

Trophic relationships among Antarctic fulmarine petrels: insights into dietary overlap and chick provisioning strategies inferred from stable-isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) analyses

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ABSTRACT: We used stable-isotope analysis (SIA) to evaluate trophic relationships in an Antarctic seabird community. We determined natural abundances of stable-nitrogen ($\delta^{15}\text{N}$) and stable-carbon ($\delta^{13}\text{C}$) isotopes from blood samples ($n = 283$) from adults and chicks of 4 Antarctic fulmarine petrel species (*Fulmarus glacialisoides*, *Thalassoica antarctica*, *Daption capense* and *Pagodroma nivea*) during 2 consecutive breeding seasons, 1994/1995 and 1995/1996, and from representative prey items. Our objectives were to use the isotope approach to infer trophic status and diet composition within and between species, addressing interspecific and temporal variability within this seabird community, and to investigate potential age-related differences in assumed trophic position within species. Prey $\delta^{13}\text{C}$ values ranged from -26.8‰ in amphipods to -23.9‰ in adult Antarctic silverfish. Seabird $\delta^{13}\text{C}$ values ranged from -25.3‰ in Antarctic petrel chicks to -23.8‰ in cape petrel adults. Prey $\delta^{15}\text{N}$ values ranged from 4.0‰ in euphausiids to 10.7‰ in adult Antarctic silverfish. Seabird $\delta^{15}\text{N}$ values ranged from 8.4‰ in Antarctic petrel adults to 12.0‰ in snow petrel chicks. There was considerable interspecific overlap in assumed trophic positions amongst the 4 petrel species, and we conclude all species consumed fish and krill. Despite this apparent overlap, the range in $\delta^{15}\text{N}$ values for petrels corresponded to the equivalent of 1 full trophic level, and estimated trophic level varied with both species and age. A simple trophic level model, constructed based on the $\delta^{15}\text{N}$ data, predicted trophic levels ranging from 2.3 in krill to 4.7 in snow petrel chicks. Snow petrels and Antarctic fulmars tended to have higher $\delta^{15}\text{N}$ values than Antarctic and cape petrels, suggesting a higher proportion of fish in their diets. Petrel chicks consistently had higher $\delta^{15}\text{N}$ values than adults, which suggests trophic segregation between adults and chicks. We discuss advantages of selectively provisioning chicks with higher trophic level prey. Extensive overlap and a relatively narrow range of $\delta^{15}\text{N}$ values are consistent with a food web comprised of few trophic steps.

KEY WORDS: Trophic relationships · Diet · Stable-isotope analysis · *Pagodroma nivea* · *Daption capense* · *Thalassoica antarctica* · *Fulmarus glacialisoides* · Antarctica · Chick-provisioning

INTRODUCTION

Trophic relations within Southern Ocean food webs are of considerable interest, yet quantitative measures

of trophic interactions remain poorly developed (Hempel 1985, Kock & Shimadzu 1994). Most quantitative characterizations of trophic structure in Antarctic marine ecosystems have focused primarily on lower trophic levels (Wada et al. 1987, but see Rau et al. 1992), with the role of upper-level predators such as seabirds receiving relatively little attention. What is known is largely based on conventional stomach-sampling analysis which, alone, may provide biased results (Hobson et al. 1994).

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In seabird or marine foodweb studies, stable-isotope analysis (SIA) offers a number of advantages over conventional diet-sampling methods (Tieszen et al. 1983, Duffy & Jackson 1986, Hobson & Sealy 1991, Hobson et al. 1994, Ben-David et al. 1997). Trophic structure in the Antarctic marine ecosystem is amenable to SIA because relatively few taxa provide key nutritional and energetic links between primary producers and upper-level consumers (Bonner 1984, Everson 1984). For example, previous studies of Antarctic seabird diets suggest that seabirds exploit a small number of common food types consisting primarily of mesopelagic and epipelagic fishes and zooplankton including *Euphausia* spp. (krill), amphipods and copepods (e.g. Whitehead 1991, Ainley et al. 1992, Rau et al. 1992).

We investigated trophic relationships within an Antarctic fulmarine petrel community using SIA. We inferred relative trophic positions of both petrels and representative prey species through analyses of nitrogen- and carbon-isotope ratios. Our objectives were to compare trophic status derived from stable-isotope analyses and diet composition within and between species, addressing interspecific and temporal variability within this seabird community.

We were also interested in potential intraspecific differences based on age, there being no good *a priori* reason to expect diets of parents and offspring to be the same. Indeed, nutritional requirements of adults and growing chicks are different (Klasing 1998), and this may translate into dietary differences. SIA provides a technique with which we can evaluate selective provisioning by adults and, when combined with conventional dietary analyses, can represent a powerful analytical tool for investigating time-integrated patterns of diet (Hobson 1993).

METHODS

We collected whole-blood samples on Hop Island (68° 50' S, 78° 43' E), Rauer Island group, East Antarctica from breeding adults and chicks of the following species: Antarctic fulmar *Fulmarus glacialisoides*, Antarctic petrel *Thalassoica antarctica*, cape petrel *Daption capense*, and snow petrel *Pagodroma nivea*. The Rauer Island group is one of 3 known areas in Antarctica in which these 4 petrel species breed sympatrically. We collected blood samples (20 to 50 µl) from 10 adults and 10 chicks of each species during each of 2 stages of the nestling period, early and late. Intervals between sampling periods ranged from 20 to 28 d to permit temporal comparisons of diets. After collection, we separated samples into plasma and cellular fractions using a hand centrifuge, and stored them in the

snow until they were transported to a freezer at Davis Station. Combined sample sizes of breeding adults and chicks in the 1994/1995 and 1995/1996 seasons were 123 and 160, respectively.

