marine food web at the Prince Edward Islands (Southern Ocean) determined by δ^{13}C and δ^{15}N analysis. Mar Ecol Prog Ser 208:13–20

Klaassen M, Lindström Å, Meltofte H, Piersma T (2001) Arctic waders are not capital breeders. Nature 413:794

Michener RH, Schell DM (1994) Stable isotope ratios as tracers in marine aquatic food webs. In: Lajtha K, Michener RH (eds) Stable isotopes in ecology and environmental Science. Blackwell Scientific Publications, Oxford, p 138–157

Minagawa M, Wada E (1984) Stepwise enrichment of 15 N along food chains: further evidence and the relation between d 15 N and animal age. Geochim Cosmochim Acta 48:1135–1140

Mizutani H, Wada E (1988) Nitrogen and carbon isotope ratios in seabird rookeries and their ecological implications. Ecology 69:340–349

Morrison RIG, Hobson KA (2004) Use of body stores in shorebirds after arrival on high-arctic breeding grounds. Auk 121:333–344

Olive PJW, Pinnegar JK, Polunin NVC, Richards G, Welch R (2003) Isotope trophic-step fractionation: a dynamic equilibrium model. J Anim Ecol 72:608–617

Owens NJP (1987) Natural variation in 15N in the marine environment. Adv Mar Biol 24:389–451

Pakhomov EA, Perissinotto R (1996) Trophodynamics of the hyperiid amphipod *Themisto gaudichaudi* in the South Georgia region during late austral summer. Mar Ecol Prog Ser 134:91–100

Pennycuick CJ, Croxall JP, Prince PA (1984) Scaling foraging radius and growth rate in petrels and albatrosses (*Procellariiformes*). Ornis Scand 15:145–154

Priddle J, Croxall JP, Everson I, Heywood RB, Murphy EJ, Prince PA, Sear CB (1988) Large-scale fluctuations in distribution and abundance of krill—a discussion of possible causes. In: Sarhage D (ed) Antarctic Ocean and resources variability. Springer-Verlag, Berlin, p 169–182

Quillfeldt P (2001) Variation of breeding success in Wilson's storm-petrels: influence of environmental factors. Antarct Sci 13:400–409

Quillfeldt P (2002) Seasonal and annual variation in the diet of breeding and non-breeding Wilson's storm-petrels on King George Island, South Shetland Islands. Polar Biol 25: 216–221

Quillfeldt P, Peter HU (2000) Provisioning and growth in chicks of Wilson´s storm-petrels *Oceanites oceanicus* on King George Island, South Shetland Islands. Polar Biol 23: 817–824

Quillfeldt P, Schmoll T, Peter HU (2000) The use of foot web coloration for the estimation of prebreeder numbers in Wilson's storm-petrels, *Oceanites oceanicus*. Polar Biol 23: 802–804

Quillfeldt P, Schmoll T, Peter HU, Epplen JT, Lubjuhn T (2001) Genetic monogamy in Wilson's Storm-Petrel. Auk 118:245–251

Rau GH, Takahashi T, Des Marais DJ, Sullivan CW (1991a) Particulate organic matter δ^{13}C variations across the Drake Passage. J Geophys Res 96:15131–15135

Rau GH, Hopkins TL, Torres JJ (1991b) ^{15}N/^{14}N and ^{13}C/^{12}C in Weddell Sea invertebrates: implications for feeding diversity. Mar Ecol Prog Ser 77:1–6

Rau GH, Ainley DG, Bengtson JL, Torres JJ, Hopkins TL (1992) ^{15}N/^{14}N and ^{13}C/^{12}C in Weddell sea birds, seals, and fish: implications for diet and trophic structure. Mar Ecol Prog Ser 84:1–8

Reinhardt K (1997) Food and feeding of Antarctic skua chicks *Catharacta antarctica lonnbergi* and *C. maccormicki*. J Ornithol 138:199–213

Roberts B (1940) The life cycle of Wilson's petrel *Oceanites oceanicus* (Kuhl). Sci Rep British Graham Land Exped 1: 141–194

Rubenstein DR, Hobson KA (2004) From birds to butterflies: animal movement patterns and stable isotopes. Trends Ecol Evol 19:256–263

Siegel V (1986) Untersuchungen zur Biologie des Antarktischen Krill *Euphausia superba*, im Bereich der Bransfield Strasse und angrenzender Gebiete. Mitt Inst Seefisch Hamburg 38:1–244

Sydeman WJ, Hobson KA, Pyle P, McLaren EB (1997) Trophic relationships among seabirds in central California: Combined stable isotope and conventional dietary approach. Condor 99:327–336

Thompson DR, Furness RW (1995) Stable-isotope ratios of carbon and nitrogen in feathers indicate seasonal dietary shifts in northern Fulmars. Auk 112:493–498

Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for d13C analysis of diet. Oecologia 57:32–37

Trivelpiece WZ, Trivelpiece SG, Volkman NJ (1987) Ecological segregation of Adélie, gentoo and chinstrap penguins at King George Island, Antarctica. Ecology 68: 351–361

Volkman NJ, Presler P, Trivelpiece W (1980) Diets of pygoscelid penguins at King George Island, Antarctica. Condor 82:373–378

Wada E, Terazaki M, Kabaya Y, Nemoto T (1987) 15N and 13C abundances in the Antarctic ocean with emphasis on the biogeochemical structure of the food web. Deep-Sea Res I 34:829–841

Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

Submitted: August 26, 2004; Accepted: January 18, 2005
Proofs received from author(s): May 23, 2005