We analyzed frozen samples of Antarctic krill *Euphausia superba* and juvenile Antarctic silverfish *Pleuragramma antarcticum* collected by the Australian Antarctic Division in 1993 and 1994 during marine science cruises in Prydz Bay. We obtained samples of a second krill species, *Euphausia crystallophias*, of adult Antarctic silverfish, and of amphipods *Themisto gaudichaudii* from diet samples collected from adult petrels using the water-offloading technique (Wilson 1984). We shipped frozen samples to Saskatoon, Canada, for analysis.

Stable-isotope measurements. We freeze-dried the cellular fraction of the blood samples and powdered them with a mortar and pestle. We used the same processes of freeze-drying and powdering for prey samples, but additionally removed lipids using a Soxhlet apparatus with chloroform solvent; we acidified krill and amphipod samples with 1 N HCl to remove carbonates before isotopic analysis. We then oven-dried samples at 60°C and placed 1 mg of each sample into a tin cup, crushed the cup into a pellet, and flash-combusted it at 1850°C in a Robo Prep elemental analyzer interfaced with a Europa 20:20 continuous-flow isotope-ratio mass spectrometer.

Stable-isotope concentrations are expressed in delta (δ) notation as parts per thousand (‰), and were calculated as:

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

where $X = {}^{15}\text{N}$ or ${}^{13}\text{C}$ and $R =$ the corresponding ratio ${}^{15}\text{N}:{}^{14}\text{N}$ or ${}^{13}\text{C}:{}^{12}\text{C}$. R_{standard} for ${}^{15}\text{N}$ and ${}^{13}\text{C} =$ atmospheric N_2 (AIR) and the PDB standard, respectively. Based on numerous measurements of organic standards, the analytical precision of these measurements is estimated to be ± 0.3 and $\pm 0.1\%$ for nitrogen and carbon, respectively (Hobson et al. 1994).

Isotopic models. Carbon is typically not a useful indicator of trophic position in marine food webs (e.g. Fry 1988, Hobson & Welch 1992) and, therefore, we did not estimate seabird trophic positions using $\delta^{13}\text{C}$ values. However, the analysis of 2 stable isotopes in consumer tissues may allow greater segregation of species than the use of a single isotope (Peterson et al. 1985, Hobson 1993). Stable-carbon isotope ratios have also been used to infer inshore or benthically linked feeding with offshore or more pelagic feeding in seabirds (Hobson et al. 1994, France 1995). Therefore, we measured $\delta^{13}\text{C}$ values in all blood samples to assess neritic versus pelagic foraging grounds.

The abundance of stable isotopes in various biochemical components of foods fractionates or changes

when incorporated into consumer tissues according to the following relationship:

$$D_t = D_d + \Delta_{dt} \quad (2)$$

where D_t = isotopic abundance in consumer tissue, D_d = the isotopic abundance in the diet, and Δ_{dt} = isotopic fractionation factor between tissue and diet. The isotopic signature of the average diet can be inferred from the isotopic abundance measurement of the consumer tissue once Δ_{dt} is known for a particular trophic relationship (Tieszen et al. 1983). We used a $\delta^{15}\text{N}$ trophic enrichment factor of 3.3‰ calculated by Wada et al. (1987) for the Ross Sea.

In a simple system in which a consumer utilizes 2 dietary options that are segregated trophically, an estimate of the relative contribution of each prey type to the diet may be calculated by:

$$P_a = (D_t - D_b)/(D_b - D_a) \quad (3)$$

where P_a = proportion of diet derived from Prey Source a, D_t = the isotopic value of consumer tissue measured, and D_b and D_a = consumer tissue isotopic values corresponding to a diet exclusively comprised of Prey Type b and a, respectively. We employed this method to estimate the relative contributions of krill and Antarctic silverfish to the diets of adult and nestling petrels. We assumed that the diets were comprised solely of these 2 trophic levels based on results from conventional diet sampling in which these 2 prey species comprised 99.8% of the diet by mass (Hodum unpubl. data).

To calculate the trophic level of a consumer (TL_{consumer}), we assumed a trophic level of 2.3 for Antarctic krill *Euphausia superba* (S. Nicol pers. comm.) and an isotopic enrichment factor between trophic levels (TL)

of 3.3‰. The trophic level in the food web may be estimated according to:

$$TL_{\text{consumer}} = 2.3 + (D_{\text{consumer}} - D_{\text{krill}})/3.3‰ \quad (4)$$

where D_{consumer} = isotopic signature of the consumer and D_{krill} = that of Antarctic krill.

Values are presented as mean \pm 1 SD. When ANOVA results were significant ($p < 0.05$), comparisons were made by a Tukey multiple-comparison test ($p < 0.05$).

RESULTS

Stable nitrogen isotope ratios

$\delta^{15}\text{N}$ concentrations ranged from $4.0 \pm 0.2‰$ in *Euphausia superba* to $12.0 \pm 0.4‰$ in snow petrel *Pagodroma nivea* chicks (Tables 1 & 2, Fig. 1). Overall, there were highly significant differences in $\delta^{15}\text{N}$ values among species and age groups (ANOVA: $F_{12, 328} = 49.2$, $p < 0.0001$). Among prey species, *Pleuragramma antarcticum* had significantly higher $\delta^{15}\text{N}$ values than amphipods and both krill species. Amphipods differed from *E. superba* and the 1 sample of *E. crystallophias*. $\delta^{15}\text{N}$ values also differed strongly between petrel species (ANOVA: $F_{7, 151} = 9.5$, $p < 0.0001$).

We compared $\delta^{15}\text{N}$ concentrations between years for each species and age group. Antarctic petrel *Thalassoica antarctica* adults were the only group to show a significant difference between years, with higher $\delta^{15}\text{N}$ values in 1995/1996 ($t_{19} = 3.16$, $p < 0.01$). There were no significant differences for any other group, although there was a consistent but non-significant trend among all 4 species and both age groups for $\delta^{15}\text{N}$ values to be 0.2 to 0.6‰ higher in 1995/1996 (Table 2).

Table 1. Stable carbon- and nitrogen-isotope concentrations (‰, mean \pm SD) of lipid-free muscle tissue of prey items from diet of petrels and results of 1-way ANOVA tests for differences among species for each isotope. Trophic level estimated by Eq. (4). Within columns, values sharing superscript letters do not differ statistically (Tukey's multiple-comparison test, $p > 0.05$); only results of this study where $n > 1$ were included in comparison. na: not applicable

Prey species	n	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Derived trophic level	Study location	Source
<i>Euphausia superba</i> (Antarctic krill)	10	4.0 ± 0.2^a	-25.0 ± 0.3^{ab}	2.3	Prydz Bay	This study
		2.3	ca -29	ca 2.2	Weddell Sea	Rau et al. (1991)
		2.7	-29.3	1.7	Australian sector	Wada et al. (1987)
		na	na	2.4	Weddell Sea	Hopkins & Torres (1989)
<i>Euphausia crystallophias</i> (krill)	1	5.1	-25.3	2.6	Prydz Bay	This study
<i>Themisto gaudichaudii</i> (amphipods)	5	6.8 ± 0.9^b	-26.8 ± 0.4^a	3.1	Prydz Bay	This study
		1.8	-27.1	1.4	Australian sector	Wada et al. (1987)
<i>Pleuragramma antarcticum</i> (juv.)	10	9.6 ± 0.4^c	-24.3 ± 0.3^{bcd}	3.9	Prydz Bay	This study
<i>Pleuragramma antarcticum</i> (ad.)	13	10.7 ± 1.2^d	-23.9 ± 0.7^{bd}	4.3	Prydz Bay	This study
		10.9 ± 9.2	-28.3 ± 0.4	4.4	McMurdo Sound	Burns et al. (1998)
ANOVA		$F_{5, 33} = 117.8$ $p < 0.0001$	$F_{5, 33} = 36.0$ $p < 0.0001$			

Table 2. Stable nitrogen ($\delta^{15}\text{N}$) and carbon isotope ($\delta^{13}\text{C}$) concentrations (‰ , mean \pm SD) of cellular fractions of petrel blood as a function of age and year. Derived trophic level (Eq. 4) and % euphausiids (Eq. 3) estimated from $\delta^{15}\text{N}$ values. ANFU: Antarctic fulmar *Fulmarus glacialisoides*; ANPE: Antarctic petrel *Thalassoica antarctica*; CAPE: cape petrel *Daption capense*; SNPE: snow petrel *Pagodroma nivea*; SIA: stable-isotope analysis

Seabird species	n	Year	Mean $\delta^{15}\text{N}$	Mean $\delta^{13}\text{C}$	Derived trophic level	Mean % euphausiid (SIA)
ANFU						
Adult	21	1994–95	10.0 \pm 1.4	-24.1 \pm 0.9	4.1	61
	20	1995–96	10.5 \pm 0.6	-24.3 \pm 0.3	4.2	53
Chick	20	1994–95	10.7 \pm 0.7	-24.9 \pm 0.3	4.3	49
	19	1995–96	11.2 \pm 1.1	-24.7 \pm 0.5	4.4	40
ANPE						
Adult	8	1994–95	8.4 \pm 0.3	-25.2 \pm 0.4	3.6	89
	20	1995–96	9.5 \pm 0.9	-24.8 \pm 0.4	3.9	70
Chick	20	1994–95	10.2 \pm 0.9	-25.2 \pm 0.4	4.1	57
	20	1995–96	10.8 \pm 1.0	-25.3 \pm 0.3	4.3	47
CAPE						
Adult	13	1994–95	9.6 \pm 0.7	-23.8 \pm 0.6	4.0	68
	20	1995–96	9.9 \pm 0.5	-24.6 \pm 0.3	4.0	64
Chick	16	1994–95	10.7 \pm 0.8	-24.9 \pm 0.6	4.3	49
	20	1995–96	11.0 \pm 2.2	-24.7 \pm 0.5	4.4	44
SNPE						
Adult	15	1994–95	9.7 \pm 1.0	-24.2 \pm 0.5	4.0	66
	20	1995–96	9.9 \pm 1.4	-24.5 \pm 0.6	4.1	62
Chick	18	1994–95	11.7 \pm 0.6	-24.6 \pm 0.5	4.6	31
	20	1995–96	12.0 \pm 0.4	-24.7 \pm 0.2	4.7	26

Interspecific comparisons revealed differences in $\delta^{15}\text{N}$ values for both adults and chicks in both years (Table 2). We found interspecific differences between adults in both 1994/1995 (ANOVA: $F_{3,56} = 4.18$, $p = 0.01$) and 1995/1996 (ANOVA: $F_{3,79} = 3.24$, $p = 0.03$). In 1994/1995, adult Antarctic fulmars *Fulmarus glacialisoides* and snow petrels had a higher $\delta^{15}\text{N}$ concentration than Antarctic petrel adults. Fulmars also had higher $\delta^{15}\text{N}$ values than Antarctic petrel adults in 1995/1996. No other species differed.

There were also interspecific differences in $\delta^{15}\text{N}$ values for chicks in both years (ANOVA: $F_{3,73} = 11.85$, $p < 0.0001$ in 1994/1995; ANOVA: $F_{3,78} = 3.01$, $p = 0.04$ in 1995/1996). $\delta^{15}\text{N}$ concentrations for snow petrel chicks were significantly higher than those for chicks of the other 3 species in 1994/1995. In 1995/1996 $\delta^{15}\text{N}$ values for snow petrel chicks were higher than those for chicks of Antarctic petrels.

We compared $\delta^{15}\text{N}$ values for early and late sampling periods within seasons for each species. Antarctic fulmar adults and chicks had higher $\delta^{15}\text{N}$ values later in the season in both 1994/1995 (adults: $t_{20} =$

-5.01, $p < 0.001$; chicks: $t_{19} = -3.87$, $p = 0.001$) and 1995/1996 (adults: $t_{19} = -5.39$, $p < 0.001$; chicks: $t_{18} = -4.07$, $p < 0.001$). Antarctic petrel adults were sampled only once during 1994/1995, and could not be compared. In 1995/1996 Antarctic petrel adults had comparable $\delta^{15}\text{N}$ values in both sampling periods ($t_{19} = 1.20$, $p = 0.24$). Antarctic petrel chicks showed no difference between periods in 1994/1995 ($t_{19} = 0.65$, $p = 0.52$) but had higher early-period $\delta^{15}\text{N}$ values in 1995/1996 ($t_{19} = 3.70$, $p = 0.002$). Cape petrels *Daption capense* showed little intraseasonal change, with only 1994/1995 chicks ($t_{15} = -2.39$, $p = 0.03$) differing between periods. Snow petrel adults and chicks were consistent between years: $\delta^{15}\text{N}$ values were higher during the late period in both 1994/1995 (adults: $t_{14} = -2.84$, $p = 0.01$; chicks: $t_{17} = -2.18$, $p = 0.04$) and 1995/1996 (adults: $t_{19} = -11.87$, $p < 0.001$; chicks: $t_{19} = -3.88$, $p = 0.001$). Because no consistent variation emerged within a season, we pooled the data by season for each species and age.

Adult and chick $\delta^{15}\text{N}$ concentrations differed for each species (Table 2), with chicks generally having higher values. In 1994/1995, Antarctic petrel ($t_{19} = 5.22$, $p < 0.001$), cape petrel ($t_{15} = 3.86$, $p < 0.001$), and snow

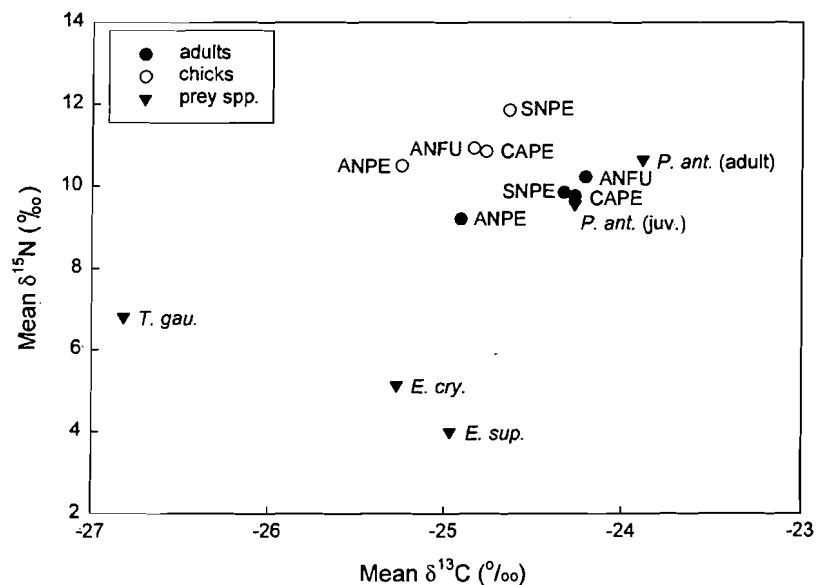


Fig. 1. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of petrels and prey species during 1994/1995 and 1995/1996 breeding seasons (error bars omitted for clarity). Standard deviations given in Table 2. Petrel abbreviations as in Table 2; prey abbreviations: *E. sup.* = *Euphausia superba*; *E. cry.* = *Euphausia crystallophias*; *T. gau.* = *Themisto gaudichaudii*; *P. ant.* = *Pleuraogramma antarcticum*

petrel ($t_{17} = 6.69$, $p < 0.001$) chicks had significantly higher $\delta^{15}\text{N}$ values than adults. Antarctic fulmar chicks showed a similar pattern, but the difference was not significant ($t_{19} = 1.93$, $p = 0.06$). In 1995/1996, chicks of all 4 species had higher $\delta^{15}\text{N}$ concentrations than adults (Antarctic petrel: $t_{19} = 4.25$, $p < 0.001$; cape petrel: $t_{19} = 2.15$, $p = 0.04$; snow petrel: $t_{19} = 5.97$, $p < 0.001$; Antarctic fulmar: $t_{19} = 2.56$, $p = 0.01$).

We tested the degree of dietary breadth using Bartlett's test for homogeneity of variances (Table 3). Antarctic fulmars and Antarctic petrels showed no difference in dietary breadth between adults and chicks. Cape and snow petrel adults and chicks, however, differed significantly in the degree of dietary variability. The diet of snow petrel chicks was less variable than that of adults ($B = 1.41$, $p < 0.0001$), while the diet of cape petrel chicks was more variable than that of adults ($B = 1.54$, $p < 0.0001$). Dietary breadth also differed between species within a season and within species between seasons, but no consistent patterns were apparent (Table 3).

Stable carbon-isotope results

$\delta^{13}\text{C}$ concentrations ranged from $-26.8 \pm 0.4\text{‰}$ in amphipods to $-23.8 \pm 0.6\text{‰}$ in cape petrel adults (Tables 1 & 2, Fig. 1). Overall, species and age groups differed significantly (ANOVA: $F_{12,328} = 19.7$, $p < 0.0001$), although a consistent pattern of trophic enrichment in $\delta^{13}\text{C}$ was not evident in this food web. There were interspecific differences in $\delta^{13}\text{C}$ concentrations among petrel species (ANOVA: $F_{7,151} = 8.1$, $p < 0.0001$); however, the similarity in $\delta^{13}\text{C}$ values be-

tween birds and pelagic prey and the overlap in values among bird species suggest that all petrel species foraged pelagically and not inshore.

DISCUSSION

The fulmarine petrel community breeding on Hop Island and its constituent prey species showed typical step-wise trophic enrichment of ^{15}N from krill to seabirds (e.g. Hobson et al. 1994). Stable carbon-isotope values did not show a similar enrichment nor did they reveal a gradient indicative of inshore/offshore foraging distributions (e.g. France 1995). Although $\delta^{13}\text{C}$ values differed statistically between species, the values were not sufficiently different as to suggest distinctive foraging distributions. This is consistent with our ship- and island-based observations that these petrel species all forage offshore rather than inshore.

There was considerable interspecific overlap in $\delta^{15}\text{N}$ values, and thus relative trophic positions, amongst the 4 petrel species. These results are consistent with those of Rau et al. (1992), who found extensive overlap in $\delta^{15}\text{N}$ values for seabirds in the Weddell Sea, including the 4 species in this study. They concluded that these higher consumers share a small number of common food resources and trophic levels. These isotopic results suggest actual dietary overlap, but trophic overlap does not necessarily indicate shared prey types. It is possible that different petrel species consumed different prey species with similar trophic positions. However, Ainley et al. (1992), using conventional stomach-sample techniques, found considerable overlap in seabird diet within the confluence of the Scotia and Weddell Seas (including the 4 species in this study), regardless of species, habitat, or year. Additional results from conventional dietary studies are also consistent with the notion of extensive dietary overlap (Ridoux & Offredo 1989, Arnould & Whitehead 1991, Whitehead 1991). Thus, our results plus those of the aforementioned studies lend support to the idea that in the Antarctic food web petrels exploit a small number of trophic levels and that a small subset of the available prey species are disproportionately important (Rau et al. 1992). Dietary overlap is influenced by both prey availability and diversity (Diamond 1983). Both of these considerations are relevant to this system, since food for upper-level predators in Antarctic marine ecosystems is generally considered to be superabundant locally but of relatively low diversity (Kock & Shimadzu 1994).

Despite extensive interspecific overlap among petrel diets, the range in $\delta^{15}\text{N}$ values is equivalent to 1 full trophic level (Fig. 2), and relative trophic level varied with both species and age. Antarctic fulmars *Fulmarus*

Table 3. Interannual and interspecific comparisons of variability, expressed as coefficient of variation (CV), in dietary breadth ($\delta^{15}\text{N}$) based on Bartlett's test for homogeneity of variances ($B =$ test statistic)

Seabird species	CV		B	p
	1994/1995	1995/1996		
Adult				
ANFU	13.86	6.26	1.29	0.001
ANPE	4.18	9.54	1.28	0.01
CAPE	7.69	5.49	1.05	0.22
SNPE	10.69	14.88	1.06	0.17
B	1.33	1.36		
p	0.002	<0.0001		
Chick				
ANFU	6.84	10.05	1.09	0.07
ANPE	9.12	9.30	1.00	0.76
CAPE	7.21	20.43	1.56	0.0001
SNPE	5.63	3.22	1.15	0.03
B	1.03	1.90		
p	0.51	<0.0001		

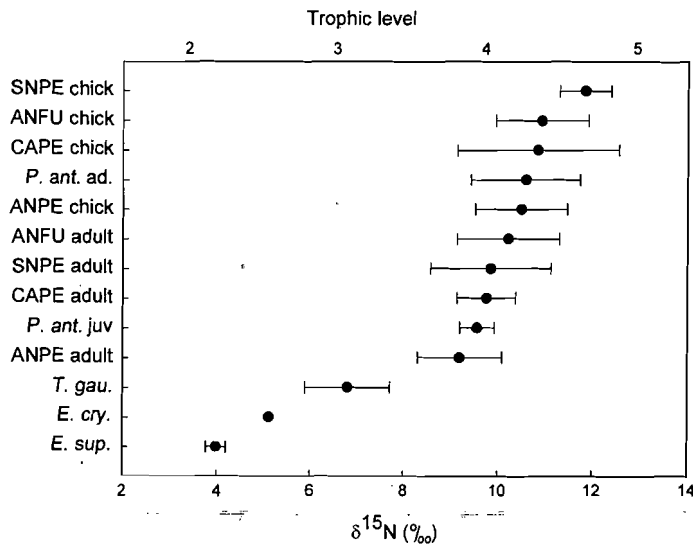


Fig. 2. Mean (\pm SD) stable nitrogen isotope values and derived trophic levels for petrels and prey species during 1994/1995 and 1995/1996 breeding seasons. Abbreviations as in Table 2 and legend to Fig. 1

glacialoides and snow petrels *Pagodroma nivea* tended to have higher $\delta^{15}\text{N}$ values than Antarctic petrels *Thalassoica antarctica* and cape petrels *Daption capense*, suggesting a higher proportion of fish in their diets. These results are consistent with those of Rau et al. (1992). The results of previous studies also suggest that snow petrels are the most piscivorous of the 4 seabird species examined, whereas cape petrels consume the highest proportion of krill, and Antarctic fulmars and petrels are intermediate (Ridoux & Offredo 1989, Arnould & Whitehead 1991).

Assessing potential trophic-level differences between adults and chicks using conventional diet-sampling methods is virtually impossible. Although it is generally believed that adults provision chicks with the same dietary items that they consume, Hobson (1993), using SIA, found that nestling thick-billed murres and black-legged kittiwakes in Lancaster Sound, Canada, occupied higher trophic positions than their parents. He found no such pattern in northern fulmars and glaucous gulls, however. Diets of adults and chicks could differ if adults provision themselves on the outward trip and collect food for chicks on the return trip.

Chicks of all 4 petrel species in this study had higher $\delta^{15}\text{N}$ values than adults, which suggests trophic segregation between adults and chicks. Chick diet was consistently one-quarter to one-half a trophic level higher than adults. This may indicate higher proportions of fish in chick diets and zooplankton in adult diets, provided diet-tissue isotopic fractionation does not change with age. We assume that isotopic fractionation does not change with age, and that the production of stom-

ach oil by adults is not a confounding factor for our $\delta^{15}\text{N}$ data.

Few previous studies have evaluated the possible effect of age on diet-tissue isotopic fractionation in consumers. Minagawa & Wada (1984) found no difference in stable nitrogen-isotope ratios of 2 mussel species with different growth rates up to an estimated age of 7 yr. Rau et al. (1991) reported a positive correlation between $\delta^{15}\text{N}$ and body mass in a marine fish, but this was also consistent with dietary change, an effect found also for Arctic char *Sylvelinus alpinus* by Hobson & Welch (1995). The few data on mammals also suggest dietary differences resulting in expected $\delta^{15}\text{N}$ shifts between adult and young. For example, Sutoh et al. (1987) found no effect of age on $\delta^{15}\text{N}$ values of tissues of cattle fed similar diets up to 10 yr of age. Elephants in South Africa showed no association between $\delta^{13}\text{C}$ values and age and only an extremely weak correlation for $\delta^{15}\text{N}$ (Tieszen et al. 1989). In addition, the isotope ratios in hair of modern Japanese are constant across all ages (Minagawa 1992). The $\delta^{15}\text{N}$ value of the tissue of neonate mammals fed exclusively on mother's milk is enriched relative to that of maternal tissue (Fogel et al. 1989, Bocherens et al. 1995, Hobson & Sease 1998), suggesting that dietary differences between adult and offspring can be detected isotopically. We lack comparable experimental studies for seabirds, but the most parsimonious explanation for relative $\delta^{15}\text{N}$ enrichment in chicks is that it reflects different trophic levels between adults and chicks rather than a systematic age-related difference in isotopic fractionation or any confounding effects of nutritional stress (Hobson 1993, Hobson et al. 1993). The available evidence from a variety of taxonomic groups thus suggests that isotopic differences between adults and young are related primarily to actual dietary or trophic differences between these age groups (reviewed by Schwarcz & Schoeninger 1991, Hobson & Welch 1995).

Further evidence for this argument is provided by stable-isotope ratios in uric acid. In bird blood plasma, uric acid can often reach the limits of solubility (Skadhauge 1983). Both uric acid and urea are waste-products of protein catabolism and are typically depleted in ^{15}N relative to body proteins (Peterson & Fry 1987). Thus, one would expect elevated levels of urea or uric acid in blood to relatively deplete blood $\delta^{15}\text{N}$ (Bearhop et al. 2000). Previous studies have found that plasma concentrations of urea and uric acid are higher in growing chicks than they are in adults, a process probably related to higher rates of protein synthesis in growing birds (Alonso et al. 1991, see also Featherston 1969, Wolf et al. 1985). Therefore, all things being equal, if chick blood contained significantly more urea or uric acid than that of adults, we would expect depleted $\delta^{15}\text{N}$ in chick blood relative to blood of adults

(Bearhop et al. 2000). Although we only examined the cellular fraction of blood, our findings that chick blood was enriched in ^{15}N compared with adult blood suggest again that such an effect was probably due to actual dietary differences between these age groups.

Stomach oil comprises only a small fraction of the total food load provided by adult fulmarine petrels to their chicks, typically less than 10 to 15% of diet-sample volume (P.J.H. pers. obs.). Although we did not measure stomach oil isotopically, we suspect that it did not contribute significantly to the differences in blood $\delta^{15}\text{N}$ content we observed between adults and chicks, since it represents such a small proportion of what is fed to chicks and is derived directly from the food rather than secreted by the adult (reviewed in Warham 1996). Thus, we feel reasonably confident that the foraging inferences we have drawn in this study are correct.

There are several possible explanations for selective provisioning and higher proportions of fish in chick diets. Antarctic fulmarine petrels experience but a short season in which environmental conditions are conducive to breeding. As such, nestlings grow relatively rapidly, 50% quicker than predicted allometrically (Croxall & Gaston 1988, Hodum 1999). Presumably there are nutritional constraints connected with rapid growth, and adults should provision offspring with higher-quality food to facilitate this growth. Vertebrate prey provide vertebrate consumers with a more complete source of nutrients than invertebrates. Although energy-density and protein values are reasonably similar for krill and fish, fish values are somewhat higher (Clarke & Prince 1980). Calcium content and the calcium to phosphorus ratio may be factors limiting chick growth in birds (Houston 1978, Clarke & Prince 1980), and calcium content, a critical factor in nestling growth, is much higher in fish than in krill (Clarke & Prince 1980, Croxall 1984). Thus, from a nutrient and energy perspective, fish are of higher quality than krill.

Krill and fish also differ in salt concentrations. Krill are isosmotic with seawater, whereas fish have lower salt concentrations. By provisioning nestlings primarily with fish, adults decrease the salt load imposed on the chicks. Increased salt loads reduce the growth rates of white ibis *Eudocimus albus* and laughing gull *Larus atricilla* chicks and possibly influence survival (Johnston & Bildstein 1990, Dosch 1997). Even if chicks can tolerate high salt loads, salt gland maintenance and excretion of excess salt are energetically expensive processes (Nyström & Pehrsson 1988).

Digestion of wax esters present in krill may also be a constraint for nestlings. Jackson (1986) demonstrated that assimilation efficiencies for krill and fish were similar for white-chinned petrels, but wax esters require a slower rate of passage for digestion. This contrasts

with the relatively rapid rate of digestion for fish (Jackson & Ryan 1986).

The assumed trophic overlap between adult petrels and *Pleuragramma antarcticum*, as inferred from our stable-isotope model, suggests they share common prey resources. Conventional diet studies indicate that euphausiids and copepods are the dominant prey items of *P. antarcticum* (Gorelova & Gerasimchuk 1981, Williams 1985). Differences in $\delta^{15}\text{N}$ greater than 5.0‰ between krill and *P. antarcticum* suggest a difference greater than 1 trophic level. This implies that the krill proportion of the *P. antarcticum* diet is supplemented with prey from a higher trophic level (e.g. amphipods and/or copepods). Our finding of similar relative trophic levels for adult petrels and *P. antarcticum* is consistent with results of other studies (Williams 1985, Ridoux & Offredo 1989, Arnould & Whitehead 1991), and suggests that euphausiids may be of primary importance in their respective diets. Higher $\delta^{15}\text{N}$ values in fulmarine petrel chicks relative to *P. antarcticum*, as found in this study, is consistent with a trophic model in which chick diet is comprised to a significant degree of fish.

We recognize that our trophic model is incomplete, but our emphasis is on relative rather than absolute trophic positions. We also recognize that factors other than trophic position can influence $\delta^{15}\text{N}$ values in marine systems (Michener & Schell 1994). Additional work needs to be done to develop a more complete trophic-structure model in this system. That said, our model seems to fit nicely what is already known of this system (e.g. Ridoux & Offredo 1989, Ainley et al. 1992, Rau et al. 1992).

To construct our isotope-derived model of trophic structure (Eq. 4), we made several assumptions, including: (1) the $\delta^{15}\text{N}$ values for primary producers remained spatially and temporally constant; (2) the whole-organism ^{15}N enrichment at each trophic step remained constant; (3) the isotopic offset between whole-organism and tissue $\delta^{15}\text{N}$ remained constant. We acknowledge that these assumptions may well lead to variability in the model, but we believe that the time-integrative nature of our samples controls for some of the potential variation attributable to the first and second assumptions. These petrel species presumably range over large distances to forage, and their blood averages several weeks of dietary integration (Hobson & Clark 1993). Thus, much of the potential fluctuation is likely to be evened out by the consumer. Also, the goal of our model is to present relative trophic positions, and thus any potential variability should affect all species and age groups equally.

Contribution of different prey items to diet composition may also be evaluated through dietary breadth indices. In our study (Table 3), dietary breadth varied

between species for adults in both years and chicks in 1 year. Within species, dietary breadth of Antarctic fulmar and petrel adults and cape and snow petrel chicks differed between seasons. One can assess the degree of foraging specialization along a continuum from specialists to opportunists using a dietary-breadth index. Dietary breadth of a species may be diagnostic, or it may vary within and between years. In a more complex food web with a correspondingly greater range of utilized prey types, measures of dietary breadth might provide insights into foraging plasticity.

Extensive overlap and a relatively narrow range of $\delta^{15}\text{N}$ values and trophic levels are consistent with a food web comprising few trophic steps. In such food webs, upper-level consumers tend to exploit a small subset of disproportionately important potential prey species. Rau et al. (1992) similarly found that many higher consumers in the Weddell Sea, including seabirds, seals, and some fish species, shared a small number of common food resources and trophic levels, thereby lending support to the concept of a simple trophic structure in Antarctic marine systems. Our results and those of Wada et al. (1987) and Rau et al. (1992) are consistent in suggesting that the trophic structure of Antarctic marine ecosystems is relatively simple at intermediate and upper trophic levels. The suggestion of selective provisioning of petrel chicks by adults certainly warrants further study. It is also a caution against the simple use of dietary data from chick-provisioning adults to infer adult diet; in actuality, the results of such studies may only reflect chick diet while breeding adults may provision themselves at different trophic levels or with different prey species.

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LITERATURE CITED

- Ainley DG, Ribic CA, Fraser WR (1992) Does prey preference affect habitat choice in Antarctic seabirds? *Mar Ecol Prog Ser* 90:207–221
- Alonso JC, Hucacas V, Alonso JA, Abelenda M, Muñoz-Pulido R, Puerta ML (1991) Hematology and blood chemistry of adult white storks (*Ciconia ciconia*). *Comp Biochem Physiol* 98A:395–397
- Arnould JPY, Whitehead MD (1991) The diet of Antarctic petrels, cape petrels, and southern fulmars rearing chicks in Prydz Bay. *Antarctic Sci* 3:19–27
- Bearhop S, Teece MA, Waldron S, Furness RW (2000) The influence of lipid and uric acid upon $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in avian blood: implications for trophic studies. *Auk* (in press)
- Ben-David M, Hanley TA, Klein DR, Schell DM (1997) Seasonal diets of coastal and riverine mink: the role of spawning Pacific salmon. *Can J Zool* 75:803–811
- Bocherens H, Fogel M, Tuross N, Zeder M (1995) Trophic structure and climatic information from isotopic signatures in pleistocene cave fauna of southern England. *J Archaeol Sci* 22:327–340
- Bonner WN (1984) Conservation and the Antarctic. In: Laws RM (ed) *Antarctic ecology*. Academic Press, London, p 821–850
- 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
- Clarke A, Prince PA (1980) Chemical composition and calorific value of food fed to mollymauk chicks *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. *Ibis* 122:488–494
- Croxall JP (1984) Seabirds. In: Laws RM (ed) *Antarctic ecology*. Academic Press, London, p 533–616
- Croxall JP, Gaston AJ (1988) Patterns of reproduction in high-latitude northern- and southern-hemisphere seabirds. *Acta XIX Congr Int Orn* 1:1176–1194
- Diamond AW (1983) Feeding overlap in some tropical and temperate seabird communities. *Stud Avian Biol* 8:24–46
- Dosch JJ (1997) Salt tolerance of nestling Laughing Gulls: an experimental field investigation. *Col Waterbirds* 20: 449–457
- Duffy DC, Jackson S (1986) Diet studies of seabirds: a review of methods. *Col Waterbirds* 9:1–17
- Everson I (1984) Marine interactions. In: Laws RM (ed) *Antarctic ecology*. Academic Press, London, p 783–819
- Featherston WR (1969) Nitrogenous metabolites in the plasma of chicks adapted to high protein diets. *Poult Sci* 48: 646–652
- Fogel ML, Tuross N, Owsley DW (1989) Annual report of the director of the Geophysical Laboratory Carnegie Institute, Washington, 1988–1989. Geophysical Laboratory, Washington, DC
- France RL (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Mar Ecol Prog Ser* 124:307–312
- Fry B (1988) Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnol Oceanogr* 33: 1182–1190
- Gorelova TA, Gerasimchuk VV (1981) Data on nutrition and daily consumption of juvenile *Pleuragramma antarcticum* Boulenger. In: Parin NV (ed) *Fishes of the open ocean*. Academy of Sciences of the USSR, Moscow, p 103–109
- Hempel G (1985) Antarctic marine food webs. In: Siegfried WR, Condy PR, Laws RM (eds) *Antarctic nutrient cycles and food webs*. Springer-Verlag, Berlin, p 266–270
- 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, Clark RG (1993) Turnover of ^{13}C in cellular and plasma fractions of blood: implications for non-destructive sampling in avian dietary studies. *Auk* 110:638–641
- Hobson KA, Sealy SG (1991) Marine protein contributions to the diet of Northern Saw-whet Owls on the Queen Charlotte Islands: a stable-isotope approach. *Auk* 108:437–440

- Hobson KA, Sease J (1998) Stable isotope analysis of tooth annuli reveals temporal dietary records: an example using Steller sea lions. *Mar Mammal Sci* 14:116–129
- Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar Ecol Prog Ser* 84:9–18
- Hobson KA, Welch HE (1995) Cannibalism and trophic structure in a high Arctic lake: insights from stable-isotope analysis. *Can J Fish Aquat Sci* 52:1195–1201
- Hobson KA, Alisauskas RT, Clark RG (1993) Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *Condor* 95:388–394
- Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63: 786–798
- Hodum PJ (1999) Foraging ecology and reproductive energetics of Antarctic fulmarine petrels. PhD dissertation, University of California, Davis
- Hopkins TL, Torres JJ (1989) Midwater food web in the vicinity of a marginal ice zone in the western Weddell Sea. *Deep Sea Res* 36:543–560
- Houston DC (1978) The effect of food quality on breeding strategy in griffon vultures. *J Zool Lond* 186:175–184
- Jackson S (1986) Assimilation efficiencies of white-chinned petrels (*Procellaria aequinoctialis*) fed different prey. *Comp Biochem Physiol* 85A:301–303
- Jackson S, Ryan PG (1986) Differential digestion rates of prey by White-chinned Petrels. *Auk* 103:617–619
- Johnston JW, Bildstein KL (1990) Dietary salt as a physiological constraint in white ibis breeding in an estuary. *Physiol Zool* 63:190–207
- Klasing KC (1998) Comparative avian nutrition. CAB International, Oxford
- Kock KH, Shimadzu Y (1994) Trophic relationships and trends in population size and reproductive parameters in Antarctic high-level predators. In: El-Sayed SZ (ed) *Southern Ocean ecology: the BIOMASS perspective*. Cambridge University Press, Cambridge, p 287–312
- Michener RH, Schell DM (1994) Stable isotope ratios as tracers in marine and 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 (1992) Reconstruction of human diet from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in contemporary Japanese hair: a stochastic method for estimating multi-source contribution by double isotopic tracers. *Appl Geochem* 7:145–158
- Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim Cosmochim Acta* 48: 1135–1140
- Nyström KGK, Pehrsson O (1988) Salinity as a constraint affecting food and habitat choice of mussel-feeding diving ducks. *Ibis* 130:94–110
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *A Rev Ecol Syst* 18:293–320
- Peterson BJ, Howarth RW, Garritt RH (1985) Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. *Science* 227:1361–1363
- Rau GH, Hopkins TL, Torres JJ (1991) $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ 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) $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. *Mar Ecol Prog Ser* 84:1–8
- Ridoux V, Offredo C (1989) The diets of five summer breeding seabirds in Adélie Land, Antarctica. *Polar Biol* 9:137–145
- Schwarcz HP, Schoeninger MJ (1991) Stable isotope analyses in human nutritional ecology. *Yearb Phys Anthropol* 34: 283–321
- Skadhauge E (1983) Formation and composition of urine. In: Freeman BM (ed) *Physiology and biochemistry of the domestic fowl*, Vol 4. Academic Press, London, p 108–135
- Sutoh M, Koyama T, Yoneyama T (1987) Variations of natural ^{15}N abundances in the tissues and diets of domestic animals. *Radio-Isotopes* 36:74–77
- Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable isotopes in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57:32–37
- Tieszen LL, Boutton TW, Ottichilo WK, Nelson DE, Brandt DH (1989) An assessment of long-term food habits of Tsavo elephants based on stable carbon and nitrogen isotope ratios of bone collagen. *Afr J Ecol* 27:219–226
- Wada E, Terazaki M, Kabaya Y, Nemoto T (1987) ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. *Deep-Sea Res* 34:829–841
- Warham J (1996) The behaviour, population biology and physiology of the petrels. Academic Press, New York
- Whitehead MD (1991) Food resource utilization by seabirds breeding in Prydz Bay, Antarctica. *Acta XX Congr Int Orn* 3:1384–1392
- Williams R (1985) Trophic relationships between pelagic fish and euphausiids in Antarctic waters. In: Siegfried WR, Condy PR, Laws RM (eds) *Antarctic nutrient cycles and food webs*. Springer-Verlag, Berlin, p 452–459
- Wilson RP (1984) An improved stomach pump for penguins and other seabirds. *J Fld Ornithol* 55:109–111
- Wolf SH, Schreiber RW, Kahana L, Torres JJ (1985) Seasonal, sexual, and age-related variation in the blood composition of the brown pelican (*Pelecanus occidentalis*). *Comp Biochem Physiol* 82A:837–846

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